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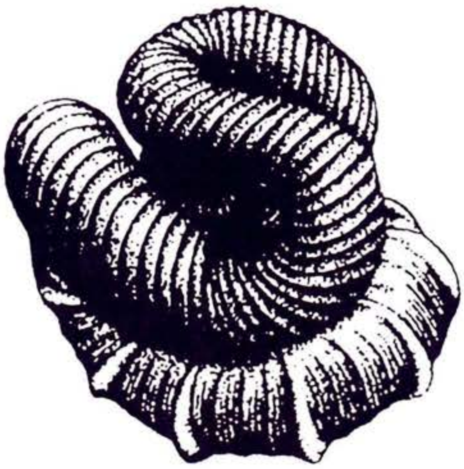

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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto,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

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A study of *Hypoturrilites* (Anmonoidea) from Hokkaido (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-XCI)

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Abstract. This paper presents the result of our study on the genus *Hypoturrilites* from the Mikasa district, Central Hokkaido. *H. gravesianus* (d'Orbigny, 1842), *H. wrighti* sp. nov., *H. komotai* (Yabe, 1904), *H. yabei* Collignon, 1964 and *H. nodiferus* (Crick, 1907) are described, giving new or revised diagnoses and comparisons with other species. As to *H. komotai* the ambiguities in the previous record of occurrence are cleared up. Hence, the described species are all early Cenomanian in age. Finally the systematic allocation of *Hypoturrilites* in the Turrilitidae is discussed.

Key words: Cenomanian, *Hypoturrilites*, *Mariella*, *Mesoturrilites*, Mikasa, Turrilitidae

Introduction

Hypoturrilites is an important genus of the Turrilitidae and more than a dozen species have been reported from various regions of the world. In Japan a magnificent specimen was described long ago under the name *Turrilites komotai* Yabe, 1904. It is nowadays referred to this genus. Recently *H.* aff. *mantelli* (Sharpe, 1857) and *H. primus* Atabekian, 1985 have been reported to occur in the lower Cenomanian of the Shuparo Valley, central Hokkaido (Matsumoto, 2000).

In this paper materials from the Mikasa district are studied. The Cenomanian rocks exposed in the Ikushunbetsu Valley of this district represent a generally shallower facies in comparison with those in the Shuparo Valley. As to the Cenomanian stratigraphy in the type section of this area readers may refer to the note by Matsumoto (1991, p. 3-5, 21-24). A supplementary note is given to a particular case concerned.

The materials of this study depend primarily on the collection of T. T. with an addition by Tamotsu Omori. The described specimens are to be held in the Kyushu University Museum with registered numbers under the abbreviated heading GK. One specimen of UMUT [the University Museum, the University of Tokyo] described by Yabe (1904) is restudied.

For brevity the following abbreviations are used in the description: D = diameter, B = breadth and H = height of the preserved last whorl; d = diameter of the whorl preceding the last one, h = height of the exposed outer face of the same whorl as above.

Systematic descriptions

Order Ammonoidea Zittel, 1884
Suborder Ancyloceratina Wiedmann, 1966
Superfamily Turrilitoidea Gill, 1871
Family Turrilitidae Gill, 1871
Genus ***Hypoturrilites*** Dubourdieu, 1953

Type species.—*Turrilites gravesianus* d'Orbigny (1842, p. 596, pl. 144, figs. 3-5) by original designation (Dubourdieu, 1953, p. 44).

Diagnosis.—More or less large, sinistrally coiled turreted shell, with high or low apical angle. Whorls in tight contact, showing convex flanks and deeply impressed interwhorl junction. Each whorl ornamented by a first row of major tubercles at about midflank and closely set second and third rows of more numerous, spirally elongated minor tubercles in the lower part of the flank. The basal surface of the whorl ornamented by radial ribs, with minor tubercles of a fourth row on its margin. Septal suture highly indented, with L at about the concave zone below the row of major tubercles. Elongated branches of the inner element (I) extend to the zone of L (see Figures 2, 7; also Atabekian, 1985, pl. 23, fig. 1).

Discussion.—The systematic position of *Hypoturrilites* in the Turrilitidae is debatable. We intend to discuss this problem after completing the descriptions of species.

Occurrence.—This genus is widespread in the lower Cenomanian of Europe (except for Northern Europe), West and Central Asia, the Middle East, North Africa, South Africa, Madagascar, South India, North Australia, New

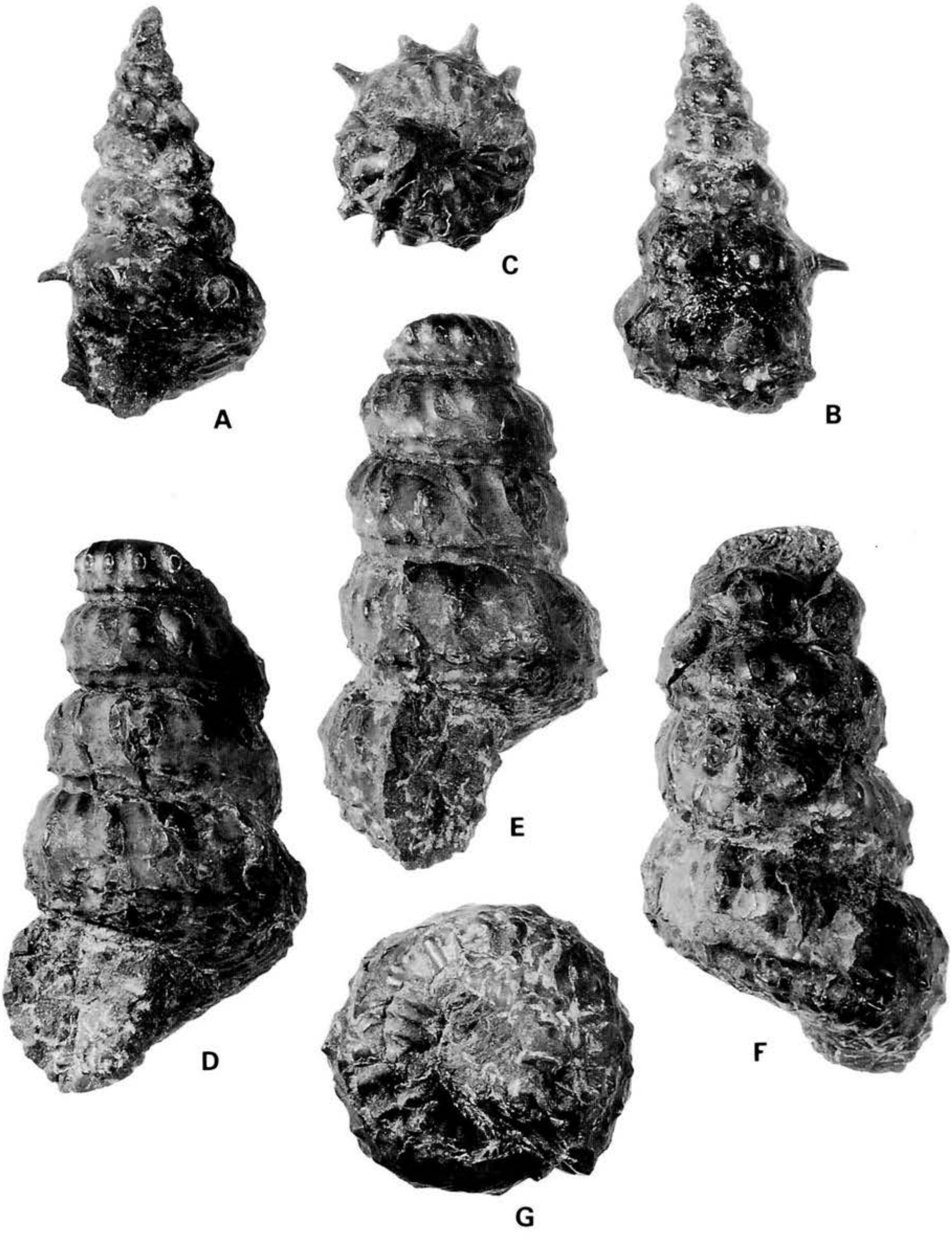


Figure 1. **A–C.** *Hypoturrilites gravesianus* (d'Orbigny, 1842). Two lateral (A and B, 180° apart each other) and basal (C) views of GK. H8543, × 1.5. **D–G.** *Hypoturrilites wrighti* sp. nov. Three lateral (D, E and F, 90° apart successively) and basal (G) views of GK. H8544 (holotype), × 1.25. Photos coutesy of M. Noda.

Zealand, Japan, Mexico and the U. S. Gulf Coast and Argentina. It seems to range upward to the middle Cenomanian in North Australia and North Africa (Wright and Kennedy, 1996, p. 364).

Hypoturrilites gravesianus (d'Orbigny, 1842)

Figure 1A-C

Turrilites tuberculatus Mantell, 1822, p. 124 (*pars*), pl. 24, fig. 6.
Turrilites gravesianus d'Orbigny, 1842, p. 596, pl. 144, figs. 3-5.
Hypoturrilites gravesianus (d'Orbigny). Dubourdieu, 1953, p. 44; Wright and Kennedy, 1996, p. 364, pl. 102, fig. 10; pl. 105, figs. 1-6; pl. 110, figs. 2, 8, 9; pl. 111, fig. 6; pl.112, figs. 1, 3; pl. 113, figs. 1, 2, 5, 7, 10-12; text-figs. 134R; 140J, R; 141E; 145F; 147E-G (with full synonymy).

Type.—The complex status of the type material of this species is explained in detail by Wright and Kennedy (1996, p. 365) and not repeated here. We agree with them in their proposal to designate BMNH C5726b as the lectotype of this species. It was illustrated by Mantell (1822, pl. 24, fig. 6) under *Turrilites tuberculatus*, but it is a well preserved syntype of d'Orbigny's species (Wright and Kennedy, 1996, pl. 113, fig. 10). We support them (Wright and Kennedy, 1996, p. 363) in favour of their application to the International Commission to designate *T. gravesianus* d'Orbigny instead of *T. giganteus* Haan, 1825 (p. 75) as type species of *Hypoturrilites.*

Material.—GK. H8543 [= previous S.36·5·14] (Figure 1A-C) collected by T. T. in 1951 at Loc. Ik1054 of the Ikushunbetsu River, from the *Mantelliceras japonicum* Zone.

Description.—This specimen is small and probably represents a young shell which corresponds to the unpreserved early part of the lectotype. Although the shell is destroyed at its top, the apical angle is roughly estimated as about 20°. The specimen preserves seven whorls which are in tight contact, showing a deeply impressed interwhorl junction. The flank of the whorl is convex and its height is less than half of the whorl diameter (h/d = 0.43).

Each whorl is ornamented by a row of large, rounded tubercles at about midflank and two rows of small, somewhat clavate tubercles in the lower part immediately above and also along the lower whorl seam. There are rounded small tubercles of a fourth row on the marginal zone of the basal surface. The large tubercles number 10 to a whorl and the small ones of each row 20. A rib arises from each of the small tubercles of the fourth row and runs further on the basal surface to the umbilicus. In this specimen the rib is faintly swollen at the edge of the umbilicus. Some of the midflank large tubercles preserve a horizontally extended spine. The spine is septate at the domelike base.

Suture is not exposed on this specimen.

Comparison. — This specimen is identified with *H. gravesianus* because of the conformity in shell form and ornamentation with the lectotype and other examples illustrated by Wright and Kennedy (1996).

Occurrence.— As for material. In contrast to the abundant occurrences of this species in the Lower Chalk of southern England, number of examples is, so far, very few in Japan.

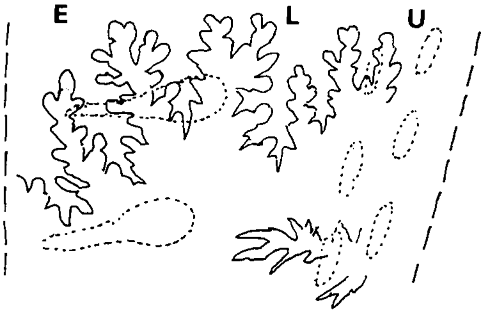


Figure 2. *Hypoturrilites wrighti* sp. nov. Suture of GK. H8544 (holotype) on the exposed flank at h = 13.0 mm. Broken line = approximate position of whorl seam; dotted line = outline of tubercle and rib; E = external lobe; L = lateral lobe; U = umbilical lobe. Figure is about × 4. Drawing by T. M.

Hypoturrilites wrighti sp. nov.

Figures 1D-G; 2

Holotype. — GK. H8544 [= previous S.51·6·26] (Figure 1D-G) collected by T. T. in 1976 from a transported nodule of the seventh branch [= Shichino-sawa] of the Kami-ichinosawa in the Ikushunbetsu Valley. The lithology and associated species of the nodule suggest a derivation from the *Mantelliceras japonicum* Zone.

Specific name.— In honour of C. W. Wright who has accomplished a revised systematics of the Cretaceous Ammonoidea in addition to a number of other palaeontological contributions.

Diagnosis.—Turreted shell with a rather small apical angle (about 20°) and tuberculate ornament like that of *H. gravesianus* and *H. tuberculatus* (Bosc, 1801), but intermediate in the number of tubercles between them. A distinct rib extends upward from each major tubercle.

Description.—This specimen is of moderate size, with D = 40 mm and H = 43 mm. It shows four whorls but lacks younger whorls and also the last part.

The whorls are in tight contact, showing a deeply impressed interwhorl junction. The outer, exposed whorl face is convex and the whorl section is subcircular (B/H = 0.92). The height of the flank is slightly less than half of the diameter (h/d = 0.47).

The whorl is ornamented by a first row of large tubercles at about the midflank, and three closely set rows of small tubercles in the lower part. The second row is slightly above and the third row just along the lower whorl seam; a fourth row is on the marginal zone of the basal surface of the whorl. The small tubercles of the second and third rows are spirally elongated, forming ridges which are separated by a narrow groove. On the basal surface radial ribs run with a gentle curvature from the tubercles of the fourth row toward the narrow umbilicus. In the upper part of the exposed whorl face a distinct rib extends upward from each major tubercle.

The number of tubercles per whorl increases slightly with growth. In the middle growth stage it is 15 or 16 for the row of large tubercles and 24 or 25 for each row of small tubercles.

Septal sutures are partly exposed, showing fairly narrow L

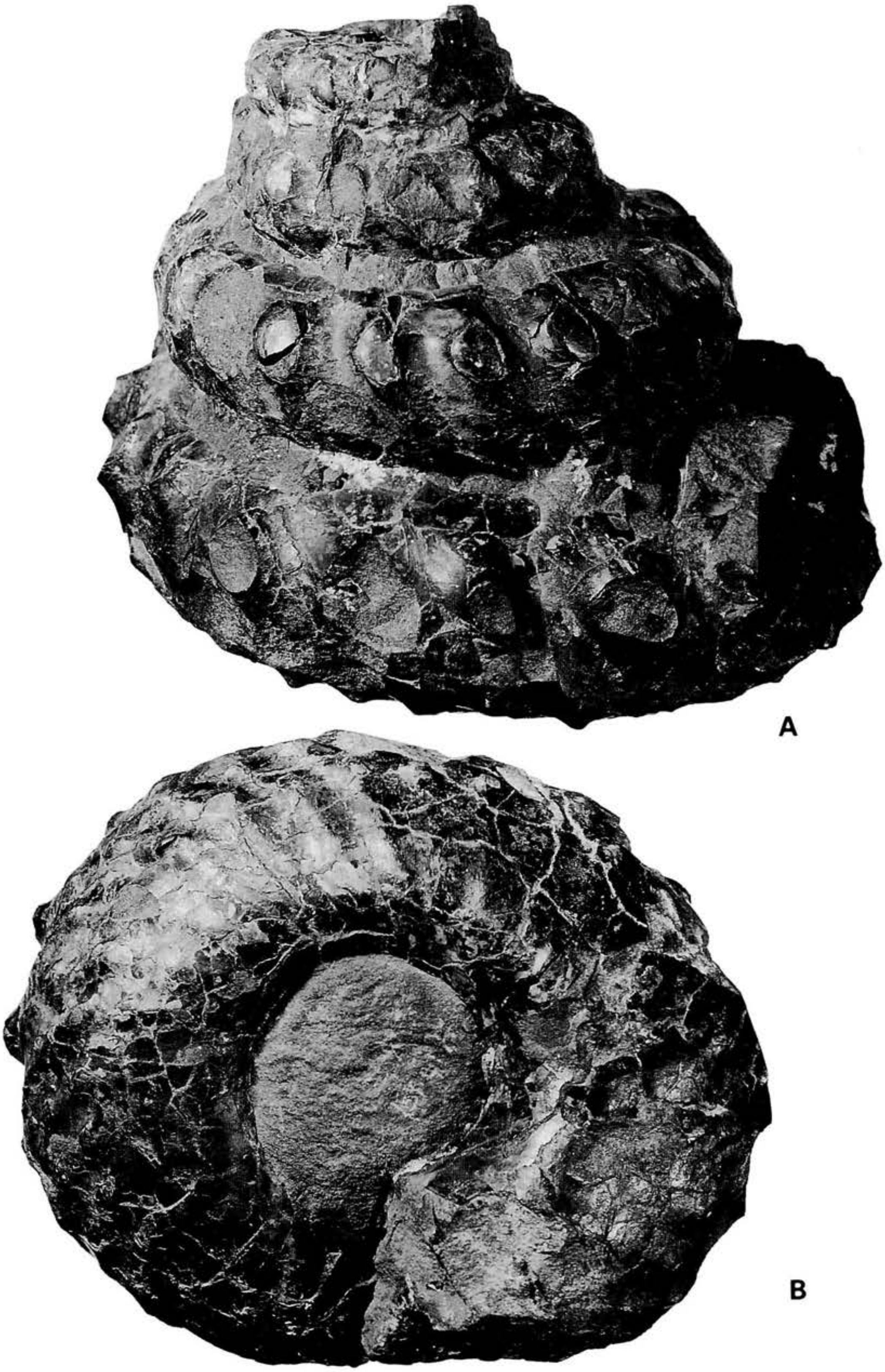


Figure 3. *Hypoturrilites komotai* (Yabe, 1904). Lateral (**A**) and basal (**B**) views of UMUT MM7458, × 0.6. Photos courtesy of M. Noda.

in the zone between the first and second rows of tubercles (Figure 2). They are fine and deeply incised even on the preserved early whorls. The septa seem to be distantly separated. On the interspace between the two sutures, a branch of an inner element extends outward to the zone of L.

Comparison.—The holotype of this species is generally similar to *Hypoturrilites gravesianus* and *H. tuberculatus* (Bosc, 1801) (redefined by Wright and Kennedy, 1996, p. 367). The number of large tubercles per whorl is about 10 to 12 in *H. gravesianus* and 20 or so in *H. tuberculatus*. It is 15 or 16 in *H. wrighti*. This number may vary to some extent, but the above difference is beyond that extent. In *H. gravesianus* and *H. tuberculatus* the upper part of the exposed whorl face is smooth, whereas in this species a distinct rib extends upward from the large tubercle.

Occurrence.— As for material. At present this species is represented by a single specimen. More material should be searched out to know clearly the stratigraphic range and geographical distribution of this species.

Hypoturrilites komotai (Yabe, 1904)

Figure 3

Turrilites komotai Yabe, 1904, p. 7, pls. 1 and 2.
Hypoturrilites komotai (Yabe, 1904). Collignon,1964, p. 44, pl. 328, fig. 1468; Wright and Kennedy, 1996, p. 367, text-fig. 145C.

Holotype.—UMUT MM7458 (Figure 3A, B), by monotypy, collected by Komota and described by Yabe (1904). Its original locality is questionable (see occurrence).

Diagnosis.— A species of *Hypoturrilites* characterized by a very large apical angle and a low ratio of flank height to diameter in each whorl, which is ornamented by spinose large tubercles of the upper row and numerous small tubercles of the lower three rows. On the basal surface of the whorl ribs run obliquely to the umbilicus.

Description.—The holotype is very large. It consists of four whorls, and several whorls of the early growth stage are not preserved. The last whorl, with D = 184 mm, is the body chamber, although its apertural part is destroyed. The estimated apical angle is as high as 70. Whorls are in tight contact; the ratio of flank height to diameter is very low (h/d = 0.34), while the cross section of the last whorl is subelliptical, with breadth slightly larger than height (B/H = 1.11). The umbilicus is fairly narrow.

The outer exposed whorl face shows a nearly flat and gently inclined upper portion and a convex main part. The latter is ornamented by a first row of large tubercles, numbering 18 or 19 per whorl. In the lower part of the exposed whorl face somewhat above and along the lower whorl seam, there are the second and the third rows of small, obliquely or spirally elongated tubercles, numbering 35 or so per whorl in each row. From the small tubercles of a fourth row on the margin of the basal surface distinct ribs run to the umbilical margin with a gentle curvature (Figure 3B). The large tubercles of the first row originally had a spine which stretched laterally with a slightly upward curvature (see Yabe, 1904, pl. 1). One of us (T. M.) actually observed the spinose tubercles when he was a student at the University of Tokyo (in 1935), but later the spines were all broken and lost. At present the exposed top of a dome-shaped large tubercle preserves the septate base of the spine (Figure 3A). The holotype does not clearly show the suture, as it is covered by a dark-colored shelly layer.

We have not observed the specimen from Madagascar, but it is identified with this species on the basis of the general conformity in the estimated apical angle and number of large tubercles, as shown by Collignon (1964, p. 44, pl. 328, fig. 1468) and also by Wright and Kennedy (1996, p. 367, text-fig. 145C). It is small and probably immature because its preserved last whorl is still septate. The suture was not drawn by these authors.

Comparison.—This species has diagnostic characters (*vide supra*), which enable us to distinguish it from other species. Comparison with *H. yabei* Collignon, 1964 is made below.

Occurrence.—Yabe (1904, p. 9) cited Komota's information that the holotype came from a loose marly nodule found below a cliff of the River Ikushunbetsu, directly upstream from the Coal Mine of Ikushunbetsu.

The above record is, however, questionable from the stratigraphic point of view. The cliff is a part of our Locality Ik1103 (Figure 4) and has yielded numerous specimens of *Calycoceras* (*Newboldiceras*) *asiaticum* (Jimbo). In fact it is the type locality of "*Acanthoceras rhotomagense* var. *asiatica*" of Jimbo (1894, p. 177, pl. 20, fig. 1). This fossiliferous part belongs to the Abundance Zone of *Calycoceras* (*Newboldiceras*) *asiaticum* in the present sense. At Loc. Ik1103 the beds with *C.* (*N.*) *asiaticum* are underlain by another fossiliferous sequence from which T. T. obtained a specimen of *Cunningtoniceras* (Matsumoto *et al.*, 1969, pl. 33, fig. 2). Thus, the fossiliferous beds of Loc. Ik1103 are as a whole referred to the middle Cenomanian. They belong to the Mikasa Formation on the western wing of the Ikushunbetsu Anticline in our present knowledge. Long ago this part was called "the Lower *Acanthoceras* zone of the *Trigonia* Sandstone" and was thought to be underlain by the "Lower Ammonite Beds" (Yabe, 1903, p. 8). Incidentally, the Upper *Acanthoceras* Zone at that date was the *Mammites*-bearing bed of an early Turonian age exposed in the Yubari Mountains.

In our present knowledge a fault of considerable magnitude is presumed to run on the east side of Ik1103 (see Matsumoto *et al.*, 1964, fig. 7) and middle Albian *Lyelliceras*-bearing strata of the Lower Yezo Subgroup are exposed for some distance (see Matsumoto, 1988, p. 157-158). Further upstream on the eastern wing of the Ikushunbetsu Anticline the successive ammonite zones in the middle part (i. e., the Member IIb) of the Mikasa Formation are exposed. They are in ascending order as follows (Matsumoto *et al.*, 1969; Matsumoto, 1991):

(1) Assemblage Zone of *Mantelliceras japonicum*-*Sharpeiceras kongo*: middle part of the lower Cenomanian.
(2) Ammonite-poor part, in which *Acomposoceras renevieri* (Sharpe, 1857) was found by T. T. (Matsumoto and Takahashi, 1992): upper part of the lower Cenomanian.
(3) Subzone of *Cunningtoniceras takahashii* and Subzone of *Calycoceras* (*Newboldiceras*) *orientale*: middle Cenomanian.

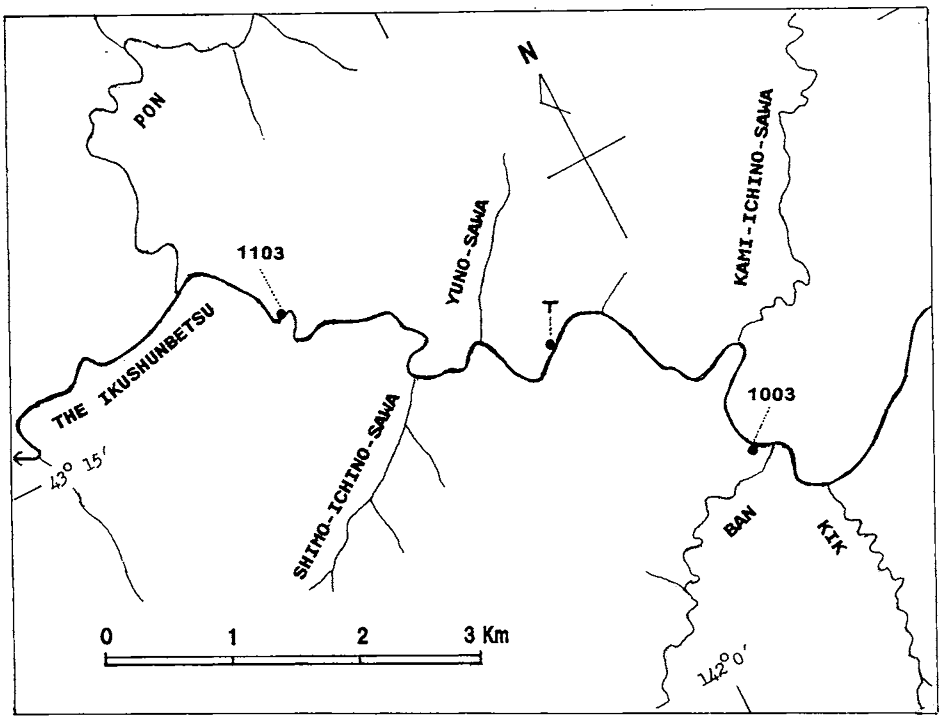


Figure 4. Outline map of the Ikushunbetsu Valley (part). The locations of Ik1103 and Ik1003 are shown. Regrettably Ik1003 (type locality of *Reesidites minimus*) was misprinted as Ik1103 in the paper by Matsumoto (1965, fig. 2 and explanation of pls. 14 and 15), but was correctly printed in figs. 4 and 34 of the same paper. For the geology of the mapped area see Yoshida and Kanbe (1955) and Matsuno *et al.* (1964), in the latter of which the distribution of the Mikasa Formation is clearly shown (Matsuno *et al.*, 1964, fig. 7). Abbreviations in this Figure: BAN = Banno-sawa, KIK = Kikumezawa, PON = R. Ponbetsu, T = type locality of the *Mantelliceras japonicum* Zone. Put Ik at the heading of 1003 and 1103.

The Zone of *M. japonicum* is prolific and several species of *Hypoturrilites* have been collected from this zone. Recently *H.* cf. *komotai* has been found in the same zone at a locality of the Ganseki-zawa, i. e. the 8th branch of the Kami-ichino-sawa, about 7 km northeast from the type outcrop (indicated as T in Figure 4) of this zone.

The Mikasa Formation on the eastern wing consists mainly of sandstones and forms a ridge on the northwest side of the Kami-ichino-sawa and also another ridge on the southeast side of the Shimo-ichino-sawa (Figure 4). There is, thus, a high possibility that Komota's nodule originated from the *M. japonicum* Zone of the Mikasa Formation exposed along the Shimo-ichino-sawa and was transported downstream for about 1.5 or 2 km.

In Madagascar *H. komotai* is recorded from the lower Cenomanian (Collignon, 1964, p. 44).

Hypoturrilites yabei Collignon, 1964

Figure 5

Hypoturrilites yabei Collignon, 1964, p. 44, pl. 328, fig, 1469; Wright and Kennedy, 1996, p. 367, text-fig. 145D.

Holotype.— Original of Collignon, 1964, p. 44, pl. 328, fig. 1469 (by original designation), from the lower Cenomanian of Antanimanga of Madagascar. It is now housed in the collection of the Département des Sciences de la Terre, Université de Bourgogne, Dijon (France).

Material.— GK. H8545 [= previous S. 40·9·4A] (Figure 5A–D) and GK. H8546 [S. 40·9·4B] (Figure 5B–H) collected by T. T. in 1960 at Loc. Ik1100, abandoned pit on the right side of the River Ikushunbetsu; also GK. H8528 collected by Tamotsu Omori (no. 86) from the Shimo-ichino-sawa, a branch of the Ikushunbetsu. They came from the fossiliferous sandstones referred to the *Mantelliceras japonicum* Zone of the Mikasa Formation.

Description.— The three specimens are smaller than the holotype. The apical angle is moderate, i. e., around 50°, and h/d is rather low, 0.40–0.42. Whorls are tightly in contact and the interwhorl junction is deeply impressed. The outer exposed whorl face is convex. The umbilicus is narrow.

Each whorl is ornamented by an upper row of large tubercles at the most convex midflank and more or less spirally elongated small ones of three closely set rows in the lower part. The large tubercles number 12–13 per whorl and the small ones in each row are nearly twice as numerous as the large ones. The large tubercle has a horizontally elongated spine as shown by GK. H8546 (Figure 5E, G), but in many cases the spine is absent and its septate base is exposed, forming a rounded domelike outline (Figure 5A, B).

A shallowly concave zone may be discernible below the

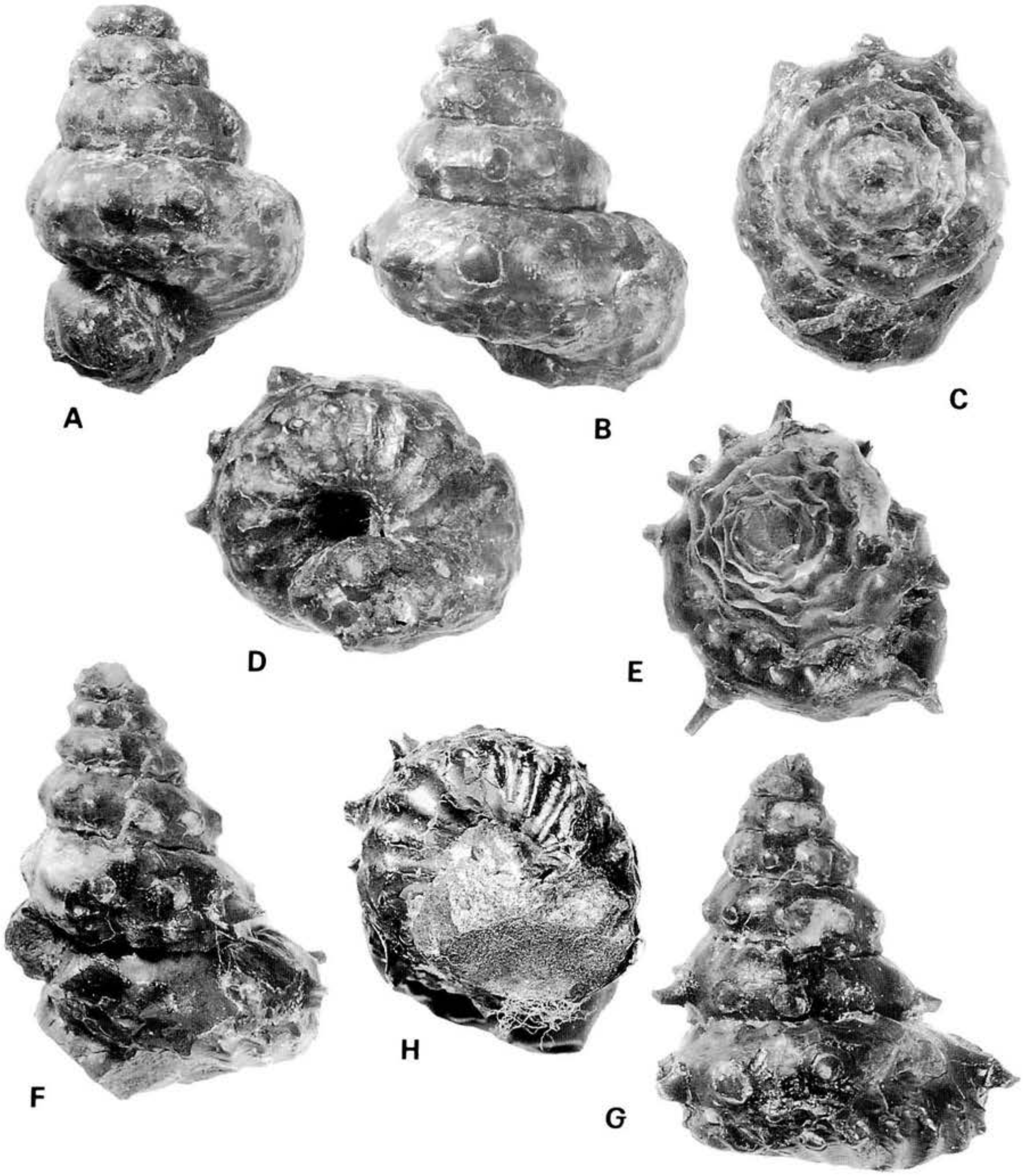


Figure 5. *Hypoturrilites yabei* Collignon, 1964. **A–D**. GK. H8545, two lateral (A and B about 180° apart), apical (C) and basal (D) views. **E–H**. GK. H8546, two lateral (E and F about 180° apart), apical (G) and basal (H) views. Figures are all × 1.25. Photos courtesy of M. Noda.

first row of large tubercles and a narrow spiral groove runs between the second and third rows of clavate tubercles. The tubercles of a fourth row are less clavate and situated at the curved outer edge of the basal rib.

There are short riblets on the uppermost part of the flank above the zone of large tubercles. They are roughly twice as numerous as the large tubercles.

The septal suture is partly exposed on a later whorl of GK. H8546. The stem of the E–L saddle is broad, whereas L is narrow and deep, resting on the zone between the first and second rows of tubercles. The extra branch exists but is not well traced.

Comparison.—The described specimens are undoubtedly identified with *H. yabei* Collignon, 1964. This species is allied to but distinguished from *H. komotai* by its somewhat smaller apical angle and less numerous tubercles. The uppermost row of riblets is faintly shown in the illustration by Collignon (1964, pl. 328, fig. 1469), although the author made no mention of this character.

Occurrence.— As for material. Despite the long distance, *H. yabei* and *H. komotai* both occur in Japan and Madagascar. In Madagascar the two species have been re-

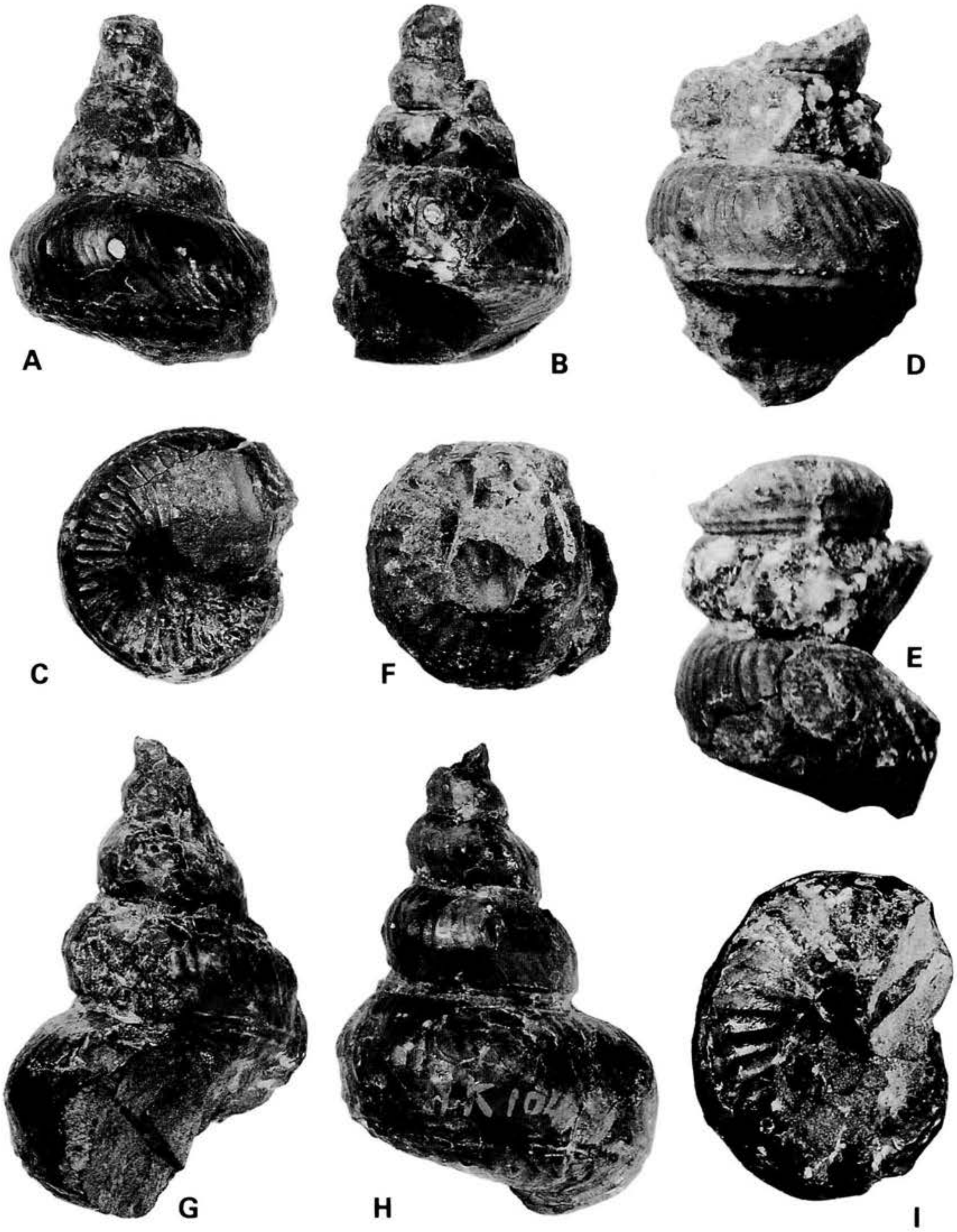


Figure 6. *Hypoturrilites nodiferus* (Crick, 1907). **A–C**. GK. H8547, two lateral (A and B about 180° apart) and basal (C) views, × 1.5. **D–F**. GK. H5570, two lateral (D and E about 90° apart) and basal (F) views, Slightly reduced(× 0.95). **G–I**. GK. H5917, two lateral (G and H about 120° apart) and basal (I) views, × 1.25. Photos courtesy of M. Noda.

corded from the same bed (Collignon, 1964, p. 44–45).

Hypoturrilites nodiferus (Crick, 1907)

Figures 6, 7

Turrilites nodiferus Crick, 1907, p. 177, pl. 11, fig. 5, 5a.

Turrilites tuberculatoplicatus Seguenza var. *tenouklensis* Pervinquière, 1910, p. 57, pl. 5, fig. 31.

Hypoturrilites nodiferus (Crick, 1907). Klinger and Kennedy, 1978, p. 22, pl.. 4, fig. 1; Collignon, 1964, p. 44, pl. 328, fig. 1466; Wright and Kennedy, 1966, text-fig. 145E.

Hypoturrilites tenouklensis (Pervinquière, 1910). Marcinowski, 1980, p. 261, pl.. 4, fig. 17; Atabekian, 1985, p. 61, pl. 28, figs. 1, 2.

Hypoturrilites laevigatus (Coquand, 1862). Wright and Kennedy, 1996 (*pars*), p. 373, pl. 102, fig. 2; text-fig. 146K–M (*non* 146P, Q).

Holotype.—Original of Crick, 1907, p. 177, pl..11, fig. 5, 5a, BMNH C18749, by monotypy.

Material.—GK. H8547 [= previous S. 51·9·25] (Figure 6A–C) collected by T. T. in 1976 from a transported nodule of the Ganseki-zawa [= the 8th branch of the Kami-ichinosawa]; GK. H5570 [= previous S. 39·6·16] (Figure 6D–F) collected in 1954 by T. T. at Loc. Ik1101; GK. H5917 [= purchased, no. A003–17] (Figure 6G–I) from Loc. Ik1049; the latter two specimens were collected in situ. The three specimens belonged to the *Mantelliceras japonicum* Zone, lower part of the Member IIb of the Mikasa Formation.

Description.— The apical angle is moderate, about 40°. The whorls are in tight contact, showing a deep junction. Each whorl has a convex flank and is subcircular in cross section.

The tubercles are in four rows as in the above-described species of *Hypoturrilites.* The first row of large tubercles, 10 to 14 per whorl, is at about or slightly below the midflank. On the exposed whorl face there are numerous transverse ribs, which are individually variable in density and number, ranging from 30 to 40 per whorl. They are weakened but run adorally across the shallowly concave zone below the row of large tubercles. Slightly above and just along the lower whorl seam there are the second and third rows of clavate, minor tubercles. They form the spiral ridges, with a narrow but distinct groove between them. The small tubercles of the fourth row are on the marginal zone of the basal surface, where radial ribs run to the umbilicus. The tubercles in each of the lower rows are approximately as numerous as the transverse ribs, but the exact correspondence in number may not be maintained as is shown on an undestroyed part of GK. H5570 (Figure 6D) and on the well preserved specimen from Madagascar (Wright and Kennedy, 1996, text-fig. 145D). The radial ribs on the basal surface are exactly as numerous as the small tubercles of the fourth row. Often a narrow riblet extends obliquely upward from the fourth tubercle to the third one.

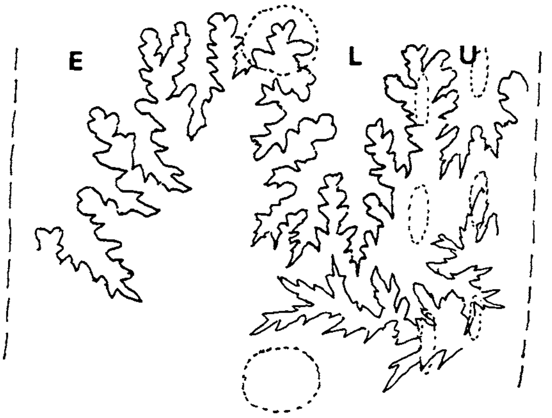


Figure 7. *Hypoturrilites nodiferus* (Crick, 1907). Suture of GK. H5570 on the flank at h = 14 mm. Legend as for Figure 2. Figure is about × 3. Drawing by T. M.

The septal suture (Figure 7) is similar to that of other species of *Hypoturrilites.*

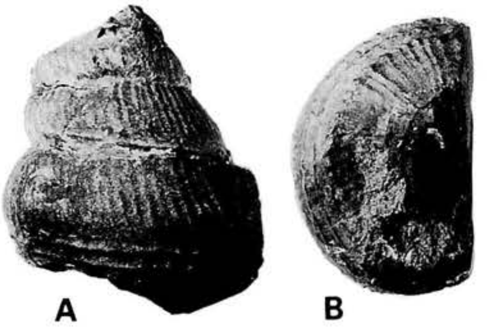
Comparison and discussion.—As there are some ambiguous points in some of the previously described taxa, discussion is given along with comparison. The holotype of this species from South Africa is represented by a single whorl. It was described at length by Klinger and Kennedy (1978, p. 22, pl. 4, fig. l), but they did not mention clearly the tubercles of the fourth row, which Crick (1907, p. 177) did mention and one of us (T. M.) confirmed on the original specimen. On the weathered part or when the lighting is inadequate, the small tubercles of the fourth row are scarcely discernible. This species is represented by a better preserved specimen of Collignon (1964, p. 44, pl. 328, fig. 1466; Wright and Kennedy, 1996, text-fig. 145E) from Madagascar.

The holotype of *Turrilites tuberculoplicatus* Seguenza var. *tenouklensis* Pervinquière (1910, p. 57, pl..14, fig. 31) (reillustrated by Wright and Kennedy, 1996, text-fig.146K–M), from the lower Cenomanian of Algeria, was referred to *H. laevigatus* (Coquand, 1862) by Wright and Kennedy (1996, p. 373). In our view it should be regarded as an example of *H. nodiferus* because of the resemblance in essential characters.

The holotype of *Turrilites laevigatus* Coquand (1862, p. 175, pl. 2, fig. 6) (reillustrated by Wright and Kennedy, 1996, text-fig. 146P, Q) is too much worn for the accurate definition of the species . It is estimated to have a taller shell shape with a higher h/d and a smaller apical angle in comparison with *H. tenouklensis* [= *H. nodiferus*].

The specimen from Crimea (Ukraine) which was identified with *H. tenouklensis* by Marcinowski (1984, p. 261, pl.. 4, fig. 17) undoubtedly shows three rows of small tubercles. It is probably another example of *H. nodiferus. H. tuberculatoplicatus* (Seguenza, 1882, p. 53, pl. 5, fig. 3), from the lower Cenomanian of Italy and England (Wright and Kennedy, 1996, p. 374, pl. 102, fig. 7; pl. 113, figs. 2, 6, 8, 9), has three rows of small tubercles as in *H. nodiferus.* It shows, however, a much taller shell shape with smaller apical angle and a higher value of h/d in comparison with *H. nodiferus.* In this respect, one of the British specimens illustrated by Wright and Kennedy (1996, pl. 113, fig. 4) might be *H. nodiferus* rather than *H. tuberculatoplicatus.*

If the large tubercles are excluded, *H. nodiferus* is considerably similar to *Mesoturrilites corrugatus* Wright and Kennedy (1996, p. 348, pl. 98, figs. 4, 17), from the lower



Figures 8. *Mesoturrilites* aff. *corrugatus* Wright and Kennedy, 1996. Lateral (**A**) and basal (**B**) views of GS. G260, × 1. Photos courtesy of M. Noda.

Cenomanian of England. In the same respect, we notice an interesting specimen (Figure 8) in the recent collection of Y. Kawashita (YKC1·11019) (registered at Saga University GS. G260) from the lower Cenomanian part of the Mikasa Formation in the Ganseki-zawa. It is tentatively called *Mesoturrilites* aff. *corrugatus*, for its ribs and small tubercles in three rows are more numerous than those of the British specimens. As to the rib density, however, there may be variation with growth and also between individuals. At any rate, this specimen (GS. G260) resembles GK. H8517 of *H. nodiferus*, if the large tubercles of the latter are ignored. Some of the transverse ribs are strengthened at or below the midflank in this specimen (GS. G260), if not forming tubercles as in *Mesoturrilites serpuliforme* (Coquand, 1862, p. 175, pl. 2, fig. 7) (see also Wright and Kennedy, 1996, p. 348, pl.. 98, fig. 10; pl. 102, fig. 5; text-figs. 138P–R, X; 146H–J).

Occurrence.—As for material.

Distribution.—If the above comments are accepted, this species is recorded widely from the lower Cenomanian of South Africa, Madagascar, North Africa, England (?), Ukraine, Azerbaijan, and Japan.

Systematic allocation of *Hypoturrilites* in the Turrilitidae

When Dubourdieu (1953, p. 41, fig. 13) established the genus *Hypoturrilites*, he was not confident about its systematic position in the family Turrilitidae. He tentatively indicated it as one of the divergences from *Pseudhelicoceras* in parallel with *Mariella* [= "*Paraturrilites*" in his paper] and *Ostlingoceras*. At about the same time, but probably after the appearance of Dubourdieu's paper, *Mesoturrilites* was proposed by Breistroffer (1953, p. 1351). Its type species, *M. aumalensis* (Coquand, 1862), is somewhat similar to *Hypoturrilites* in having an upper row of fairly large tubercles at about the midflank and three rows of small tubercles in the lower part. In many species of *Hypoturrilites*, however, the large tubercles of the upper row at about the midflank are less numerous than the small ones in each of the lower three rows. In *M. aumalensis* and many other species of *Mesoturrilites* the small tubercles in each row are equal in number to the large ones of the upper row. In morphological terms the typical species of *Mesoturrilites* can be regarded as a development of *Mariella* in which the ribbing was reduced and the tubercles in the lower rows are spirally elongated, as Wright and Kennedy (1996, p. 346) mentioned as one of the possible cases. In some other cases the ribbing remained in such ways as in *Mesoturrilites boerssumensis* (Schlüter, 1876), *M. serpuliforme* (Coquand, 1862) and *M.* aff. *corrugatus*. The latter subgroup of *Mesoturrilites* is fairly similar to *H. nodiferus* or to *H. tuberculatoplicatus*, in which, however, the midflank tubercles are enlarged and reduced in number.

The relationship of *Hypoturrilites* with *Mariella* takes a more definite shape. An actual morphological, if not phylogenetical, transition is observed between such a form of *Mariella* (*M.*) *bergeri* (Brongniart, 1822) as illustrated by Kennedy (1996, fig. 28p, o) from the uppermost part of the Albian and the typical form of *Hypoturrilites primus* Atabekian (1985, p. 60, pl. 16, fig. 1; pl. 17, fig. 1; Matsumoto, 2000, p. 6, fig. 2–3) from the lower Cenomanian.

Hypoturrilites betaitraensis Collignon, 1964 (p. 13, pl. 320, figs. 1387, 1388) (Wright and Kennedy, 1996, p. 375, pl. l02, fig. 12; text-fig. 134F–I), from the lower Cenomanian of Madagascar, South Africa, Algeria, West Europe and Turkmenistan, shows a pair of delicate ribs, of which one runs from the large tubercle upward to the interwhorl junction while the other is intercalatory between the large tubercles. Its small tubercles are conical or obliquely clavate as in many species of *Mariella*. The riblets similar to the above-mentioned delicate ribs are discernible and the small tubercles of the second and third rows are spirally elongated in *H. yabei*.

Although the details of the phylogenetical relations are practically unknown, it is interesting to note that *Mariella* extended from the Albian to the Cenomanian and that numerous species of *Hypoturrilites* and several species of *Mesoturrilites* evolved almost simultaneously in early Cenomanian time.

Conclusions

(1) In this paper *Hypoturrilites* is studied based on materials from the Ikushunbetsu Valley of the Mikasa district. As a result, *H. gravesianus* (d'Orbigny, 1842), *H. wrighti* sp. nov., *H. komotai* (Yabe, 1904), *H. yabei* Collignon, 1964, and *H. nodiferus* (Crick, 1907) are distinguished.

(2) In addition to the establishment of a new species , *H. wrighti*, the revised descriptions have made clear the distinction between *H. komotai* and *H. yabei*. *H. nodiferus* was proposed long ago on the basis of a fragmentary whorl but it is now well defined, showing its diagnosis, variation, and affinities with other species.

(3) Doubts about the occurrence of *H. komotai* are cleared up by ascribing its derivation to a lower Cenomanian bed. Thus, the number of described species from Hokkaido, including the recently reported *H.* aff. *mantelli* (Sharpe, 1857) and *H. primus* Atabekian, 1985 from the Shuparo area (Matsumoto , 2000), is altogether seven, about half of the described species from various regions of the world.

(4) The systematic allocation of *Hypoturrilites* in the family

Turrilitidae is discussed. As a conclusion, numerous species of *Hypoturrilites* seem to have evolved almost simultaneously from *Mariella* in the early Cenomanian age. At about the same time several species of *Mesoturrilites* may have evolved also from *Mariella*. A few atypical species of *Hypoturrilites* show a morphologically intermediate appearance between typical *Hypoturrilites* and *Mesoturrilites*.

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Late Miocene ostracodes from the Kubota Formation, Higashi-Tanagura Group, Northeast Japan, and their implications for bottom environments

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Abstract. Sixty-seven ostracode species including those in open nomenclature are identified in thirty-six samples from the upper Miocene Kubota Formation, Higashi-Tanagura Group, distributed in Fukushima Prefecture, northeastern Japan. The lower part of the Kubota Formation yields *Spinileberis* sp. dominantly. In the middle to upper part of the formation, dominant species are *Schizocythere kishinouyei* (Kajiyama), *Kotoracythere abnorma* Ishizaki, *Hanaiborchella triangularis* (Hanai), *Cytheropteron miurense* Hanai, *Paracytheridea neolongicaudata* Ishizaki and *Finmarchinella japonica* (Ishizaki). Most of these species live off southwestern Japan under a subtropical to warm marine climate regime, but cryophilic and circumpolar species also occur sparsely in the middle to upper part. The ostracode assemblages indicate that the lower and the middle to upper parts of the Kubota Formation were deposited in an enclosed inner bay influenced by warm water and a warm shallow sea, respectively. Principal component analysis reveals that the influence of open sea water became strong in the upward sequence of the middle part. Analyses of ostracode faunas indicate that the Shiobara fauna from the Kubota Formation flourished in warm-water conditions.

Key words: Kubota Formation, Late Miocene, Ostracoda, Shiobara fauna

Introduction

The Kubota Formation is known as one of the units containing the Shiobara fauna (Iwasaki, 1970), which flourished in Northeast Japan during the middle to late Miocene.

Chinzei and Iwasaki (1967) and Iwasaki (1970) considered that the Akasaka and Kubota Formations of the Higashi-Tanagura Group were deposited contemporaneously in an inner bay. Furthermore, these authors reconstructed a Higashi-Tanagura Bay on the basis of the lithology and geometry of the basin, discussing the paleoecology of the molluscan assemblages. In their discussion, Chinzei and Iwasaki (1967) compared the molluscan assemblages in the eastern Tanagura area with ones belonging to the Kadonosawa and Tatsunokuchi faunas, and recognized parallel communities. Iwasaki (1970) made a comparison with the molluscan assemblages in the eastern Tanagura, Shiobara, and Takasaki areas, where nearly contemporaneous deposits are distributed. Consequently, he recognized parallel communities between them and defined the Shiobara-type fauna (Shiobara fauna).

The Shiobara fauna was defined as a cold-water fauna which lived in inner bays or coastal areas (e.g. Chinzei, 1963; Chinzei and Iwasaki, 1967; Chinzei, 1986). Recently some workers, however, pointed out that the fauna flourished in warm- to mild-temperate realms rather than cold-temperate ones, or contained warm-water species as well as cold-water ones (e.g. Ogasawara *et al.*, 1985; Ogasawara, 1994; Ozawa *et al.*, 1996). Thus, the Shiobara fauna has been studied by many workers paleoecologically.

Many studies on the Miocene paleoenvironments have been made using molluscan fossils. For example, Chinzei (1986) and Ogasawara (1994) summarized the molluscan faunas of the late Cenozoic of Japan in the light of paleoclimates. Chinzei (1986) stated that Northeast Japan was influenced by cold water during the middle to late Miocene, since he regarded the Shiobara fauna as a cold-water fauna. On the other hand, Ogasawara (1994) thought

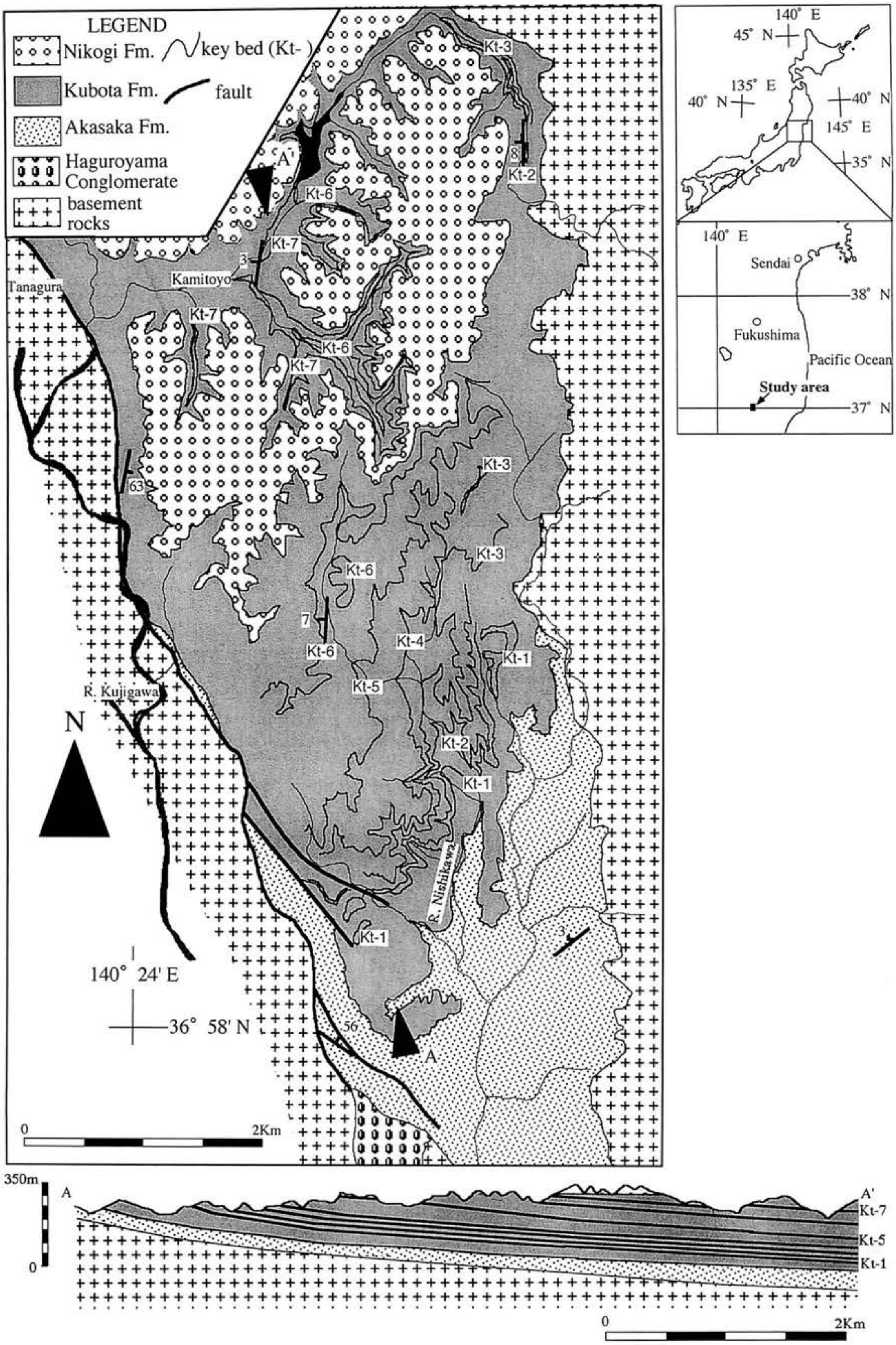
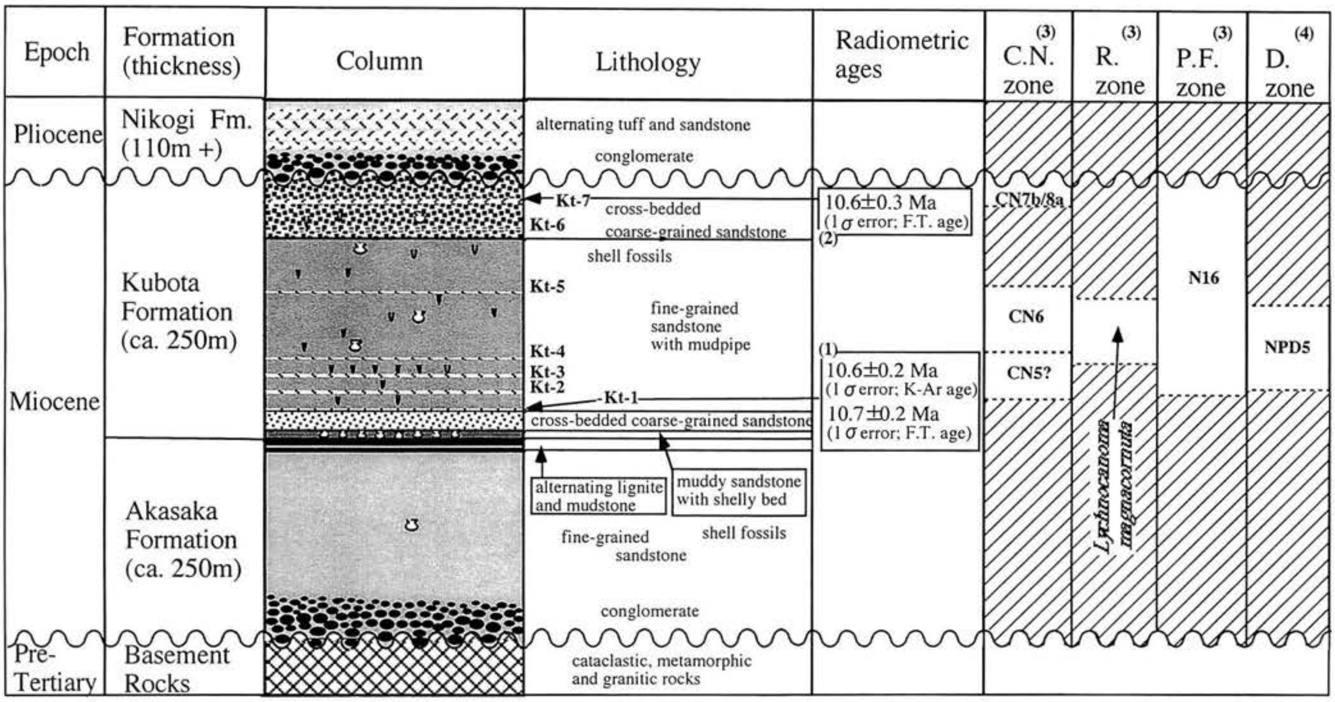


Figure 1. Geological sketch map and geological cross section of the eastern Tanagura area. Partly modified after Shimamoto *et al.* (1998) for the geological map.



(1) Takahashi *et al.* (2001) (2) Takahashi *et al.* (in press) (3) Shimamoto *et al.* (1998) (4) Yanagisawa *et al.* (2000)

Figure 2. Diagram showing the Neogene sequence in the eastern Tanagura area and biostratigraphy and radiometric ages of tuff layers of the Kubota Formation. Compiled after Shimamoto *et al.* (1998) and Yanagisawa *et al.* (2000) for biostratigraphy and Takahashi *et al.* (2001) and Takahashi *et al.* (in press) for radiometric ages.

that marine climates in Northeast Japan were warm- to mild-temperate during the middle to late Miocene, based on the modern distribution of molluscan genera and the marine zoogeographic divisions of Nishimura (1981). Paleoclimates suggested by molluscan fossils have been based on their biogeography and phylogeny. However, only a few studies have been made on other fossil groups from deposits yielding the Shiobara fauna.

To approach the problems mentioned above, we quantitatively examined ostracodes from the upper Miocene Kubota Formation of the Higashi-Tanagura Group.

Geological setting

The eastern Tanagura area lies about 70 km south of Fukushima City, Fukushima Prefecture, northeastern Japan (Figure 1).

The geology of the eastern Tanagura area has been studied by many workers (e.g., Chinzei and Iwasaki, 1967; Iwasaki, 1970; Otsuki, 1975; Shimamoto *et al.*, 1998). The Miocene distributed in the eastern Tanagura area comprises two formations: the Akasaka and Kubota Formations (Figures 1, 2). The Kubota Formation overlies conformably the Akasaka Formation and is overlain unconformably by the Pliocene Nikogi Formation. On the basis of lithology, the Kubota Formation is divided into three parts (Shimamoto *et al.*, 1998): the lower part is composed of muddy fine-grained sandstone, yielding abundant molluscan fossils, and medium- to coarse-grained sandstone; the middle part muddy fine-grained sandstone with mud-pipes and tuffaceous sandstone; the upper part cross-bedded coarse-grained sandstone. Many felsic tuff layers are intercalated in the middle to upper part, in which Shimamoto *et al.* (1998) recognized seven layers as keybeds (Kt-1 to Kt-7 tuff layers).

The geological age of the Kubota Formation has been determined by means of planktonic microfossils and radiometric dating of tuff layers (e.g. Aita, 1988; Takahashi and Amano, 1989; Taketani and Aita, 1991; Shimamoto *et al.*, 1998; Yanagisawa *et al.*, 2000; Takahashi *et al.*, 2001; Takahashi *et al.*, in press). Shimamoto *et al.* (1998) verified that the middle and upper parts of the Kubota Formation can be assigned to the calcareous nannofossil Zone CN6 to CN7/8a of Okada and Bukry (1980), planktonic foraminifer Zone N16 of Blow (1969) and the radiolarian *Lychnocanoma magnacornuta* Zone of Motoyama and Maruyama (1996). Yanagisawa *et al.* (2000) studied the diatom assemblages from the Kubota Formation for the first time and correlated the middle part with the diatom Zone NPD5C of Yanagisawa and Akiba (1998) (Figure 2).

On the other hand, Takahashi *et al.* (2001) dated the radiometric ages of a biotite-rich tuff layer, recognized as a keybed, the Kt-1 tuff layer, by Shimamoto *et al.* (1998). They reported the zircon fission-track age (F.T. age) and biotite potassium-argon age (K-Ar age) of the Kt-1 tuff layer to be 10.7±0.2 Ma (1 σ error) and 10.6±0.2 Ma (1 σ error). Moreover, Takahashi *et al.* (in press) dated the zircon fis-

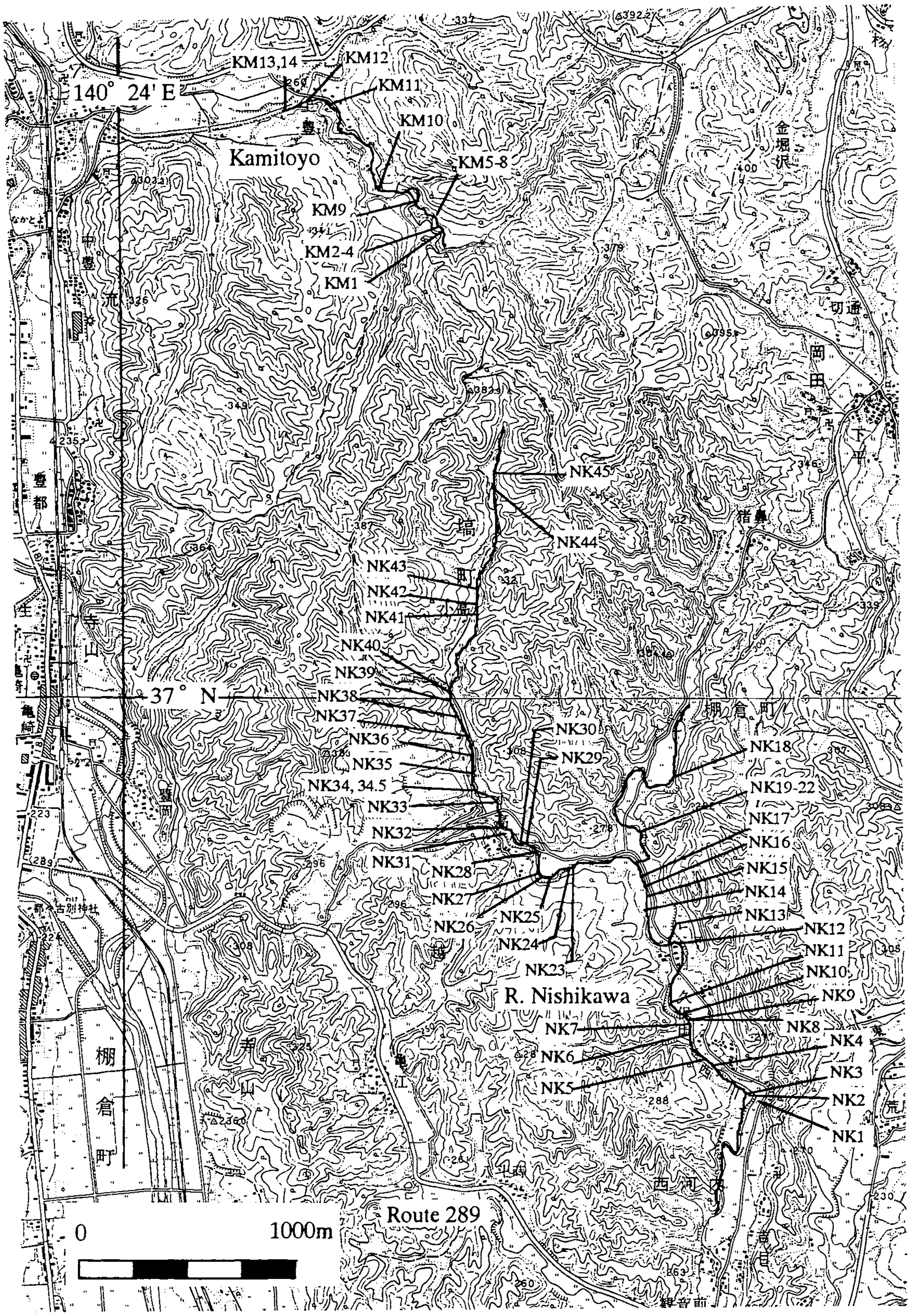


Figure 3. Map showing the ostracode fossil localities (a part of 1:25,000 map of "Tanagura" and "Hanawa" published by Geographical Survey Institute of Japan).

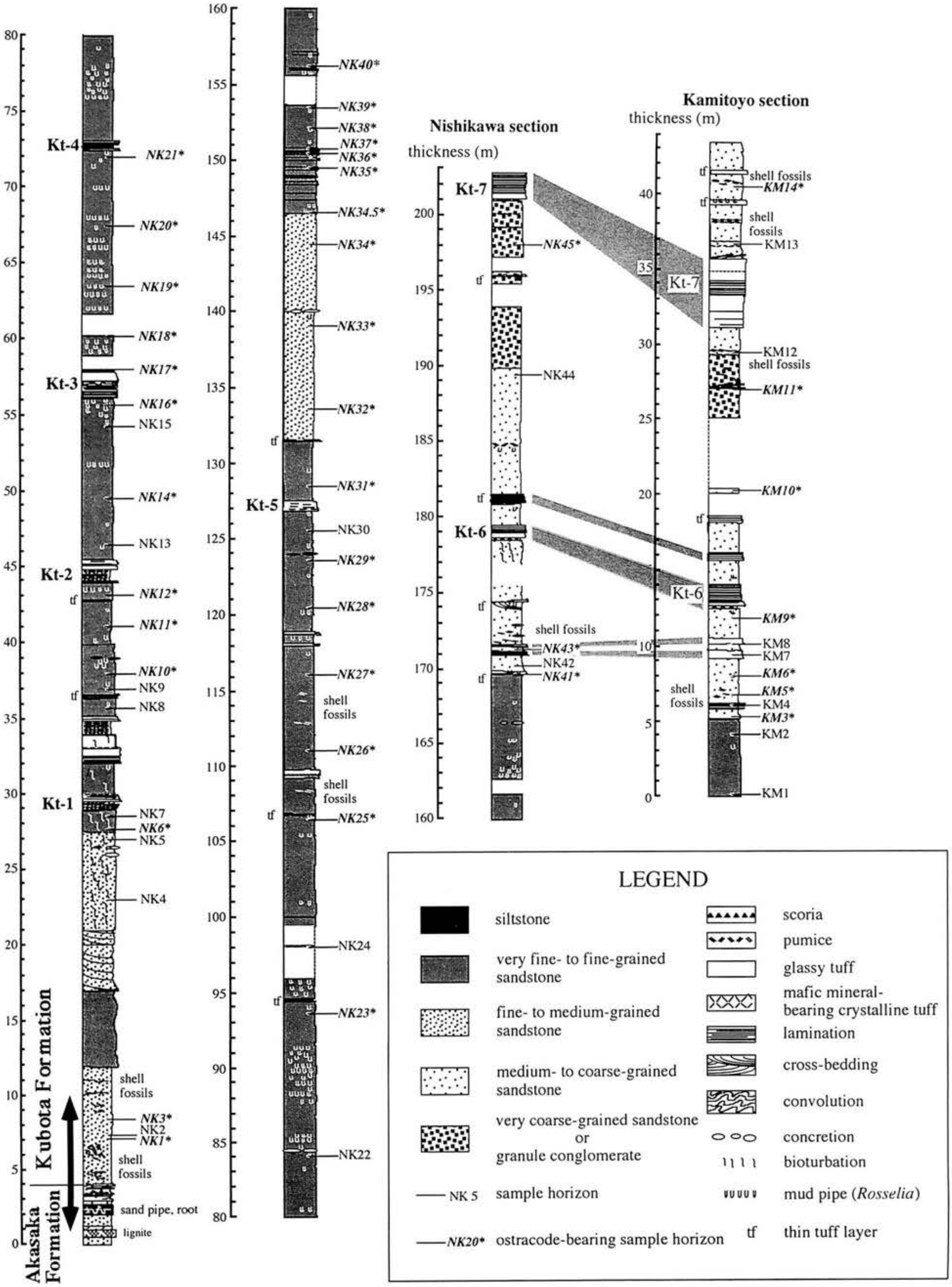


Figure 4. Columnar sections of the Kubota Formation. Bold italic numbers with asterisk marks indicate the ostracode samples in this study.

sion-track age of a felsic tuff, Kt-7, to be 10.6±0.3 Ma (1 σ error) (Figure 2). These reported microfossil and radiometric ages do not contradict the biochronology of Saito (1999).

Materials and methods

We collected 60 sediment samples from two sections of the Kubota Formation (Figures 3, 4) and examined 40 samples: 33 samples from the Nishikawa section and 7 samples from the Kamitoyo section. The Nishikawa section along the Nishikawa River is typical of the Kubota Formation (Shimamoto *et al.*, 1998). The upper part is better exposed in the Kamitoyo section along the Hokkawa River. We collected sediment samples from the Kamitoyo section to examine fossil ostracodes from the upper part of the Kubota Formation. These two sections are well correlated to each other by virtue of five keybeds.

Eighty grams of dried sediments were treated by using a saturated sodium sulfate solution and naphtha (Maiya and Inoue, 1973; Oda, 1978), washed through a 200 mesh sieve screen, and dried again. These procedures were repeated until the whole sediment sample became disintegrated. A fraction coarser than 125μm (115 mesh) was sieved and divided by a sample splitter into aliquot parts, from which 100 to 200 individuals were picked with a fine brush under the binocular microscope. We took micrographs with a JEOL Field Emission Scanning Electron Microscope, JSM-6330F to identify the taxonomic relationships of the fossil ostracodes (Figures 5, 6). The results of our identifications are listed in Figure 7. In this figure, the estimated preservation of ostracodes in each sample is as follows: good means the sample contained abundant specimens easily identified to species level; poor, the sample contained mostly specimens identified with difficulty to species level; moderate indicates somewhere between good and poor.

We examined ostracode assemblages in detail from those samples, each represented by more than fifty individuals by means of the proportions (relative abundance) of major species, species diversity and equitability and performed principal component analysis on data for abundance of major forty species.

Ostracode assemblages from the Kubota Formation

Ostracodes occurred in 36 samples and did not occur in 4 samples (samples NK1, 17, 18 and 45). We identified 67 ostracode taxa including those left in open nomenclature (Figure 7).

The ostracode assemblages from the Kubota Formation can be distinctly divided into two groups (Figure 8). In the lower part of the formation, *Spinileberis* sp. accounts for more than 90% of the assemblage. The genus *Spinileberis* has been reported to occur abundantly on muddy bottoms in Recent enclosed inner bays (e.g. Hanai, 1961; Ikeya and Shiozaki, 1993).

In the middle to upper part, *Schizocythere kishinouyei* (Kajiyama), *Kotoracythere abnorma* Ishizaki, *Hanaiborchella triangularis* (Hanai), *Cytheropteron miurense* Hanai, *Paracytheridea neolongicaudata* Ishizaki, *Finmarchinella japonica* (Ishizaki) and so on occurred. *S. kishinouyei* occurs most dominantly, forming 20 to 40% of the number of specimens in the assemblage. Subordinate are *K. abnorma* and *H. triangularis*, accounting for 10 to 20% of the number of specimens in the assemblage. Other species represent less than 10%. Most species are reported to live in coastal areas and the open sea under the influence of the Kuroshio Warm Current (e.g. Hanai, 1957, 1970; Ishizaki, 1981; Zhou, 1995; Tsukawaki *et al.*, 1997, 1998). All of these species are known to represent the Shiobara fauna (Ishizaki, 1966; Irizuki and Matsubara, 1994, 1995; Ishizaki *et al.*, 1996; Irizuki *et al.*, 1998). Through the upper horizons of the middle part to the upper part, the relative abundance of *Kotoracythere abnorma* increases (Figure 8).

Faunal structures

The faunal structures of ostracode assemblages were expressed by the following four indices: species diversity [*H* (*S*)], equitability (*Eq.*), the number of species, and number of individuals per 10 g sediment sample. These indices have been used extensively in paleoecology. Figure 9 shows vertical changes of these indices. Changes in faunal structures may be related to environmental changes (e.g., Buzas and Hayek, 1998). Species diversity [*H*(*S*)] and equitability (*Eq.*) are expressed by the Shannon-Wiener formula and the equation of Buzas and Gibson (1969), respectively:

$$H(S) = -\Sigma p_i \ln p_i \text{ and } Eq. = \exp[H(S)]/S$$

where p_i means the proportion (relative abundance) of the i-th species in a sample and S the number of species.

In the middle part of the Kubota Formation, the values of *H*(*S*) and *Eq.* range from 2.08 to 3.00 and from 0.44 to 0.64, respectively. The number of species in each sample varies from 20 to 40. Vertical changes of *Eq.* values are little. *H*(*S*) values and the number of species change synchronously. Through the upper horizon of the middle to upper part (samples NK41 and KM3) , *H*(*S*) values and the number

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➡ **Figure 5.** Scanning electron micrographs of selected ostracode species from the Kubota Formation. All specimens, expect for one juvenile one (7), represent adult valves. All scale bars indicate 100 μm. RV = right valve; LV = left valve. **1:** *Aurila* sp., RV, loc. NK27. **2:** *Callistocythere hatatatensis* Ishizaki, RV, loc. NK34.5. **3:** *Callistocythere kotorai* Ishizaki, RV, loc. NK35. **4:** *Callistocythere* sp.2, LV, loc. NK36. **5:** *Coquimba* cf. *ishizakii* Yajima, RV, loc. NK25. **6:** *Coquimba* sp.1, RV, loc. NK10. **7:** *Coquimba* sp.2, RV, loc. NK27. **8:** *Cornucoquimba saitoi* (Ishizaki), LV, loc. NK35. **9:** *Cornucoquimba moniwensis* (Ishizaki), LV, loc. NK21. **10:** *Cythere omotenipponica* Hanai, RV, loc. NK27. **11:** *Cytheropteron miurense* Hanai, LV, loc. KM3. **12:** *Cytheropteron* cf. *sawanense* Hanai, LV, loc. NK10. **13:** *Cytheropteron subuchioi* Zhao, LV, loc. NK27. **14:** *Eucytherura neoalae* Ishizaki, RV, loc. NK21. **15:** *Finmarchinella japonica* (Ishizaki), RV, loc. NK27. **16:** *Hanaiborchella triangularis* (Hanai), RV, loc. NK27. **17:** *Yezocythere gorokuensis* (Ishizaki), LV, loc. NK27. **18:** *Trachyleberis* sp., RC, loc. NK35.


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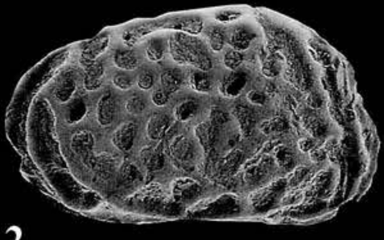
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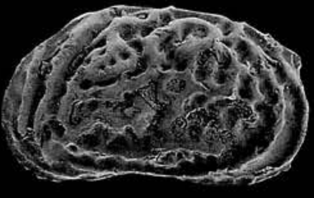
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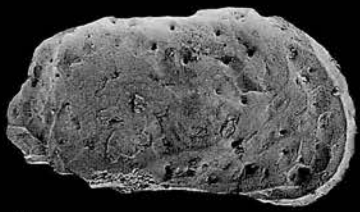
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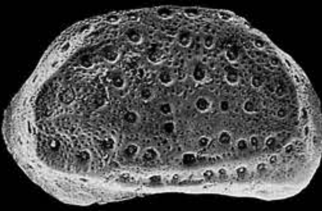
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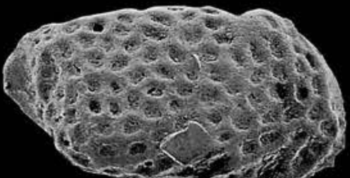
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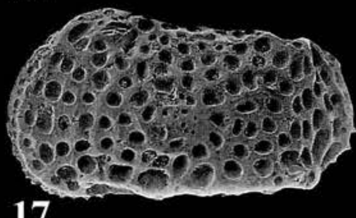
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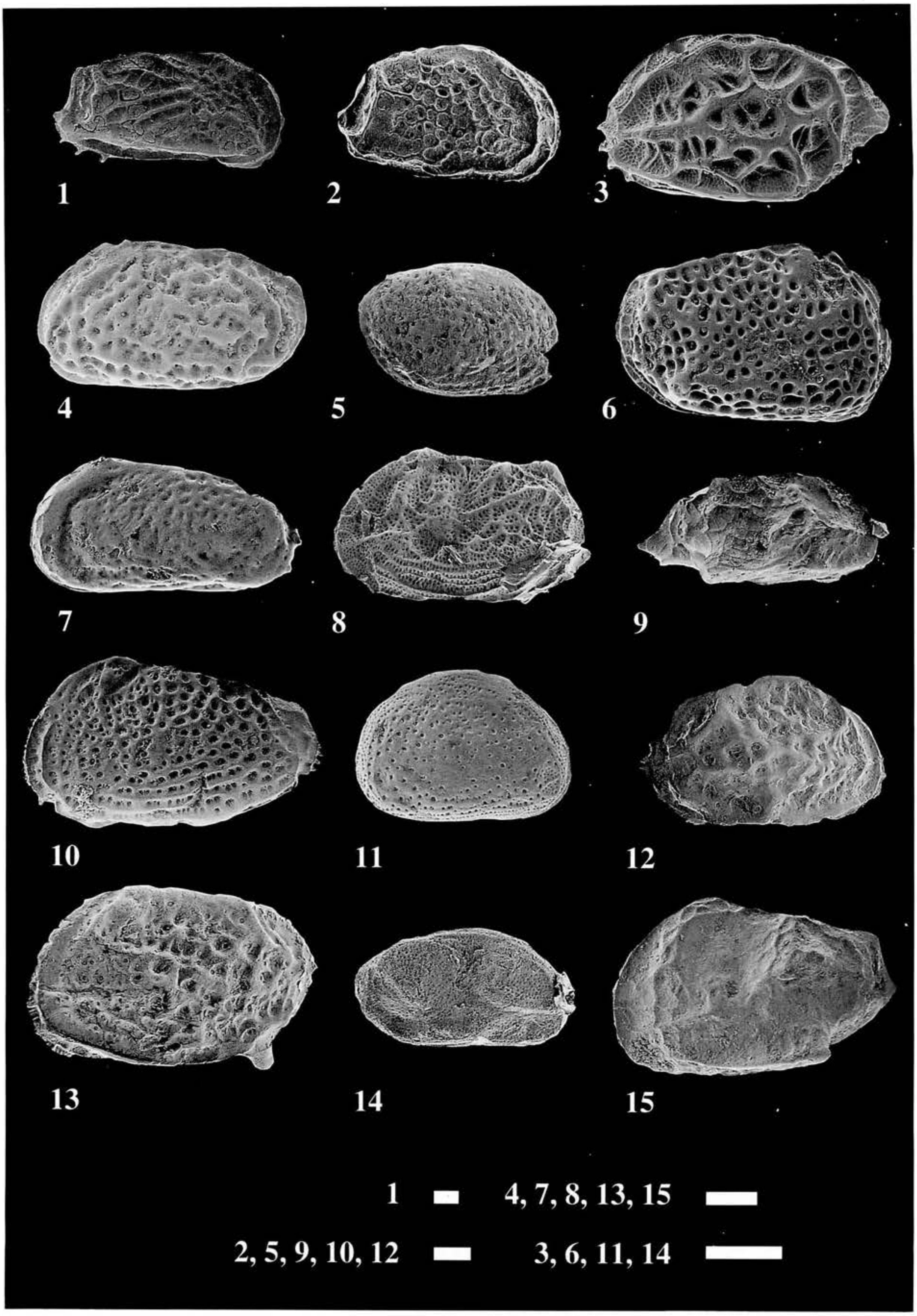
4, 7, 9, 12 — 1, 2, 3, 5, 6, 8, 10, 11, 14, 15, 18 — 13, 16, 17 —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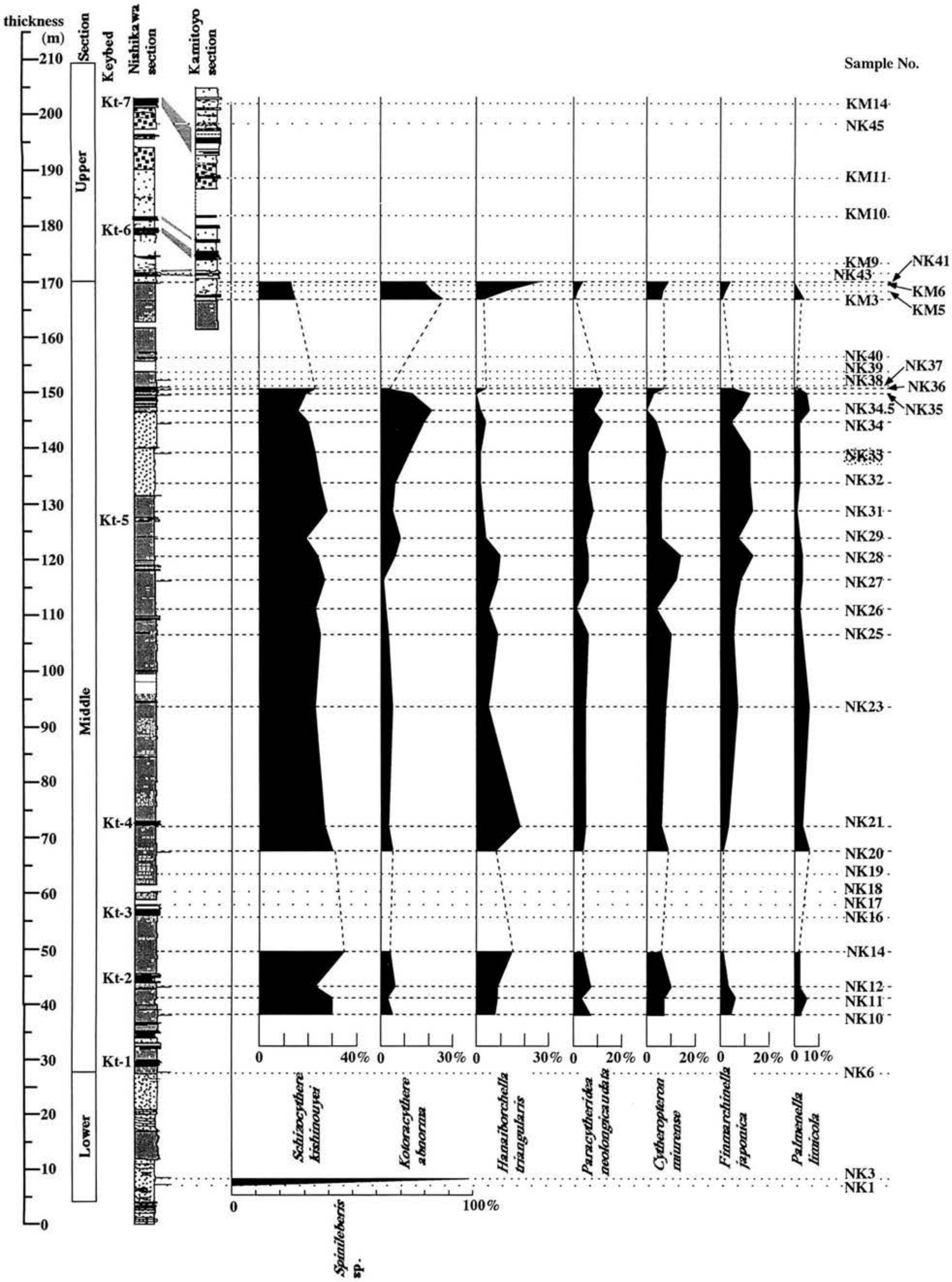
3, 6, 11, 14

species/sample	NK3	NK6	NK10*	NK11*	NK12*	NK14*	NK16	NK19	NK20*	NK21*	NK23*	NK25*	NK26*	NK27*	NK28*	NK29*	NK31*	NK32*	NK33*	NK34*	NK34.5*	NK35*	NK36*	NK37	NK38	NK39	NK40	NK41*	NK43	KM3*	KM5	KM6	KM9	KM10	KM11	KM14
Acanthocythereis spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Aurila cymba (Brady)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
* *Aurila* sp.	0	0	5	1	0	0	0	0	0	0	0	2	2	11	5	7	12	5	6	4	4	10	6	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Aurila* spp.	1	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	2	0	0	3	3	0	3	0	0	0	0	0	2	1	0	0	0	0	0	0
Callistocythere kotorai Ishizaki	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0
* *Callistocythere hatatatensis* Ishizaki	0	0	1	1	0	0	0	0	0	0	1	1	0	0	2	0	2	0	3	14	4	11	8	0	0	0	0	1	0	0	0	0	0	0	0	0
* *Callistocythere rugosoforma* Ishizaki	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	3	0	0	0	1	0	0	0	0	0	0	0	0	0
* *Callistocythere subsetanensis* Ishizaki	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Callistocythere undulatifacialis Hanai	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callistocythere sp.1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Callistocythere* sp.2	0	0	3	1	0	0	0	0	0	0	0	2	0	3	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callistocythere spp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
* *Coquimba* cf. *ishizakii* Yajima	0	0	0	0	1	0	0	0	0	0	0	1	4	2	0	0	0	0	3	5	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Coquimba* sp.1	0	0	1	2	0	0	0	0	0	1	4	5	12	3	0	14	14	12	10	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Coquimba sp.2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Coquimba spp.	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Coquimba* ? spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Cornucoquimba moniwensis* (Ishizaki)	0	0	5	7	8	5	0	0	5	4	12	0	4	4	2	8	7	2	10	1	0	3	5	0	0	0	0	0	1	0	1	0	0	0	0	1
* *Cornucoquimba saitoi* (Ishizaki) s.l.	0	0	8	9	2	1	0	0	6	7	14	16	4	13	14	6	5	4	0	7	19	9	7	0	0	0	0	1	4	14	9	1	0	5	0	2
* *Cornucoquimba* spp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Cythere omotenipponica* Hanai	0	0	0	7	1	0	0	0	0	0	2	2	2	3	3	1	2	2	1	1	5	4	12	0	0	0	1	0	1	3	2	0	0	0	0	1
* *Cythere* spp.	0	0	1	6	1	0	0	0	6	4	14	1	9	10	4	3	6	4	6	2	8	9	0	2	1	0	0	3	0	0	1	1	0	0	0	0
Cythere ? spp.	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Cytheropteron miurense* Hanai	0	0	11	12	10	6	0	0	10	8	18	17	6	28	24	11	15	10	18	9	1	6	14	0	0	0	0	7	0	5	2	0	0	0	0	2
* *Cytheropteron sawanense* Hanai	0	0	2	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cytheropteron cf. *sawanense* Hanai	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cytheropteron subuchioi Zhao	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Cytheropteron uchioi* Hanai	0	0	1	3	3	0	0	0	3	2	6	1	0	1	0	1	0	3	4	0	1	2	4	0	0	0	0	0	2	0	0	0	0	0	0	0
Cytheropteron sp.1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cytheropteron spp.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
* *Eucytherura neoalae* Ishizaki	0	0	4	4	3	1	0	0	0	3	2	1	2	0	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Finmarchinella japonica* (Ishizaki) s.l.	0	0	7	10	3	1	0	0	1	4	16	8	10	19	22	14	33	22	26	9	17	24	7	0	0	0	7	3	0	1	0	0	0	1	0	0
Finmarchinella sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Finmarchinella spp.	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Finmarchinella* ? spp.	0	0	0	0	3	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Hanaiborchella triangularis* (Hanai)	0	1	13	16	9	14	1	2	8	23	11	15	8	22	17	7	7	4	5	8	5	1	7	2	2	1	2	20	1	3	0	0	0	0	0	1
* *Hemicythere kitanipponica* Tabuki	0	0	2	3	0	0	0	0	1	0	3	0	10	0	0	4	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemicythere spp.	0	0	0	1	0	0	0	0	2	0	1	1	1	1	0	2	1	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemicytherura clathrata (Sars)	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
* *Hemicytherura cuneata* Hanai	0	0	0	1	0	0	0	0	0	0	0	0	1	0	3	2	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
* *Hemicytherura kajiyamai* Hanai	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Hemicytherura yamaguchii (Tabuki)	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Hermanites posterocostatus* Ishizaki	0	0	2	3	1	0	0	0	0	0	1	1	3	2	0	2	3	2	5	0	1	4	2	0	0	0	0	0	0	1	0	0	0	0	0	0
* *Kotoracythere abnorma* Ishizaki	0	5	9	5	6	4	0	0	5	4	12	8	4	3	10	16	12	10	27	37	42	27	4	1	0	1	2	14	4	23	13	1	1	2	1	4
* *Kotoracythere* spp.	0	0	0	0	0	0	0	0	0	0	6	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Loxoconcha nozokiensis* Ishizaki	0	0	0	1	0	0	0	0	0	0	1	0	3	1	4	8	4	5	17	10	7	0	7	0	0	0	0	0	0	3	1	0	0	0	0	0
* *Loxoconcha* spp.	0	0	0	0	9	7	0	0	0	1	0	0	0	0	0	0	7	0	0	0	1	0	1	0	0	0	1	0	0	3	0	0	0	0	0	0
* *Loxocorniculum* sp.	0	0	3	6	0	0	1	0	6	0	3	0	4	0	0	11	1	4	4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Metacytheropteron sp.	0	0	0	0	1	1	0	0	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Munseyella hatatatensis* Ishizaki	0	0	1	0	0	0	0	0	0	0	0	2	0	1	0	1	0	0	0	0	2	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0
Munseyella spp.	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	2	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Neonesidea sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Palmenella limicola* (Norman)	0	1	3	9	2	2	0	0	6	4	14	5	3	6	6	3	3	4	4	4	12	10	2	0	0	0	0	0	0	4	0	0	0	0	0	0
* *Paracytheridea neolongicaudata* Ishizaki	0	0	12	5	7	4	0	1	5	6	14	9	1	14	8	11	22	10	11	26	17	25	22	2	0	0	3	3	1	1	1	0	0	0	0	1
Pontocythere sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	1	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Robertsonites* sp.	0	0	0	0	0	0	0	0	0	3	0	2	0	0	0	1	0	1	0	1	2	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
* *Rotundracythere* ? sp.	0	0	12	5	1	9	4	6	6	11	3	11	7	7	0	2	4	2	0	0	0	0	0	3	0	0	1	5	0	0	0	0	0	0	0	0
* *Schizocythere hatatatensis* Ishizaki	0	0	1	0	0	1	0	0	0	0	0	1	1	2	1	3	1	1	3	5	2	3	4	0	0	0	0	0	0	6	2	0	0	0	0	1
Schizocythere cf. *hatatatensis* Ishizaki	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Schizocythere kishinouyei* (Kajiyama)	0	1	50	55	23	33	2	0	32	34	54	42	37	64	42	38	78	48	51	45	39	40	48	0	0	0	7	10	4	17	10	0	0	1	1	4
Schizocythere spp.	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2	0	2	0	0	0
* *Semicytherura henryhowei* Hanai and Ikeya	0	0	7	6	4	5	0	0	1	2	5	3	7	3	2	2	3	2	0	1	0	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Spinileberis sp.	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Trachyleberis* sp.	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	3	1	0	1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	2	0	0
Trachyleberis spp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* *Yezocythere gorokuensis* (Ishizaki)	0	0	0	0	1	0	0	0	0	2	0	1	5	1	2	6	6	6	7	2	4	4	3	0	0	0	0	6	0	0	0	0	0	0	0	0
Yezocythere spp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total speciments	22	8	169	181	101	95	8	9	105	127	229	163	164	234	176	200	259	182	223	200	209	203	195	10	3	2	30	76	25	87	46	3	3	12	3	19
Preservation	G	M	G	G	G	M	M	M	M	G	M	G	G	G	M	G	G	M	G	G	M	M	G	M	P	M	G	M	G	G	G	P	P	G	M	G

Figure 7. List of ostracode species from the Kubota Formation. Asterisk marks indicate samples and species used for with principal component analysis. Abbreviation for preservation: G = good, M = moderate and P = poor.

← **Figure 6.** Scanning electron micrographs of selected ostracode species from the Kubota Formation. All are adult specimens. All scale bars indicate 100 µm. RC = right lateral view of carapace. **1**: *Hermanites posterocostatus* Ishizaki, RV, loc. NK27. **2**: *Hemicythere kitanipponica* (Tabuki), RV, loc. NK34.5. **3**: *Hemicytherura cuneata* Hanai, LV, loc. NK27. **4**: *Kotoracythere abnorma* Ishizaki, LV, loc.NK35. **5**: *Loxoconcha nozokiensis* Ishizaki, RV, loc. NK36. **6**: *Loxocorniculum* sp., LV, loc. NK27. **7**: *Munseyella hatatatensis* Ishizaki, LV, loc. NK40. **8**: *Palmenella limicola* (Norman), LV, loc. NK21. **9**: *Paracytheridea neolongicaudata* Ishizaki, RV, loc. NK34. **10**: *Robertsonites* sp., LV, loc. NK35. **11**: *Rotundracythere* ? sp., RV, loc. NK27. **12**: *Schizocythere kishinouyei* (Kajiyama), RV, loc. KM3. **13**: *Schizocythere hatatatensis* Ishizaki, LV, loc. KM3. **14**: *Semicytherura henryhowei* Hanai and Ikeya, RV, loc. NK21. **15**: *Spinileberis* sp., LV, loc. NK3.


thickness (m)
210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
Section
Upper
Middle
Lower
Keybed
Kt-7
Kt-6
Kt-5
Kt-4
Kt-3
Kt-2
Kt-1
Nishikawa section
Kamitoyo section
Sample No.
KM14
NK45
KM11
KM10
KM9
NK43
NK41
KM6
KM5
KM3
NK40
NK39
NK38
NK37
NK36
NK35
NK34.5
NK34
NK33
NK32
NK31
NK29
NK28
NK27
NK26
NK25
NK23
NK21
NK20
NK19
NK18
NK17
NK16
NK14
NK12
NK11
NK10
NK6
NK3
NK1
0 40%
0 30%
0 30%
0 20%
0 20%
0 20%
0 10%
0 100%
Schizocythere kishinouyei
Kotoracythere abnorma
Hanaiborchella triangularis
Paracytheridea neolongicaudata
Cytheropteron miurense
Finmarchinella japonica
Palmenella limicola
Spinileberis sp.

of species decrease.

The number of individuals in sample NK3 is 0.2 per 10 g sediment. Samples from the middle and upper parts contain about 40 to 400 and less than about 10 individuals per 10g, respectively.

Principal component analysis

In order to elucidate bottom environments of the Kubota Formation, 21 samples which contained more than 50 individuals and 40 species represented by more than three individuals at least in a sample were subjected to Q-mode principal component analysis. The analysis was carried out to obtain clues to the intersample relationship and to identify end members (samples having extreme properties). However, the correlation coefficient may be considered inappropriate as a measure of similarity between samples because it requires calculation of variance across variables (Davis, 1986). Therefore, the analysis in this study was based on the covariance matrix. The computer program used in this study was a modified version written by Furuya and Obata (1996). The results of the analysis show that the first two components account for about 85 % of the total variation, which should be sufficient for discussion of general distribution patterns of the ostracode assemblages (Table 1). Figure 10 shows the stratigraphic distribution of eigenvectors in relation to the first two components.

The first component

This component explains more than 77% of the total variation. *Schizocythere kishinouyei* (score = +113.9), *Kotoracythere abnorma* (score = +35.9), *Hanaiborchella triangularis* (score = +34.5) and *Cytheropteron miurense* (score = +32.6) contribute greatly to this component. They are abundant in most of the samples examined. Recent representatives of these species are mostly known to occur predominantly in littoral to sublittoral habitats, which are influenced by the Kuroshio Warm Current (e.g. Hanai, 1957, 1970; Ishizaki, 1966, 1981; Zhou, 1995; Tsukawaki *et al.*, 1997, 1998). The first component is interpreted to represent the abundance of ostracode species.

The second component

This component explains more than 7% of the total variation. *Kotoracythere abnorma* (score = +32.0) and *Cornucoquimba saitoi* s.l. (score = +8.8) have high positive scores of the second component. *Hanaiborchella triangularis* (score = −8.1), *Rotundracythere*? sp. (score = −7.9) and *Schizocythere kishinouyei* (score = −7.1) have high negative scores of the second component. *K. abnorma* and *C. saitoi* are extinct species. *K. abnorma* occurs in the middle Miocene Hatatate Formation, but does not occur in the Moniwa Formation, which is overlain conformably by the Hatatate Formation (Ishizaki, 1966). Kitamura *et al.* (1986) suggested that the Hatatate and Moniwa Formations were deposited in lower sublittoral to bathyal and upper sublittoral settings, respectively, based on sedimentary facies and benthic foraminifer assemblages. Hence, *K. abnorma* is considered as having lived in the lower sublittoral zone under the influence of open sea water. Because *C. saitoi* also occurs in the Hatatate Formation, it is regarded as having lived under the influence of open sea water (Ishizaki, 1966). Thus, species having high positive scores are considered as having lived in the open sea. On the other hand, species having high negative scores are reported from Recent seas, except for *Rotundracythere*? sp. *H. triangularis* is reported from the mouth of Ise and Mikawa Bays (Bodergat and Ikeya, 1988). *Rotundracythere*? sp. occurs in the Pleistocene Sasaoka Formation (Ishizaki and Matoba, 1985). Because *Rotundracythere*? sp. occurs with shallow marine molluscs, it is regarded as having likewise lived in shallow marine waters. *S. kishinouyei* is reported from an upper sublittoral zone under the influence of coastal currents in the eastern China sea (Ishizaki, 1981). Therefore, species having high negative scores are considered as having lived in shallow seas influenced by coastal currents. Consequently, the second component is interpreted as signalling changes of water mass: positive and negative eigenvectors represent the stronger and weaker influence of open sea water, respectively.

Discussion

Water depths

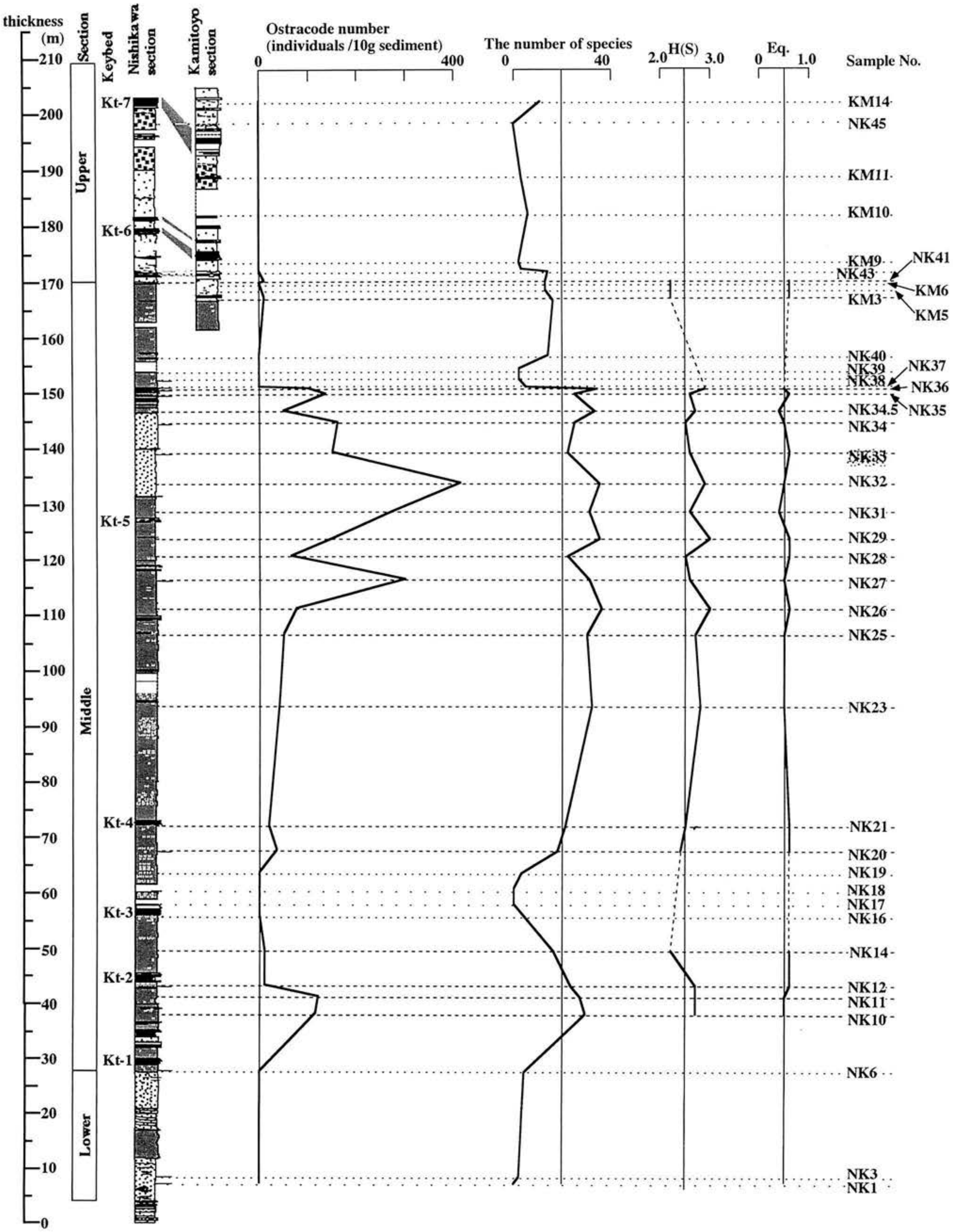
In the lower part of the Kubota Formation, *Spinileberis* sp. occurs dominantly. This fact suggests that the lower part was a deposit in an enclosed inner bay (e.g. Ikeya and Shiozaki, 1993).

Most of the ostracode species from the middle part of the formation are reported in Recent shallow seas, as mentioned above. Moreover, the faunal structures of the ostracode assemblages from the unit indicate high values of $H(S)$, $Eq.$ and the number of species. For example, the faunal structures of ostracode assemblages in the outer part of Uranouchi Bay show values of $H(S)$, $Eq.$ and the number of species that are 2.0 to 3.0, 0.4 to 0.6 and 20 to 40, respectively (Ishizaki, 1979). These values approximate those of the middle part. Thus, the ostracode assemblage from the middle part of the Kubota Formation represents a sublittoral setting. Vertical changes of the second component eigenvectors indicate that the influence of open sea water became stronger in the upward sequence.

In the upper part, the low occurrence of ostracodes means that paleodepths cannot be assessed, except for the horizon of the sample KM3. The sample KM3 has a positive second-component eigenvector and the horizon of the sample was deposited under the influence of open sea water.

As already mentioned, Iwasaki (1970) studied the molluscan fauna from the Kubota Formation. He reported

← **Figure 8.** Diagram showing the vertical changes for the relative abundance of major species. Broken lines show samples containing more than 50 individuals of ostracodes. Dotted lines represent samples containing less than 50 individuals. Loose dotted lines represent samples containing no ostracode. For explanation of columnar sections see the legend of Figure 4.


thickness (m)
210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
Section
Upper
Middle
Lower
Keybed
Kt-7
Kt-6
Kt-5
Kt-4
Kt-3
Kt-2
Kt-1
Nishikawa section
Kamitoyo section
Ostracode number (individuals /10g sediment)
0
400
The number of species
0
40
H(S)
2.0
3.0
Eq.
0
1.0
Sample No.
KM14
NK45
KM11
KM10
KM9
NK43
NK41
KM6
KM3
KM5
NK40
NK39
NK38
NK37
NK36
NK35
NK34.5
NK34
NK33
NK32
NK31
NK29
NK28
NK27
NK26
NK25
NK23
NK21
NK20
NK19
NK18
NK17
NK16
NK14
NK12
NK11
NK10
NK6
NK3
NK1

the *Ostrea* and *Anadara-Dosinia* assemblages from the lower part, the *Lucinoma-Turritella* assemblage from the middle part and the *Mizuhopecten-Chlamys* assemblage from the upper part. These molluscan assemblages represent the following habitat conditions, referring to the paleobathymetric indices of molluscan fossils shown by Ogasawara and Masuda (1989): 1) the lower part represents an inner-bay environment with water depths shallower than 30 m; 2) the middle part represents depths between 100 and 200m; 3) the upper part represents depths of 30 m or less under the influence of the open sea. These estimates based on molluscan fossils from the Kubota Formation are generally consistent with the water depths suggested by ostracodes.

Shimamoto *et al.* (1998) examined foraminifer, radiolarian and molluscan fossils and showed the successive changes of the planktonic/benthic foraminifer ratio (P/B ratio). They thought that the lower part was deposited in an inner bay because of the occurrence of *Ostrea* of *in-situ* origin, while the middle part was in an open sea shallower than about 100 m based on P/B ratios. Consequently, they concluded that the Kubota Formation represents a sequence of marine transgression and regression. Vertical changes of water depths suggested by ostracodes are largely consistent with their views. On the other hand, decreasing frequency of radiolarians in the upward sequence of the middle part suggests that influence of the open sea water became feeble. This representation contradicts one based on vertical changes of second-component eigenvectors. Some workers have pointed out that radiolarian assemblages from the Kubota Formation contain many reworked individuals (Taketani and Aita, 1991; Shimamoto *et al.*, 1998). Therefore, the reported frequency of radiolarians is regarded as not sufficiently representing paleoenvironmental settings during deposition of the middle part. Consequently, the middle part was subject to the strong influence of open sea water in its upward sequence.

Marine climates

In the lower part of the Kubota Formation, the only dominant species is *Spinileberis* sp. Recent species of this genus are widely distributed from southern China to northern Japan and occur abundantly in bays influenced by warm coastal waters (e.g. Hanai, 1961; Ishizaki, 1971; Ikeya and Shiozaki, 1993). Hence, the lower part is considered to have been deposited under the influence of warm coastal waters.

In the middle part, Recent representatives of *Schizocythere kishinouyei*, *Hanaiborchella triangularis* and *Cytheropteron miurense* among the dominant species are reported from shallow seas under the influence of the Kuroshio Warm Current (e.g. Ishizaki, 1981; Zhou, 1995). However, such circumpolar and cryophilic species as *Hemicytherura clathrata*, *Munseyella hatatatensis*, *Palmenella limicola*, *Finmarchinella japonica* s.l. and *Hemicythere kitanipponica* also occurred sparsely (Figure 10). Circumpolar and cryophilic species are members of high-latitude genera (Cronin and Ikeya, 1987). Irizuki and Matsubara (1995) and Irizuki *et al.* (1998) also reported that circumpolar and cryophilic species occurred with warm-water species in the Miocene deposits. They considered that the Miocene circumpolar and cryophilic species may not have experienced such subfrigid to frigid environments as their Recent counterparts and lived in slightly colder conditions than the other species because of the absence of fossil records for them from the mid-Neogene climatic optimum horizon of southwestern Japan (Ishizaki, 1963; Yajima, 1988, 1992). Hence, the middle part of the formation was deposited in a warm shallow sea under the feeble influence of cooler currents.

Ostracodes are sparse in the upper part of the formation. However, species forming assemblages do not show any distinct change, comparing with the assemblages from the middle part. Hence, the upper part may also have been deposited in warm-water conditions.

As mentioned above, Ogasawara (1994) studied the relations between marine climates and Neogene molluscan faunas, considering their tolerance for marine climates. Moreover, he divided the Shiobara fauna into older and younger faunas based on characteristic species of each fauna. The molluscan fauna from the Kubota Formation belongs to the younger Shiobara fauna, because *Mizuhopecten paraplebejus* and *Kaneharaia kaneharai*, both of which characterize the younger fauna, were reported (Iwasaki, 1970). Ogasawara (1994) mentioned that the younger Shiobara fauna had lived in the warm- to mild-temperate realms of Nishimura's (1981) zoogeographical classification of modern marine faunas around the Japanese Islands.

Marine paleoclimates represented by ostracode fauna from the Kubota Formation strongly supported Ogasawara's (1994) views.

Conclusions

1) Sixty-seven ostracode species including those left in open nomenclature were reported for the first time from the upper Miocene Kubota Formation. The fauna is characterized by the abundance of warm-water species.

2) The ostracode fauna from the Kubota Formation reveals an enclosed inner bay paleoenvironment influenced by warm water for the lower part and a warm shallow sea under the feeble influence of cold water for the middle to upper part. Hence, the Shiobara fauna from the Kubota Formation flourished in a warm shallow sea.

3) Results of principal component analysis of successively collected ostracode samples suggest that the middle part of the Kubota Formation was strongly influenced by

← **Figure 9.** Diagram showing the vertical changes of the ostracode abundance of individuals per 10g sediment, number of species, species diversity (*H*(*S*)) and equitability (*Eq.*). Broken lines show samples containing more than 50 individuals of ostracodes. Dotted lines represent samples containing less than 50 individuals. Loose dotted lines represent samples containing no ostracode. For explanation of columnar sections see the legend of Figure 4.

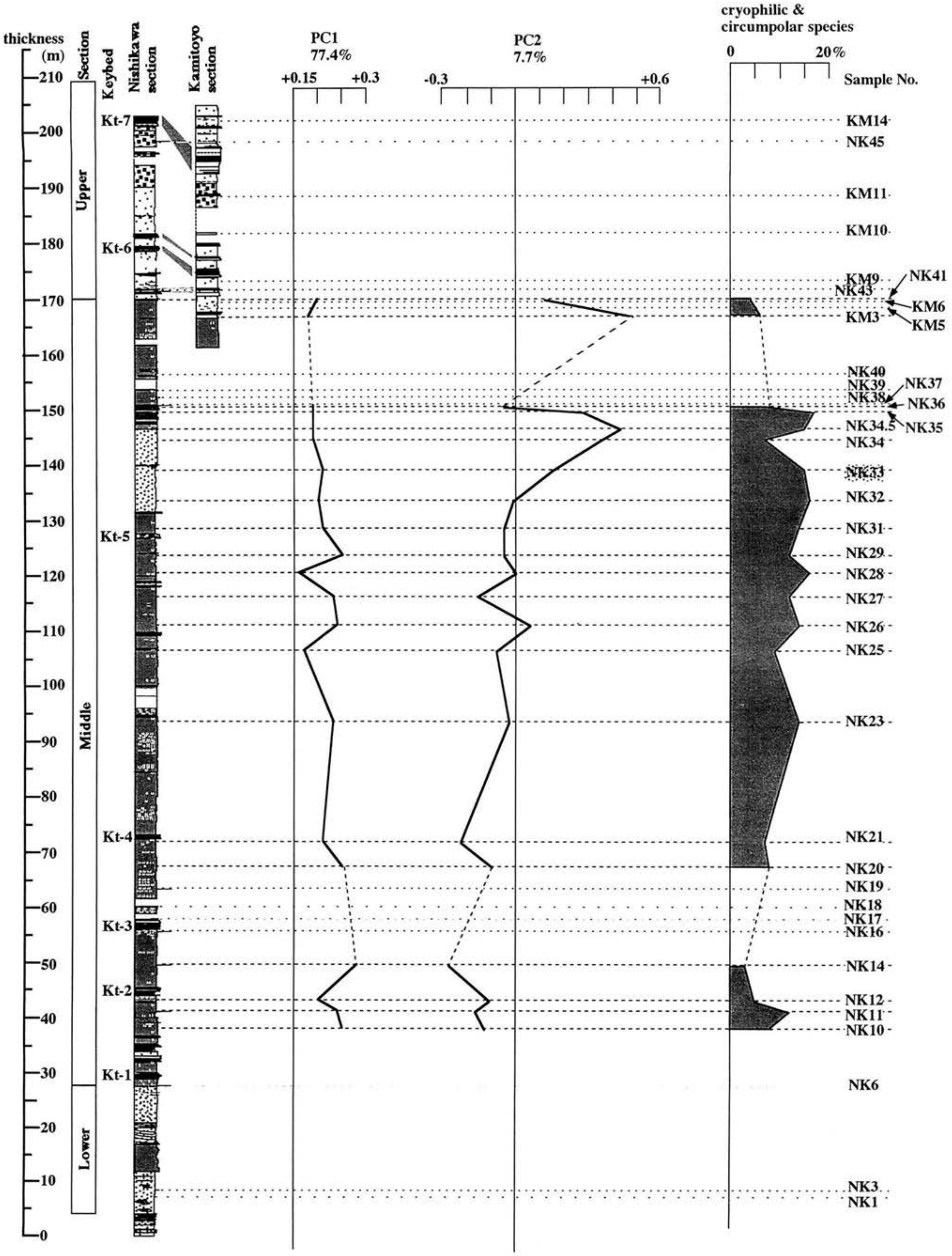

thickness (m)
210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
Section
Upper
Middle
Lower
Keybed
Kt-7
Kt-6
Kt-5
Kt-4
Kt-3
Kt-2
Kt-1
Nishikawa section
Kamitoyo section
PC1
77.4%
+0.15
+0.3
PC2
7.7%
-0.3
+0.6
cryophilic & circumpolar species
0
20%
Sample No.
KM14
NK45
KM11
KM10
KM9
NK43
NK41
KM6
KM5
KM3
NK40
NK39
NK38
NK37
NK36
NK35
NK34.5
NK34
NK33
NK32
NK31
NK29
NK28
NK27
NK26
NK25
NK23
NK21
NK20
NK19
NK18
NK17
NK16
NK14
NK12
NK11
NK10
NK6
NK3
NK1

Table 1. Summary of principal component analysis.

	Eigenvalue	Percentage	Cumulative Percentage
PC 1	380.5	77.4	77.4
PC 2	37.8	7.7	85.1

open sea water in its upward sequence.

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← **Figure 10.** Diagram showing vertical changes of eigenvectors with respect to the first two components and the proportion of cryophilic and circumpolar ostracode species. Broken lines show samples containing more than 50 individuals of ostracodes. Dotted lines represent samples containing less than 50 individuals. Loose dotted lines represent samples containing no ostracode. For explanation of columnar sections see the legend of Figure 4.

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The systematic status of the genus *Miosesarma* Karasawa, 1989 with a phylogenetic analysis within the family Grapsidae and a review of fossil records (Crustacea: Decapoda: Brachyura)

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Abstract. The genus *Miosesarma* Karasawa (Decapoda: Brachyura: Grapsidae) known from the Miocene of Japan is redefined. A phylogenetic analysis of 22 genera of the family Grapsidae MacLeay is provided based on 41 adult morphological characters. A single tree is produced (length = 85, CI = 0.565, RI = 0.807, RC = 0.456). The analysis supports the monophyly of the subfamilies Plagusiinae Dana, Grapsinae MacLeay and Varuninae H. Milne Edwards. The analysis suggests that the Sesarminae Dana is polyphyletic and that *Cyclograpsus* H. Milne Edwards, *Helice* De Haan, *Metaplax* H. Milne Edwards and *Miosesarma* are derived as sister taxa to varunines. The tribe Cyclograpscaea H. Milne Edwards is treated as a subfamily Cyclograpsinae (*nomen. transl.*) consisting of *Cyclograpsus* (type genus), *Helice*, *Heterograpsus* Campbell and Griffin, *Metaplax*, *Miosesarma* and *Paragrapsus* H. Milne Edwards, which were previously placed within the Sesarminae. Within the Grapsidae, the Varuninae and Cyclograpsinae are sister groups nested as the most derived clade, followed by the Sesarminae, Grapsinae, and the most basal Plagusiinae. Five subfamilies within the Grapsidae are redefined based on the phylogenetic analysis. During a review of fossil records of the Grapsidae, 25 species, 17 genera and four subfamilies are recognized as fossils. *Maingrapsus* Tessier *et al.*, *Palaeograpsus* Bittner, and *Telphusograpsus* Lőrenthey, known from the European Eocene, are referred to the family Goneplacidae H. Milne Edwards and *Sculptoplax* Müller and Collins from the Eocene of Hungary is referred to the Xanthidae MacLeay. Fossil grapsids exhibiting the dorsal carapace only can not confidently be referred to subfamilies.

Key words: Brachyura, Crustacea, Decapoda, Grapsidae, Phylogeny

Introduction

The genus *Miosesarma* Karasawa, 1989 is an endemic genus known from the lower-middle Miocene of Japan (Karasawa, 1989, 1999; Kato, 1996). Karasawa (1989) originally placed the genus within the subfamily Sesarminae Dana, 1851 (Decapoda: Brachyura: Grapsidae) and demonstrated its close resemblance to extant sesarmines, *Helice* De Haan, 1835 and *Metaplax* H. Milne Edwards, 1852. Pereyra Lago (1993) and Schubart and Cuesta (1998) indicated that larval characters of *Helice* were similar to those of the grapsid subfamily Varuninae H. Milne Edwards, 1853. Schubart *et al.* (2000) suggested reclassification and phylogeny of the Grapsidae based upon molecular data, and that *Helice* and *Metaplax* should be classified within Varuninae.

The purpose of the present paper is to redefine the genus *Miosesarma* based on newly obtained specimens and to provide an adult morphology-based phylogenetic analysis for 22 genera of the Grapsidae. A review of fossil records of the Grapsidae is included.

Phylogenetic analysis of the family Grapsidae MacLeay, 1838

Materials and methods

A total of 25 species were examined with representatives from 22 genera including one extinct genus, *Miosesarma*, within the Grapsidae. Among these, extant species were collected from Japan, Thailand and Malaysia. The analyses were based on the examination of material deposited in the Mizunami Fossil Museum, Mizunami, Japan and the

Table 1. Taxa included in the analysis.

- Family Grapsidae MacLeay, 1838
  - Subfamily Grapsinae MacLeay, 1838
    - Genus *Geograpsus* Stimpson, 1858
      - *Geograpsus grayi* (H. Milne Edwards, 1853)
    - Genus *Grapsus* Lamarck, 1801
      - *Grapsus albolineatus* Lamarck, 1818
      - *Grapsus tenuicrustatus* (Herbst, 1783)
    - Genus *Metopograpsus* H. Milne Edwards, 1853
      - *Metopograpsus thukuhar* (Owen, 1839)
    - Genus *Pachygrapsus* Randall, 1840
      - *Pachygrapsus minutus* A. Milne Edwards, 1873
    - Genus *Planes* Bowdich, 1825
      - *Planes cyaneus* Dana, 1851
  - Subfamily Sesarminae Dana, 1851
    - Genus *Chasmagnathus* De Haan, 1833
      - *Chasmagnathus convexus* De Haan, 1833
    - Genus *Cyclograpsus* H. Milne Edwards, 1837
      - *Cyclograpsus intermedius* Ortmann, 1894
    - Genus *Helice* de Haan, 1835
      - *Helice leachi* Hess, 1865
    - Genus *Metaplax* H. Milne Edwards, 1852
      - *Metaplax crenulata* (Gerstecker, 1856)
    - Genus *Miosesarma* Karasawa, 1989
      - *Miosesarma japonicum* Karasawa, 1989
      - *Miosesarma naguraense* Kato, 1996
    - Genus *Nanosesarma* Tweedie, 1950
      - *Nanosesarma minutum* (De Man, 1887)
    - Genus *Sesarma* Say, 1817
      - *Sesarma* (*Perisesarma*) *bidens* (De Haan, 1835)
      - *Sesarma* (*Parasesarma*) *pictum* (De Haan, 1835)
    - Genus *Sesarmops* Sèrene and Soh, 1970
      - *Sesarmops intermedium* (De Haan, 1835)
  - Subfamily Varuninae H. Milne Edwards, 1853
    - Genus *Acmaeopleura* Stimpson, 1858
      - *Acmaeopleura parvula* Stimpson, 1858
    - Genus *Eriocheir* De Haan, 1835
      - *Eriocheir japonica* (De Haan, 1835)
    - Genus *Gaetice* Gistl, 1848
      - *Gaetice depressus* (De Haan, 1833)
    - Genus *Hemigrapsus* Dana, 1851
      - *Hemigrapsus sanguinensis* (De Haan, 1835)
    - Genus *Pseudograpsus* H. Milne Edwards, 1837
      - *Pseudograpsus* sp.
    - Genus *Ptychognathus* Stimpson, 1858
      - *Ptychognathus* sp. aff. *P. ishii* Sakai, 1939
    - Genus *Varuna* H. Milne Edwards, 1830
      - *Varuna litterata* (Fabricius, 1798)
  - Subfamily Plagusiinae Dana, 1851
    - Genus *Percnon* Gistl, 1848
      - *Percnon planissimum* (Herbst, 1804)
    - Genus *Plagusia* Latreille, 1804
      - *Plagusia dentipes* De Haan, 1833

- Family Xanthidae MacLeay, 1838
  - Genus *Leptodius* A. Milne Edwards, 1873
    - *Leptodius nudipes* (Dana, 1852)
- Family Cancridae Latreille, 1803
  - Genus *Cancer* Linnaeus, 1758
    - *Cancer amphioetus* Rathbun, 1898

Natural History Museum and Institute, Chiba, Japan. The material examined is listed in Table 1. The subfamilial arrangement of the genera conforms to Sakai (1976), Manning and Holthuis (1981) and Karasawa (1989). Outgroups included two heterotrematous crabs, *Cancer amphioetus* Rathbun, 1898 (Cancridae) and *Leptodius nudipes* (Dana, 1852) (Xanthidae) outside of the Grapsidae (Table 1). Table 2 lists 41 adult morphological characters and character states used in the analysis. The missing data were scored unknown. The data matrix is provided in Table 3.

The phylogenetic analysis used PAUP version 3.1.1 (Swofford, 1993), utilizing a data matrix originating in MacClade version 3 (Maddison and Maddison, 1992). Heuristic search analyses were performed with the following options in effect: addition sequence, simple; one tree held at each step during stepwise addition; tree-bisection-reconnection (TBR) branch stepping performed; MULPARS option activated; steepest descent option not in effect; branches having maximum length zero collapsed to yield polytomies; topological constraints not enforced; tree unrooted; multistate taxa interpreted as uncertain; character state optimization, accelerated transformation (ACCTRAN). All characters were unordered, unscaled and equally weighted.

Characters

Forty-one characters were included in the data matrix (Table 3). There are 34 binary characters and 7 multistate characters. In the text, characters and character states are indicated by numbers in parentheses (e.g. 1-0 = character 1+character state 0).

Carapace.—In examined material the carapace is usually smooth (3-0; Figures 1.1, 1.2, 1.5-1.8, 4.11, 4.12, 4.15); however, all grapsine genera and a sesarmine *Sesarma* bear oblique ridges dorsally (3-1; Figure 1.3, 1.4). One outgroup taxon, *Cancer*, and two plagusiines, *Plagusia* and *Percnon*, possess frontal teeth (4-0; Figure 1.1, 1.2), while all other examined taxa have a straight frontal margin without teeth (4-1; Figure 1.3-1.8). Most taxa have a narrow orbital margin (5-0; Figure 1.1-1.4, 1.6), but a varunine *Hemigrapsus* and three sesarmines, *Chasmagnathus, Metaplax* and *Miosesarma*, possess wide orbital margins (5-1: Figures 1.5, 1.7, 1.8, 4.5, 4.11, 4.12, 4.15). Both outgroup taxa, all plagusiines and all grapsines lack infraorbital ridges (6-0; Figure 2.9-2.11); however, all sesarmines and all varunines bear infraorbital ridges (6-1;

Table 2. Characters and states used in the phylogenetic analysis.

Carapace
1 Ratio of carapace length/width: wider than long (0); about equal (1); long (2)
2 Maximum carapace width: midlength (0); anterior (1); posterior (2)
3 Carapace with oblique ridges dorsally: absent (0); present (1)
4 Frontal margin with frontal teeth: present (0); absent (1)
5 Orbital width: narrow (0); wide (1)
6 Infraorbital ridge: absent (0); present (1)
7 Upper orbital margin with notch: present (0); absent (1)
8 Lateral teeth: present (0); absent (1)
9 Pterygostomian and ventrolateral surfaces with oblique striae: absent (0); present (1)
Eye stalk and antennule
10 Eye stalk: short (0); long (1)
11 Antennule: not visible dorsally (0); visible dorsally (1)
Maxilliped 3
12 Ratio of merus/ischium: short (0); subequal (1); very short (2)
13 Anterolateral margin of merus: quadrate (0); expanded (1); convex (2)
14 merus and ischium with oblique, hairy ridge: absent (0); present (1)
15 Maxilliped 3 with wide rhomboidal gap: absent (0); present (1)
16 Exopod: wide (0); narrow (1)
17 Articulation of palp: anteromesial angle of merus (0); anterior margin of merus (1)
18 Dactylus: long (0); short (1)
Abdomen
19 Male abdomen: fused somites (0); 7 somites (1)
20 Male abdomen width; narrow (0); wide (1)
Thoracic sternum
21 Thoracic sternum width: narrow (0); wide (1)
22 Sternites 1 and 2: distinct (0); indistinct (1)
23 Suture between sternites 3 and 4: distinct (0); indistinct (1)
24 Median groove on sternite 3: present (0); absent (1)
25 Median groove on sternite 4: present (0); absent (1)
26 Button: present (0); absent (1)
27 Anterior end of sterno-abdominal cavity: shallow (0); sternite 4 (1); sternite 3 (2)
28 Cristiform margin of anterior sterno-abdominal cavity: absent (0); present (1)
29 Deeply concave lateral margin of sternites 3-4: absent (0); present (1)
30 Transverse groove on sternite 8: absent (0); present (1)
31 Sternite 8 visible in ventral view: indistinct (0); distinct (1)
32 Sternite 8 visible in posterior view: indistinct (0); distinct (1)
33 Location of male gonopore: coxae (0); sternite 8 (1)
34 Location of male gonopore on sternite 8: excluded (0); lateral (1); inner (2)
Gonopod
35 Gonopods 1: sinuous (0); twist (1); linear (2)
Pereiopods
36 Cheliped with elongate, slender palm: absent (0): present (1)
37 Chelipeds with pectinated crests on dorsal margin of propodus: absent (0); present (1)
38 Chelipeds with hairs on lateral surfaces of propodus near base of fingers: absent (0); present (1)
39 Chelipeds with tubercles on dorsal margin of dactylus: absent (0); present (1)
40 Pereiopods 2-5 meri with longitudinal ridge on lateral surface: absent (0); present (1)
41 Pereiopods 2-5 meri with oblique ridges on lateral surface: absent (0); present (1)

Table 3. Input data matrix of 41 characters and 24 genera. The last two taxa are outgroups. Missing character states are shown by ?.

Characters	0 0 0 0 0 0 0 0 0 1	1 1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 2 2 3	3 3 3 3 3 3 3 3 3 4	4
Taxa	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1
Geograpsus	0 1 1 1 0 0 1 0 0 0	0 1 1 0 1 1 1 0 1 1	1 0 1 1 1 0 1 0 0 0	0 0 1 1 1 0 0 0 0 0	1
Grapsus	1 2 1 1 0 0 1 0 0 0	0 1 1 0 1 1 1 0 1 1	1 0 1 1 1 0 1 0 0 0	0 0 1 1 1 0 0 0 0 0	1
Metopograpsus	0 1 1 1 0 0 1 1 0 0	0 0 1 0 1 1 1 0 1 1	1 0 1 1 1 0 2 1 0 0	0 0 1 1 1 0 0 0 0 0	1
Pachygrapsus	0 1 1 1 0 0 1 1 0 0	0 0 1 0 1 1 1 0 1 1	1 0 1 1 1 0 1 0 0 0	0 0 1 1 1 0 0 0 0 0	1
Planes	2 0 1 1 0 0 1 0 0 0	0 0 1 0 1 0 1 0 1 1	1 0 1 1 1 0 1 0 0 0	0 0 1 1 1 0 0 0 0 0	1
Chasmagnathus	0 0 0 1 1 1 1 0 0 1	0 1 2 1 1 1 1 1 1 1	1 0 1 1 1 0 2 1 1 0	0 0 1 1 2 0 0 0 0 0	0
Cyclograpsus	0 0 0 1 0 1 1 0 0 0	0 1 2 1 1 1 1 1 1 0	1 0 1 1 1 1 2 1 0 1	1 1 1 2 2 0 0 0 0 0	0
Helice	0 0 0 1 1 1 1 0 0 1	0 1 2 1 1 1 1 1 1 0	1 0 1 1 1 1 2 1 0 1	1 1 1 2 2 0 0 0 0 0	0
Metaplax	0 0 0 1 1 1 1 0 0 1	0 1 2 1 1 1 1 1 1 0	1 0 1 1 1 1 2 1 0 1	1 1 1 2 2 1 0 0 0 0	0
Miosesarma	0 0 0 1 1 1 1 0 0 1	0 1 2 ? 1 1 1 ? 1 0	1 ? 1 1 1 ? 2 1 0 1	1 1 1 2 2 1 0 ? 0 0	0
Nanosesarma	0 1 0 1 0 1 1 0 1 0	0 1 2 1 1 1 1 1 1 1	1 0 1 1 1 1 2 1 1 0	0 0 1 1 2 0 0 0 0 0	0
Sesarma	0 1 1 1 0 1 1 0&1 1 0	0 1 2 1 1 1 1 1 1 1	1 0 1 1 1 0 2 1 1 0	0 0 1 1 2 0 1 0 1 0	1
Sesarmops	1 0 0 1 0 1 1 0 1 0	0 1 2 1 1 1 1 1 1 1	1 0 1 1 1 1 2 1 1 0	0 0 1 1 2 0 1 0 1 0	0
Acmaeopleura	0 0 0 1 0 1 1 1 0 0	0 1 1 0 0 0 1 0 1 0	1 0 1 1 1 1 2 1 0 1	1 1 1 2 2 0 0 1 0 0	0
Eriocheir	1 2 0 1 0 1 1 0 0 0	0 0 1 0 0 0 1 0 1 1	1 0 1 1 1 0 2 1 0 1	1 1 1 2 2 0 0 0 0 0	0
Gaetice	0 0 0 1 0 1 1 0 0 0	0 1 1 0 0 0 1 0 1 0	1 0 1 0 1 1 2 1 0 1	1 1 1 2 2 0 0 0 0 0	0
Hemigrapsus	0 0 0 1 1 1 1 0 0 1	0 1 1 0 1 1 1 0 1 0	1 0 1 1 1 0 2 1 0 1	1 1 1 2 2 0 0 1 0 0	0
Pseudograpsus	1 0 0 1 0 1 1 0 0 0	0 1 1 0 0 0 1 0 1 0	1 0 1 1 1 1 2 1 0 1	1 1 1 2 2 0 0 1 0 0	0
Ptychognathus	0 1 0 1 0 1 1 0 0 0	0 1 1 0 0 0 1 0 1 0	1 0 1 1 1 1 2 1 0 0	1 1 1 2 2 0 0 1 0 0	0
Varuna	1 0 0 1 0 1 1 0 0 0	0 0 1 0 0 0 1 0 1 1	1 0 1 1 1 0 2 1 0 1	1 1 1 2 2 0 0 0 0 0	0
Percnon	2 2 0 0 0 0 1 0 0 0	1 2 2 0 0 1 0 0 0 1	1 1 1 1 1 0 1 0 0 0	1 0 1 1 2 0 0 0 0 1	0
Plagusia	2 2 0 0 0 0 1 0 0 0	1 0 2 0 0 1 0 0 0 1	1 0 1 1 1 0 1 0 0 0	1 0 1 1 1 0 0 0 0 1	0
Leptodius	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 1 0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0	0
Cancer	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0

Figures 2.12–2.16, 4.5, 4.8). Upper orbital fissures are present in both outgroup taxa (7–0), and absent in all taxa of the Grapsidae (7–1; Figures 1.1–1.8, 4.11, 4.12, 4.15). Two grapsines, *Metopograpsus* and *Pachygrapsus*, and a varunine *Acmaeopleura* possess the anterolateral margin without teeth (8–1), but all other taxa have anterolateral teeth (8–0; Figures 1.1–1.8, 4.11, 4.12, 4.15). The pterygostomian and ventrolateral surfaces in three sesarmines, *Nanosesarma*, *Sesarma*, and *Sesarmops*, are ornamented with oblique striae (9–1), while those in remaining taxa are without oblique striae (9–0). A ratio of the carapace width/length [character 1; Figure 1.1–1.8] and a maximum carapace width [character 2, Figure 1.1–1.8] are variable in examined taxa and both characters seem to be consistent at the generic level.

Eye stalk and antennule.—In examined taxa a varunine *Hemigrapsus* and three sesarmines, *Chasmagnathus*, *Metaplax* and *Miosesarma* have slender, long eye stalks (10–1; Figures 1.5, 1.7, 1.8, 4.15), but others have stout, short ones (10–0; Figure 1.1–1.4, 1.6). The antennule in all plagusiines is visible dorsally in deep clefts of the front (11–1; Figure 1.1, 1.2), and this character defines the Plagusiinae (Alcock, 1900 and subsequent workers). In all other taxa antennules are not visible dorsally (11–0; Figures 1.3–1.8, 4.11, 4.12, 4.15).

Maxilliped 3.—The merus is shorter than the ischium in both outgroup taxa, three grapsines, *Metopograpsus*, *Pachygrapsus* and *Planes*, a plagusiine *Plagusia*, and two varunines, *Gaetice* and *Varuna* (12–0; Figure 2.9); it is much shorter than the ischium in only plagusiine *Percnon* (12–2; Figure 2.10). In remaining taxa its length is about equal to the ischium length (12–1; Figures 2.11–2.16, 4.10). The anterolateral corner of the merus is quadrate in both outgroups (13–0), is more or less expanded and strongly convex anterolaterally in all grapsines and all varunines (13–1; Figure 2.11, 2.15, 2.16), and is not expanded but convex in all plagusiines and all sesarmines (13–2; Figures 2.9, 2.10, 2.12–2.14, 4.10). The possession of an oblique, hairy ridge on the merus and ischium is a definitive character of the Sesarminae (Alcock, 1900 and subsequent workers). In examined taxa, all extant sesarmines possess this oblique, hairy ridge (14–1; Figure 2.12–2.14), which all other taxa lack. In all grapsines, all sesarmines and a varunine *Hemigrapsus*, a wide rhomboidal gap separates maxillipeds 3 (15–1; Figure 2.11–2.15), while maxillipeds 3 are completely closed together or leave a narrow gape in all other taxa (15–0; Figures 2.9, 2.10, 2.16, 4.10). The exopods are wide in two outgroup taxa and most varunines (16–0; Figure 2.16), but narrow in most grapsines, all plagusiines and all sesarmines (16–1; Figures 2.9–2.15, 4.10). In both

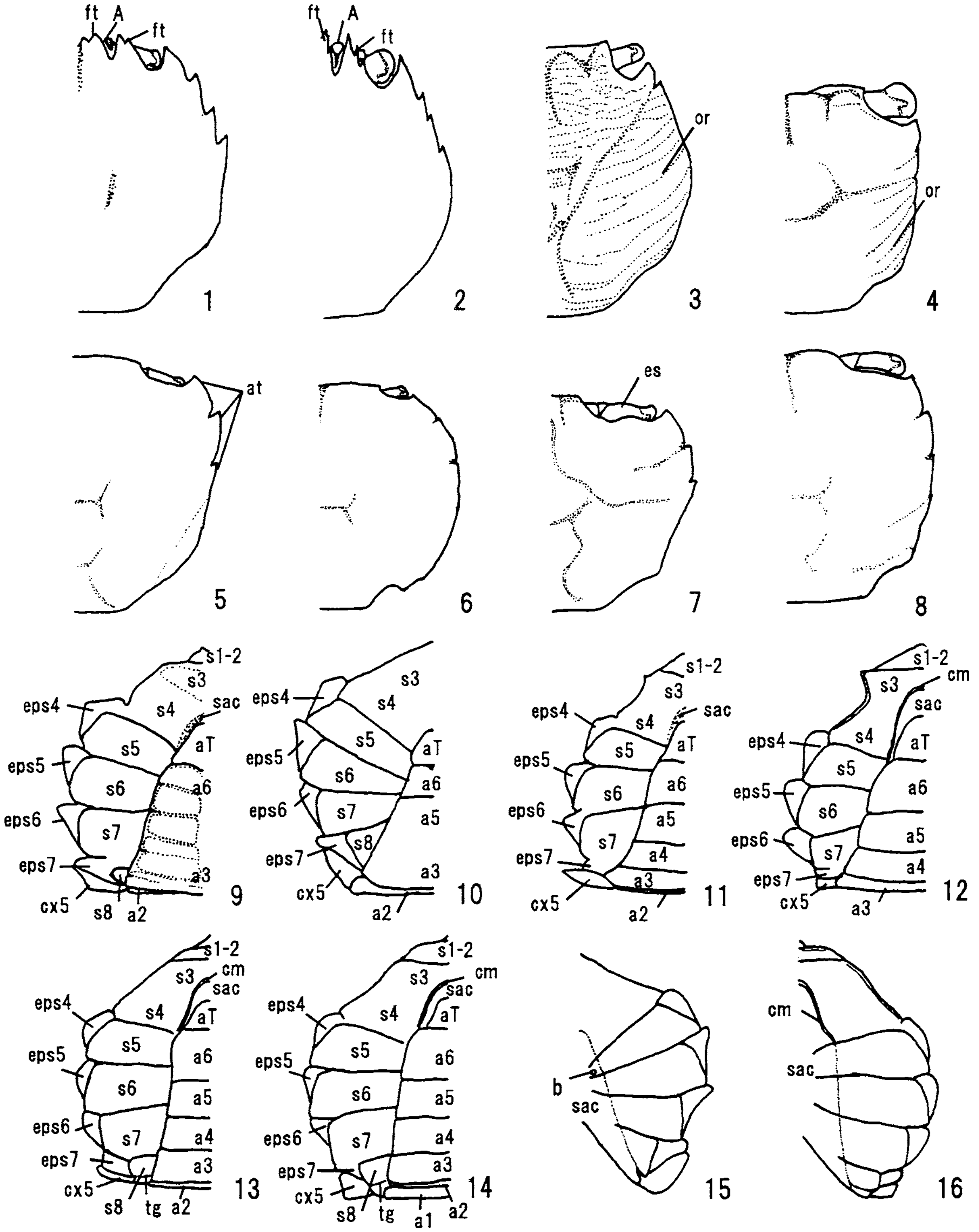

Figure 1. Diagrammatic representation of selected extant grapsid morphological characters. **1-8.** Dorsal view of carapace. **9-14.** Thoracic sternum and abdomen of male. **15, 16.** Thoracic sternum of male. **1, 9**: *Plagusia dentipes* De Haan, 1833 (CL = 43.5 mm). **2, 10, 15**: *Percnon planissimum* (Herbst, 1804) (CL = 33.8 mm). **3**: *Grapsus albolineatus* Lamarck, 1818 (CL = 57.6 mm). **4**: *Sesarma (Perisesarma) bidens* (De Haan, 1835) (CL = 12.5 cm). **5, 13, 16**: *Hemigrapsus sanguinensis* (De Haan, 1835) (CL = 18.9 mm). **6, 13**: *Cyclograpsus intermedius* Ortmann, 1894 (CL = 18.3 mm). **7**: *Metaplax crenulata* (Gerstecker, 1856) (CL = 29.4 mm). **8**: *Helice leachi* Hess, 1865 (CL = 14.6 mm). **12**: *Sesarmops intermedium* (De Haan, 1835) (CL = 24.1 cm). **Abbreviations**: **A**, antennule; **a1**, abdominal somite 1; **a2**, abdominal somite 2; **a3**, abdominal somite 3; **a4**, abdominal somite 4; **a5**, abdominal somite 5; **a6**, abdominal somite 6; **aT**, telson; **at**, anterolateral tooth; **b**, button; **cm**, cristiform margin of anterior sterno-abdominal cavity; **cx5**, coxa of pereiopod 5; **eps4**, episternite 4; **eps5**, episternite 5; **eps6**, episternite 6; **eps7**, episternite 7; **es**, eye stalk; **ft**, frontal tooth; **or**, oblique ridge; **s1-2**, thoracic sternites 1-2; **s3**, thoracic sternite 3; **s4**, thoracic sternite 4; **s5**, thoracic sternite 5; **s6**, thoracic sternite 6; **s7**, thoracic sternite 7; **s8**, thoracic sternite 8; **sac**, sterno-abdominal cavity; **tg**, transverse groove on sternite 8.

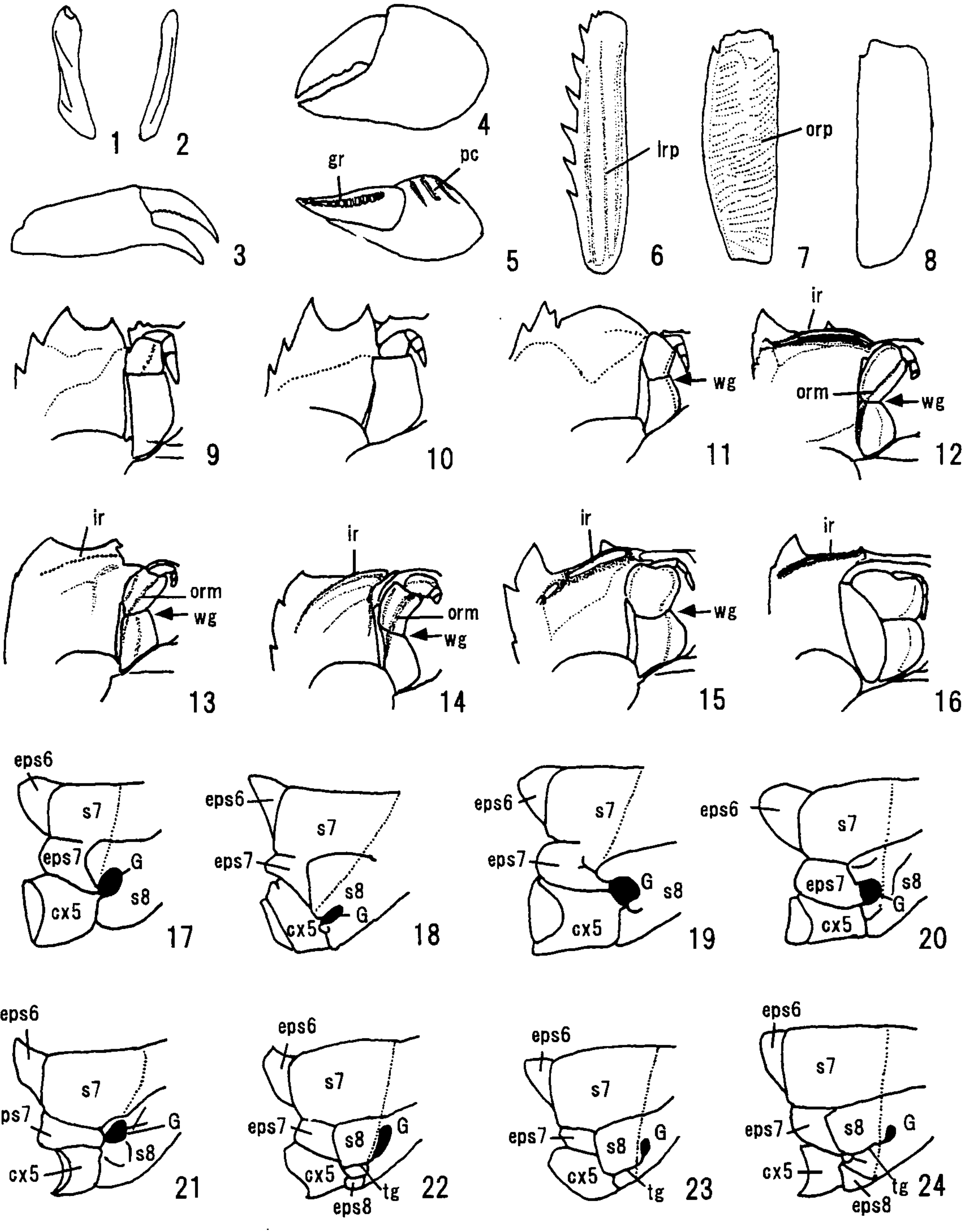

Figure 2. Diagrammatic representation of selected extant grapsid morphological characters. **1, 2.** Gonopod 1. **3-5.** Cheliped. **6-8.** Merus of pereiopod 4. **9-16.** Ventral view of carapace and maxilliped 3. **17-24.** Thoracic sternites 7 and 8. **1, 11, 19**: *Grapsus tenuicrustatus* (Herbst, 1783) (CL = 36.1 mm). **2, 13, 23**: *Cyclograpsus intermedius* Ortmann, 1894 (CL = 18.3 mm). **4, 5**: *Sesarma (Parasesarma) pictum* (De Haan, 1835) (CL = 17.4 mm). **6, 9, 17**: *Plagusia dentipes* De Haan, 1833 (CL = 43.5 mm). **7**: *Grapsus albolineatus* Lamarck, 1818 (CL = 57.6 mm). **8**: *Helice leachi* Hess, 1865 (CL = 14.6 mm). **10, 18**: *Percnon planissimum* (Herbst, 1804) (CL = 33.8 mm). **12, 20**: *Sesarmops intermedium* (De Haan, 1835) (CL = 24.1 mm). **14, 24**: *Metaplax crenulata* (Gerstecker, 1856) (CL = 29.4 mm). **15, 22**: *Hemigrapsus sanguinensis* (De Haan, 1835) (CL = 18.9 mm). **16**: *Ptychognathus* sp. aff. *P. ishii* Sakai, 1939 (CL = 8.3 mm). **21**: *Chasmagnathus convexus* De Haan, 1833 (CL = 40.1 mm). **Abbreviations**: **cx5**, coxa of pereiopod 5; **eps6**, episternite 6; **eps7**, episternite 7; **eps8**, episternite 8; **G**, gonopore; **gr**, tubercles on dorsal margin of dactylus; **ir**, infraorbital ridge; **lrp**, longitudinal ridge on lateral surface of pereiopod 4; **orm**, oblique, hairy ridge on merus and ischium of maxilliped 3; **orp**, oblique ridge on lateral surface of pereiopod 4; **pc**, pectinated crests on dorsal margin of propodus; **s7**, thoracic sternite 7; **s8**, thoracic sternite 8; **tg**, transverse groove on sternite 8; **wg**, wide rhomboidal gap between maxillipeds 3.

outgroup taxa and all plagusiines the palp articulates at an anteromesial angle of the merus (17-0; Figure 2.9, 2.10); however, in all other taxa it articulates at an anterior margin (17-1; Figures 2.11-2.16, 4.10). The dactyli are long in both outgroup taxa, all plagusiines, all grapsines and all varunines (18-0; ; Figure 2.9-2.11, 2.15, 2.16), but is reduced and short in all extant sesarmines (18-1; Figure 2.12-2.14).

Abdomen.—In all grapsines, all sesarmines and all varunines, the male abdomen consists of seven unfused abdominal somites (19-1; Figures 1.11-1.14, 4.9, 4.14), while the outgroup taxa and all plagusiines possess fused somites (19-0; Figure 1.9, 1.10). The outgroup taxa, most varunines and four sesarmines, *Cyclograpsus*, *Helice*, *Metaplax* and *Miosesarma*, have a narrow male abdomen (20-0; Figures 1.13, 1.14, 4.3, 4.9, 4.14), while the male abdomen is wide and fills the entire space between pereiopods 5 in all grapsines, all plagusiines, two varunines, *Varuna* and *Eriocheir*, and three sesarmines, *Nanosesarma*, *Sesarma* and *Sesarmops* (20-1; Figure 1.9-1.12).

Thoracic sternum.—All grapsids possess a wide thoracic sternum (21-1; Figures 1.9-1.14, 4.2, 4.3, 4.6, 4.7, 4.9, 4.10, 4.13, 4.14, 4.16), but the two outgroup taxa have a narrow sternum (21-0). In the outgroup taxa and most extant grapsids, thoracic sternites 1-2 are distinct (22-0; Figure 1.9, 1.11-1.14), while in only plagusiine *Percnon* they are reduced and indistinct (22-1; Figure 1.10). In both outgroup taxa, a suture between sternites 2 and 3 is distinct and well defined as a deep groove (23-0); however, the suture in all grapsids is indistinct and poorly defined (23-1; Figures 1.9-1.14, 4.13, 4.14). A median groove on sternite 3 is present in one outgroup taxon, *Cancer*, and a varunine *Gaetice* (24-0) , but it is absent in all other examined taxa (24-1; Figures 1.9-1.14, 4.6, 4.13). A median groove on sternite 4 is present in both outgroup taxa (25-0), but is absent in all grapsid taxa (25-1; Figures 1.9-1.14, 4.6). Guinot and Bouchard (1998) described the button on the male thoracic sternum within the Brachyura and indicated that in their examined material plagusiines and grapsines possessed the button on the sternum (Figure 1.15), but that the button was either present or absent within the Varuninae and Sesarminae (Figures 1.16, 4.6). In our examined material the button [character 26] is present in both outgroup taxa, all grapsines and all plagusiines, and present or absent in sesarmines and varunines. The outgroup taxon, *Cancer*, possesses a shallow sterno-abdominal cavity (27-0), while all other examined taxa have a deep sterno-abdominal cavity (Figures 1.9-1.16, 4.6). The anterior end of the sterno-abdominal cavity reaches the anterior sternite 4 in one outgroup, *Leptodius*, most grapsines and all plagusiines (27-1; Figure 1.9-1.11, 1.15), and reaches sternite 3 in all sesarmines, all varunines and a grapsine *Metopograpsus* (27-2; Figures 1.12-1.14, 1.16, 4.6, 4.13, 4.14). Guinot and Bouchard (1998) mentioned that in the Thoracotremata a deep sterno-abdominal cavity was often anteriorly delimited by a cristiform margin. In our examined material, the cristiform margin is well defined in all sesarmines, all varunines and a grapsine *Metopograpsus* (28-1; Figures 1.12-1.14, 1.16, 4.6, 4.13), but absent in both outgroup taxa, all plagusiines and most grapsines (28-0; Figure 1.9-1.11, 1.15). *Nanosesarma*, *Sesarma* and *Sesarmops*, members of the Sesarminae, possess deeply concave lateral margins of sternites 3-4 (29-1; Figure 1.12). In both outgroup taxa and the sesarmine genera, *Chasmagnathus*, *Nanosesarma*, *Sesarma* and *Sesarmops*, the male abdomen covers entirely the sternite 8 (31-0, 32-0; Figure 1.9-1.12). The sternite 8 is not covered entirely by the abdomen and is visible in ventral and posterior view in all varunines and four sesarmines, *Cyclograpsus*, *Helice*, *Metaplax* and *Miosesarma* (31-1, 32-1; Figures 1.13, 1.14, 4.14), but in both plagusiine taxa the male abdomen fills the entire space between pereiopods 5 (31-0; Figure 1.9, 1.10) and is visible in ventral view (32-1; Figure 1.9, 1.10).

In members of the section Heterotremata Guinot, 1977, male gonopores are located on coxae and/or the thoracic sternite 8, and the gonopores in all representatives within the Thoracotremata Guinot, 1977 are on sternite 8 (Guinot, 1977; Guinot and Richer de Forges, 1997). If male gonopores are situated on the inner part of sternite 8, the sternite is traversed by a groove which arises from the coxa and joins the gonopore or is interrupted (Figure 2.22-2.24) (Guinot, 1979; Tavares, 1992; Jamieson, Guinot and Richer de Forges, 1996). Both outgroups, all grapsines, all plagusiines, and the sesarmine genera, *Chasmagnathus*, *Nanosesarma*, *Sesarma* and *Sesarmops*, lack a transverse groove on the sternite 8 (30-0; Figure 2.17-2.20); however, most varunines and four sesarmines, *Cyclograpsus*, *Helice*, *Metaplax* and *Miosesarma*, have a groove on sternite 8 (30-1; Figures 2.22-2.24, 4.13, 4.14). In all grapsids of the Thoracotremata male gonopores are opened on thoracic sternite 8 (34-1; Figures 2.17-2.24, 4.13, 4.14), but in both outgroup taxa belonging to the Heterotremata they are located on the coxae (34-0). When male gonopores are situated on sternite 8, they are opened on lateral parts of sternite 8 in all plagusiines, all grapsines and the sesarmines, *Chasmagnathus*, *Nanosesarma*, *Sesarma* and *Sesarmops* (34-1; Figure 2.17-2.21). The male gonopores are located on the inner part of sternite 8 (34-2; Figures 2.22-2.24, 4-13, 4.14) in all varunines and the sesarmines, *Cyclograpsus*, *Helice*, *Metaplax* and *Miosesarma*.

Gonopod.—Only one character is found to be informative. Male gonopods 1 are sinuous (35-0) in both outgroup taxa, twisted (35-1; Figure 2.1) in a plagusiine *Plagusia* and all grapsines, and linear (35-2; Figures 2.2, 4.7, 4.13, 4.14, 4.16) in a plagusiine *Percnon*, all sesarmines and all varunines.

Pereiopods. — Two sesarmine genera, *Metaplax* and *Miosesarma*, possess a slender, elongate palm of the male chelipeds (36-1; Figures 2.3, 4.4), while all other taxa possess a short, massive palm (36-0; Figure 2.4). In examined material two sesarmines, *Sesarma* and *Sesarmops*, have chelipeds with pectinated crests on the dorsal margin of the propodus (37-1; Figure 2.5) and with tubercles on the dorsal margin of the dactylus (39-1; Figure 2.5). Four varunines, *Acmaeopleura*, *Hemigrapsus*, *Pseudograpsus* and *Ptychognathus*, bear hairs on the lateral surface of the propodus of the cheliped near the base of fingers (38-1), which all other extant taxa lack. Longitudinal ridges on the lateral surface of meri of pereiopods 2-5 are present in the Plagusiinae (40-1; Figure 2.6), but absent in all other taxa (40-0; Figures

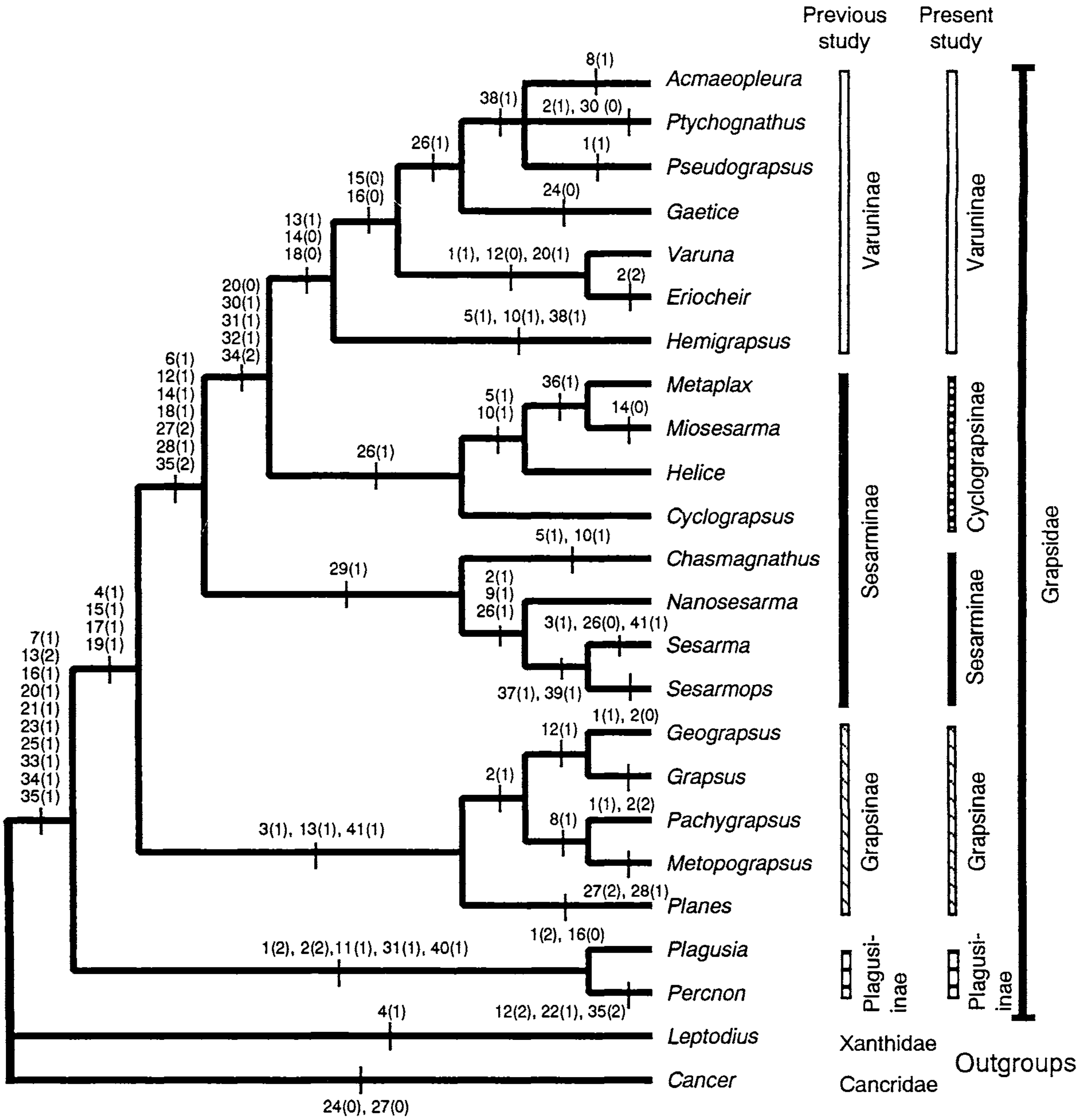

Figure 3. Single parsimonious tree of 22 genera within the Grapsidae. Length = 85, Consistency index = 0.565, Retention index = 0.807, Rescaled consistency index = 0.456. Character changes are indicated.

2.8, 4.15). All taxa within the Grapsinae and a sesarmine *Sesarma* possess oblique ridges on the lateral surface of meri of pereiopods 2-5 (41-1; Figure 2.7), which all other taxa lack.

Results

The present analysis yielded a single parsimonious tree, 85 steps long with a consistency index (CI) of 0.565, a retention index (RI) of 0.807 and a rescaled consistency index (RC) of 0.456 (Figure 3). The monophyly of the Grapsidae is well supported by ten characters, five of which are unique and unreversed: the upper orbital margin without distinct notches (7-1), a wide thoracic sternum (21-1), the absence of a suture between thoracic sternites 3 and 4 (23-1), the absence of a median groove on the thoracic sternite 4 (25-1), and male gonopores opened on thoracic sternites 8 (33-1). Our analysis suggests that within the Grapsidae the Plagusiinae is the most basal clade, followed by the Grapsinae, Sesarminae and the most derived Varuninae. The Plagusiinae is united by five characters, three of which are unique: antennules which are visible dorsally (11-1), sternite 8 which is visible ventrally (31-1), and the possession of longitudinal ridges on meri of pereiopods 2-5 (40-1).

The Grapsinae+Sesarminae+Varuninae clade is unambiguously united by four synapomorphies, three of which are never reversed: the absence of frontal teeth (4-1), the palp of the maxilliped 3 which articulates at an anterior margin of the merus (17-1), and the male abdomen with seven free somites (19-1). Three synapomorphies, the carapace with oblique ridges dorsally (3-1), an expanded anterolateral corner of the merus of the maxilliped 3 (13-1), and the presence of meri of pereiopods with oblique ridges on the lateral surface (41-1), well support the monophyly of the Grapsinae. The analysis shows the sister-group relationship of the Grapsinae and Sesarminae+Varuninae clades. The Sesarminae+Varuninae clade is unambiguously united by seven characters of which four are never reversed: the possession of the infraorbital ridge (6-1), an anterior margin of the sterno-abdominal cavity reaching the thoracic sternite 3 (27-2), the presence of the cristiform margin of an anterior sterno-abdominal cavity (28-1), and linear gonopods 1 (35-2).

Our analysis suggests that the Sesarminae as customarily defined is a polyphyletic group. The monophyly of the *Chasmagnathus*+*Nanosesarma*+*Sesarma*+*Sesarmops* clade is united by only one character, deeply concave lateral margins of thoracic somites 3 and 4 (29-1), and is derived as the sister to the Varuninae+four remaining sesarmines (*Cyclograpsus*, *Metaplax*, *Helice*, *Miosesarma*) clade. The Varuninae and *Metaplax*+*Miosesarma*+*Helice*+*Cyclograpsus* clades are unambiguously united by four unique synapomorphies: the presence of a transverse groove on the thoracic sternite 8 (30-1), the thoracic sternite 8 which is visible in ventral and posterior view (31-1, 32-1), and male gonopores located on the inner part of the thoracic sternite 8 (34-2). The Varuninae clade is the sister to the *Metaplax* +*Miosesarma*+*Helice*+*Cyclograpsus* clade and is united by three characters, an expanded anterolateral corner of the merus of maxilliped 3 (13-1), the absence of oblique, hairy ridges on the merus and ischium of maxilliped 3 (14-0) and a long dactylus of maxilliped 3 (18-0).

Discussion

The family Grapsidae is presently divided into four subfamilies, Grapsinae, Plagusiinae, Sesarminae and Varuninae, based on the adult morphology (i.e., Alcock, 1900, Rathbun, 1918, Sakai, 1976, Guinot, 1979, Manning and Holthuis, 1981). However, the subfamilial arrangement of some genera within the Grapsidae has been questioned by recent contributions based on larval morphology (Pereyra Lago, 1993, Schubart and Cuesta, 1998 and many more) and molecular data using the 16S rRNA (Schubart *et al.*, 2000). Guinot and Bouchard (1998) mentioned that both Sesarminae and Varuninae were artificial groups. Rice (1980) noted that the Grapsinae seemed to have the most advanced zoeae within the Grapsidae and thought that the four subfamilies within the Grapsidae evolved independently from a more primitive stock of which there is no larval evidence. Schubart, Neigel and Felder (2000) and Schubart *et al.* (2000) provided molecular phylogenies of the Grapsidae. Although Schubart *et al.* (2000) treated four subfamilies within the Grapsidae as families, we place four subfamilies within the Grapsidae according to previous studies of Alcock (1900), Sakai (1976), Manning and Holthuis (1981) and others.

The adult morphology-based phylogeny presented herein and the molecular phylogeny of Schubart *et al.* (2000) each of which supports monophyly of the Grapsidae, are each largely supported, but they differ somewhat in topology. Ten characters, five of which are unique and unreversed, well support the monophyly of the family Grapsidae in this study. Schubart, Neigel and Felder (2000) showed the paraphyly of the family based on molecular data using 16S rRNA but the subsequent study of Schubart *et al.* (2000) suggested the monophyly of the family; we concur that the Grapsidae is monophyletic.

Our morphology-based phylogenetic analysis suggests the Plagusiinae is the earliest derived crown-group subfamily, followed by the Grapsinae. These results support the molecular phylogeny of the family by Schubart *et al.* (2000). The Plagusiinae and Grapsinae are monophyletic by our analysis. The monophyly of the Grapsinae is well supported by molecular data (Schubart *et al.*, 2000) and larval morphology (Rice, 1980, Cuesta and Schubart, 1999). Schubart *et al.* (2000) showed that the Plagusiinae was polyphyletic and that only *Percnon* was the most basal clade. However, the larval morphology of *Percnon* is most similar to that of *Plagusia* within the Grapsidae (Rice, 1980) which supports our tree in which *Percnon* and *Plagusia* occur together on one clade.

The subfamily Sesarminae is polyphyletic. The *Metaplax* +*Miosesarma*+*Helice*+*Cyclograpsus* clade is readily distinguished from the *Chasmagnathus*+*Nanosesarma*+*Sesarma* +*Sesarmops* clade by having four unique synapomorphies and the former is derived as the sister to the Varuninae clade. One unique synapomorphy supports the monophyly of the latter sesarmine clade. The Sesarminae was previously discriminated from the other three subfamilies by the possession of an oblique, hairy ridge on the merus and ischium of the maxilliped 3 (Alcock, 1900 and subsequent workers). In our analysis the presence of this ridge [character 14] is not a unique character and the character state in the Varuninae clade is the absence of the ridge, a reversal of the state identified as a synapomorphy of the Sesarminae+Varuninae clade. Guinot (1979) indicated that male gonopores of *Cyclograpsus*, *Helice* and *Metaplax* together with those of varunine genera were located on the inner part of thoracic sternite 8. Examination of American sesarmine genera based on molecular data (Schubart *et al.*, 2000) suggested that *Chasmagnathus* and *Cyclograpsus* should be classified within the Varuninae and that the remaining Sesarminae group was monophyletic. Pereyra Lago (1993) and Schubart and Cuesta (1998) also showed that larval characters of three genera, *Chasmagnathus*, *Cyclograpsus* and *Helice*, were similar to those of members within the Varuninae rather than *Sesarma* sensu lato. However, our adult-morphology based analysis indicates that *Chasmagnathus* remains within the "Sesarminae" clade and that *Cyclograpsus* and *Helice* belong to another clade which is derived as the sister to the Varuninae clade and are more derived than the "Sesarminae" clade.

The present analysis separates the *Metaplax*+*Miose-*

sarma+Helice+Cyclograpsus clade from the "Sesarminae" clade and strongly suggests that genera placed within the clade should be classified in another subfamily. H. Milne Edwards (1853) erected a new tribe Cyclograpscaea within his subfamily Grapsinae (= Grapsidae see Alcock, 1900). Six genera, *Pseudograpsus*, *Heterograpsus* Lucas, 1849 (= *Brachynotus* de Haan, 1833), *Cyclograpsus*, *Paragrapsus* H. Milne Edwards, 1853, *Pralynotus* de Haan, 1835 (= *Gaetice*), and *Chasmagnathus* were originally included in the Cyclograpscaea. Subsequently, Alcock (1900) redefined four subfamilies within the Grapsidae, and synonymized the Cyclograpscaea with the Sesarminae and Varuninae. He moved *Pseudograpsus*, *Brachynotus* and *Gaetice* to the Varuninae and *Cyclograpsus* and *Chasmagnathus* to the Sesarminae. Tesch (1918) referred *Paragrapsus* to the Sesarminae. In our phylogenetic analysis, *Pseudograpsus* and *Gaetice* are classified within the Varuninae, and *Chasmagnathus* is placed within the Sesarminae. Two genera, *Brachynotus* and *Paragrapsus*, were not examined in our analysis. We treat the tribe Cyclograpscaea which contains a remaining genus *Cyclograpsus* as a subfamily Cyclograpsinae H. Milne Edwards, 1853 *nomen. transl. herein* (type genus: *Cyclograpsus* by present designation). Three additional genera, *Helice*, *Miosesarma* and *Metaplax* are included in the Cyclograpsinae based on the present analysis. The Cyclograpsinae is distinguished from the Sesarminae in that male gonopores are located on the inner part of thoracic sternite 8, sternite 8 is visible in ventral and poserior view, and bears a distinct transverse groove that extends from the articulation of the coxa-sternal junction to the gonopore. The present subfamily differs from the Varuninae derived as its sister group by the presence of an oblique, hairy ridge on the merus and ischium and a short, reduced dactylus of maxilliped 3, and the absence of an anterolateral expansion of the merus of maxilliped 3. *Paragrapsus and Heterograpsus* Campbell and Griffin, 1966 have an oblique, hairy ridge on the merus and ischium of maxilliped 3, male gonopores located on the inner part of the thoracic sternite 8, and a transverse groove on sternite 8; therefore, it is suggested that both genera should be referred to the Cyclograpsinae.

Within examined material the Varuninae is at least monophyletic. However, Schubart *et al.* (2000) showed using molecular data that the subfamily was polyphyletic, *Euchirograpsus* H. Milne Edwards, 1853, a non Northwestern Pacific genus, was the sister taxon of *Plagusia*, and *Platychirograpsus* de Man, 1896 and *Glyptograpsus* Smith, 1870, which both are American endemic genera, were derived as the sister to the Sesarminae. The reexamination of the systematic position of these three genera is beyond the scope of our study, whilst examination of the detail adult morphology would be necessary to confirm the reassignment of these genera.

The location of gonopores on thoracic sternite 8 [character 34] and the possession of the infraorbital ridge [character 6] are supported as useful phylogenetic characters. The gonopores are located on the lateral margin of sternite 8 in the Plagusiinae, Grapsinae and Sesarminae, and on the inner part of sternite 8 in the Cyclograpsinae and Varuninae. The Plagusiinae and Grapsinae lack the infraorbital ridge, while the Sesarminae, Cyclograpsinae and Varuninae possess the infraorbital ridge.

The following diagnosis is given for five subfamilies based on our phylogenetic analysis:

Subfamily Plagusiinae Dana, 1851.—Front with teeth. Antennule visible dorsally. Infraorbital ridge absent. Maxillipeds 3 without wide rhomboidal gap and oblique, hairy ridge on merus and ischium; anterolateral corner not expanded, convex; palp articulating at anteromesial corner of merus; exopod narrow. Male abdomen wide, filling entire space between pereiopods 5. Anterior margin of sterno-abdominal cavity reaching thoracic sternite 4. Sternal button present in male. Male gonopore located on lateral margin of thoracic sternite 8. Meri of pereiopods usually bearing longitudinal ridges laterally and spines dorsally (modified from Rathbun, 1918).

Subfamily Grapsinae MacLeay, 1838. — Front usually strongly deflexed. Carapace usually with oblique ridges dorsally. Infraorbital ridge absent. Maxillipeds 3 usually separated by wide rhomboidal gap, without oblique, hairy ridge on merus and ischium; anterolateral corner of merus usually expanded; palp articulating at anterior margin of merus; exopod narrow. Male abdomen wide, filling entire space between pereiopods 5. Anterior margin of sterno-abdominal cavity usually reaching thoracic sternite 4. Strernal button present in male. Male gonopore located on lateral margin of thoracic sternite 8 (modified from Rathbun, 1918).

Subfamily Sesarminae Dana, 1851. — Front strongly deflexed. Infraorbital ridge present. Maxillipeds 3 separated by wide rhomboidal gap, and with oblique, hairy ridge on merus and ischium; anterolateral corner of merus not expanded, convex; palp articulating at anterior margin of merus; exopod narrow. Male abdomen wide, filling entire space between pereiopods 5. Anterior margin of sterno-abdominal cavity reaching thoracic sternite 3. Sternal button present or absent in male. Male gonopore located on lateral margin of thoracic sternite 8 (modified from Rathbun, 1918).

Subfamily Varuninae H. Milne Edwards, 1853.—Front moderately or little deflexed. Infraorbital ridge present. Maxillipeds 3 moderately or slightly gaping, without oblique, hairy ridge on merus and ischium; anterolateral corner of merus expanded; palp articulating at anterior margin of merus; exopod usually wide. Male abdomen rarely filling entire space between pereiopods 5. Anterior margin of sterno-abdominal cavity reaching thoracic sternite 3. Transverse groove usually present on sternite 8. Sternal button usually present in male. Male gonopore located on inner part of thoracic sternite 8 (modified from Rathbun, 1918).

Subfamily Cyclograpsinae H. Milne Edwards, 1853 [nom. transl. *of Tribe Cyclograpscaea*].—Front strongly deflexed. Infraorbital ridge present. Maxillipeds 3 separated by wide rhomboidal gap, with oblique, hairy ridge on merus and ischium; anterolateral corner of merus not expanded, convex; palp articulating at anterior margin of merus; exopod narrow. Male abdomen not filling entire space between pereiopods 5. Anterior margin of sterno-abdominal cavity

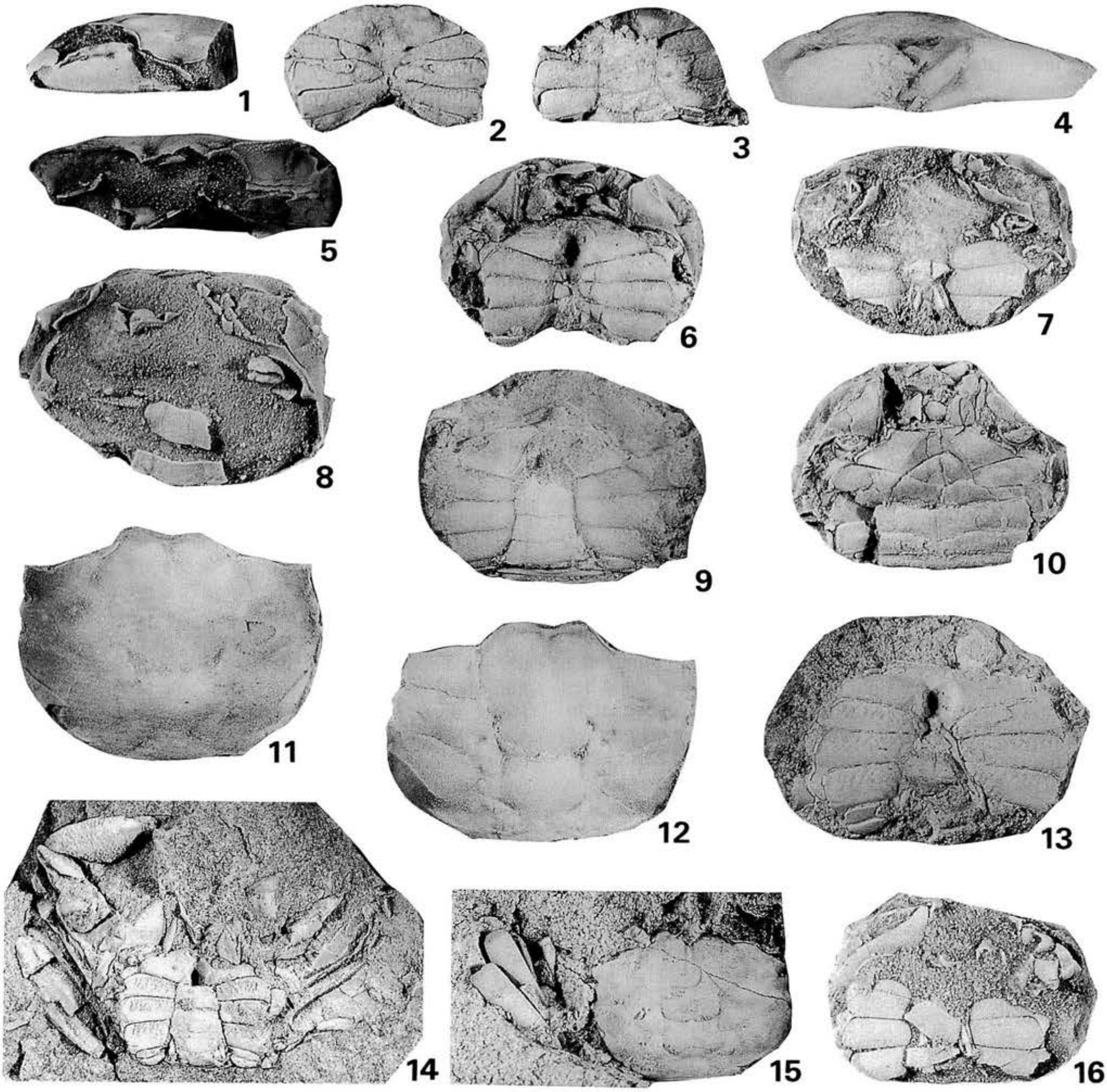

Figure 4. **1-13, 15, 16.** *Miosesarma japonicum* Karasawa, 1989. **1:** MFM83343, middle Miocene Masuda Group, frontal view of carapace and lateral view of cheliped, female, ×2.5. **2:** MFM39154, middle Miocene Bihoku Group, ventral view of thoracic sternum, female, ×2.5. **3:** MFM39155, middle Miocene Bihoku Group, ventral view of thoracic sternum and abdomen, male, ×2.5. **4:** MFM9146, lower Miocene Mizunami Group, lateral view of chelipeds, male, ×1.5. **5:** MFM83344, middle Miocene Masuda Group, frontal view of carapace, male, ×2.5. **6:** MFM39156, middle Miocene Bihoku Group, ventral view of carapace, thoracic sternum and maxillipeds 3, male, ×2.5. **7:** MFM83345, middle Miocene Masuda Group, ventral view of carapace, thoracic sternum and gonopods 1, male, ×2.5. **8:** MFM83344, middle Miocene Masuda Group, ventral view of carapace and abdomen, male, ×2.5. **9:** MFM9017 (paratype), lower Miocene Mizunami Group, ventral view of thoracic sternum and abdomen, male, ×2.5. **10:** MFM39157, middle Miocene Bihoku Group, ventral view of carapace, thoracic sternum, abdomen and maxillipeds 3, female, ×2.5. **11:** MFM9016 (paratype), lower Miocene Mizunami Group, dorsal view of carapace, male, ×2.5. **12:** MFM9015 (holotype), lower Miocene Mizunami Group, dorsal view of carapace, male, ×2.5. **13:** MFM9147, lower Miocene Mizunami Group, ventral view of thoracic sternum, abdomen and gonopods 1, male, ×2.5. **15:** MFM39158, middle Miocene Bihoku Group, dorsal view of carapace and eye stalk, and lateral view of pereiopods, male, ×2.5. **16:** MFM83346, middle Miocene Masuda Group, ventral view of carapace, thoracic sternum, abdomen and gonopods 1, male, ×2.5. **14.** *Miosesarma naguraense* Kato, 1996, MFM83347, middle Miocene Nagura Formation, ventral view of thoracic sternum, abdomen and gonopods 1, male, ×1.5.

reaching thoracic sternite 3. Transverse groove present on sternite 8. Sternal button usually absent in male. Male gonopore located on inner part of thoracic sternite 8 (redefined here).

Redefinition of the genus *Miosesarma* Karasawa, 1989

Subfamily Cyclograpsinae H. Milne Edwards, 1853

Genus *Miosesarma Karasawa, 1989*

Type species.—Miosesarma japonica Karasawa, 1989 by monotypy.

Species included. — *Miosesarma japonicum* Karasawa, 1989 (Figure 4.1 - 4.13, 4.15, 4.16) and *Miosesarma naguraense* Kato, 1996 (Figure 4.14).

Revised diagnosis. — Carapace rectangular in outline, length about 3/4 width, widest at midlength. Front deflexed, about 1/4 carapace width. Frontal margin bilobed. Upper orbital margin sinuous, occupying about 3/4 carapace width. Anterolateral margins nearly straight, almost parallel, with 4 forwardly directed teeth. Posterolateral margin sinuous. Dorsal surface smooth, moderately vaulted transversely and weakly vaulted longitudinally. Regions well defined; epibranchial lobe more inflated; mesobranchial lobe with ridge extending from 4th anterolateral tooth; metabranchial lobe with weak ridge parallel to posterolateral margin. Infraorbital ridge present with prominence laterally. Thoracic sternum wide; sterno-abdominal cavity of male deep, reaching sternite 3; sternite 8 of male with transverse groove. Male abdomen narrow, not filling entire space between pereiopods 5. Merus of maxilliped 3 subequal to ischium with convex anterolateral margin; exopod narrow. Male gonopod linear; gonopore opened on inner part of thoracic sternite 8. Chelipeds dissimilar in both sexes; female chelae much smaller than male; propodus slender, elongate. Pereiopods flattened.

Remarks. — Karasawa (1989) originally placed *Miosesarma* in the subfamily Sesarminae. Examination of new specimens shows that the genus is referred to the subfamily Cyclograpsinae because the infraorbital ridge is present, the gonopore is located on the inner part of the thoracic sternite 8, a narrow male abdomen does not fill all of the space between pereiopods 5, and the merus of maxilliped 3 has a convex anterolateral margin. Karasawa (1989) showed that the genus had close affinities with Recent cyclograpsines, *Helice* and *Metaplax.* Our phylogenetic analysis also suggests that *Miosesarma* and *Metaplax* are sister taxa nested as the most derived clade, followed by *Helice* and the most basal *Cyclograpsus* within the Cyclograpsinae.

Most extant members of the Grapsidae live in intertidal waters and adapt to freshwater or terrestrial habitats (Guinot and Bouchard, 1998); however, *Planes* is known from pelagic waters (Manning and Holthuis, 1981) and *Euchirograpsus* from depths between 10 and 359 m (Manning and Holthuis, 1981). *Miosesarma* appears to have inhabited sublittoral and upper bathyal waters based on associated decapods and molluscs (Karasawa, 1993; Kato, 1996).

Distribution. — Early-early Middle Miocene of Honshu, Japan; Ayugawa Group (Karasawa, 1997), Bihoku Group (Karasawa, 1993), Hokutan Group (Karasawa, 1997), Katsuta Group (Karasawa, 1993), Masuda Group (Karasawa, 1993), Mizunami Group (Karasawa, 1989), Chichibumachi Group (Kato, 1996), Nenokami Sandstone Member (Kato, 1996), Numanouchi Formation (Kato in prep.), Yatsuo Group (Karasawa, 1993).

A review of fossil records of the family Grapsidae

Previously known fossil records within the family Grapsidae have included 34 species and 21 genera. Fossil records of the Grapsinae comprise three genera: *Metopograpsus* from the lower Miocene of Hungary (Müller, 1998); *Pachygrapsus* from the middle Miocene of Hungary and Poland (Müller, 1974, 1996) and from the Pleistocene of Jamaica (Morris, 1993); and *Planes* from the lower Miocene of the Caucasus (Smirnov, 1929; Glaessner, 1969).

The genus *Sesarma* (s.l.) of the Sesarminae is represented by three fossil species, *Sesarma paraensis* Beurlen, 1958, from the upper Oligocene-lower Miocene of Brazil, *Sesarma smithi* H. Milne Edwards, 1853, from the Pleistocene of Australia (Etheridge and McCulloch, 1916) and *Sesarma* sp. from the middle Miocene of Japan (Karasawa, 1993). According to Serène and Soh's 1970 reclassification of the genus *Sesarma* (s.l.), *S. smithi* now belongs to *Neosarmatium* Serène and Soh, 1970.

Varunine genera known as fossils are *Brachynotus* from the middle Miocene of Hungary (Müller, 1974), *Eriocheir* from the Pliocene of Japan (Karasawa and Narita, 2000), *Hemigrapsus* from the Pleistocene of U.S.A. (Rathbun, 1926), *Miograpsus* Fleming, 1981 from the upper Miocene of New Zealand, *Varuna* from the middle Eocene of Jamaica (Withers, 1924), and *Utica* White, 1847 from the Pleistocene of Australia (Wintle, 1886). Among these genera *Miograpsus* is the only known extinct genus.

Glaessner (1969) showed that *Telphusograpsus* Lőrenthey, 1902, from the Eocene of Rumania, was referable to *Varuna*; however, *Telphusograpsus* is an independent genus by virture of having an inflated carapace with two upper orbital fissures and with a distinct inner orbital angle, and lacking a posterolateral facet on the branchial region. Members of the Grapsidae lack a distinct inner orbital angle and upper orbital fissures. The genus is probably referred to the family Goneplacidae H. Milne Edwards, 1852. Withers (1924) reported *Varuna* ? sp. from the Eocene of Jamaica, but that occurrence was based only upon a portion of the merus of the cheliped; therefore, the systematic position of the species is doubtful. Karasawa (1993) described a new species, *Varuna angustifrons*, from the lower Oligocene of Japan; however, the species was moved from *Varuna* to *Carinocarcinoides* Karasawa and Fudouji, 2000 of the family Goneplacidae (Karasawa and Fudouji, 2000).

Fossil records of the Cyclograpsinae comprise three genera, *Cyclograpsus*, *Miosesarma* and *Helice,* all known from the Miocene of Japan (Karasawa, 1989; Karasawa and Inoue, 1992; Karasawa, 1993; Kato, 1996).

The extinct genus *Palaeograpsus* Bittner, 1875 has not been placed within any of the grapsid subfamilies (Glaessner, 1969). Previously known species of the genus include: *Palaeograpsus attenuatus* Bittner, 1875, *P.*

Table 4. Distributions and geologic ranges of recognized fossil species of the family Grapsidae.

Taxa	Range	Locality
Family Grapsidae MacLeay, 1838		
Subfamily Grapsinae MacLeay, 1838		
Genus *Metopograpsus* H. Milne Edwards, 1853		
Metopograpsus traxleri Müller, 1998	L. Miocene	Austria
Genus *Pachygrapsus* Randall, 1840		
Pachygrapsus hungaricus Müller, 1974	M. Miocene	Hungary, Poland
Pachygrapsus sp., Morris, 1993	Pleistocene	Jamaica
Genus *Planes* Bowdich, 1825		
Planes prior (Smirnov, 1929)	L. Miocene	Caucasus
Subfamily Sesarminae Dana, 1851		
Genus *Sesarma* Say, 1917		
Sesarma paraensis Beurlen, 1958	U. Oligo.- L. Mio.	Brazil
Sesarma (s.l.) ? sp., Karasawa, 1993	M. Miocene	Japan
Genus *Neosarmatium* Sèrene and Soh, 1970		
Neosarmatium smithi (H. Milne Edwards, 1853)	Pleistocene	Australia
Subfamily Cyclograpsinae H. Milne Edwards, 1853		
Genus *Cyclograpsus* H. Mine Edwards, 1837		
Cyclograpsus directus Karasawa, 1989	L. Miocene	Japan
Cyclograpsus rectangularis Karasawa, 1989	M. Miocene	Japan
Genus *Helice* De Haan, 1835		
Helice sp., Karasawa and Inoue, 1992	M. Miocene	Japan
Genus *Miosesarma* Karasawa, 1989		
Miosesarma japonicum Karasawa, 1989	L.- M. Miocene	Japan
Miosesarma naguraense Kato, 1996	M. Miocene	Japan
Subfamily Varuninae H. Milne Edwards, 1853		
Genus *Brachynotus* De Haan, 1833		
Brachynotus febrarius Müller, 1974	M. Miocene	Hungary
Genus *Eriocheir* De Haan, 1835		
Eriocheir japonica (De Haan, 1835), Karasawa and Narita, 2000	L. Pliocene	Japan
Genus *Hemigrapsus* Dana, 1851		
Hemigrapsus oregonensis (Dana, 1851), Rathbun, 1926	Pleistocene	U.S.A.
Hemigrapsus nudus (Dana, 1851), Rathbun, 1926	Pleistocene	U.S.A.
Hemigrapsus sp., Rathbun, 1926	Pleistocene	U.S.A.
Genus *Miograpsus* Fleming, 1981		
Miograpsus papaka Fleming, 1981	L. Miocene	New Zealand
Genus *Varuna* H. Milne Edwards, 1830		
Varuna ? sp., Withers, 1924	M. Eocene	Jamaica
Genus *Utica* White, 1847		
Utica haswelli Wintle, 1886	Pleistocene	Australia
Utica yarraensis Wintle, 1886	Pleistocene	Australia
Subfamily uncertain		
Genus *Daragrapsus* Müller and Collins, 1991		
Daragrapsus trispinosus Müller and Collins, 1991	U. Eocene	Hungary
Genus *Daranyia* Lōrenthey, 1901		
Daranyia granulata Lōrenthey, 1901	U. Eocene	Hungary
Daranyia fabiani Di Salvo, 1933	M. Eocene	Italy
Genus *Pseudodaranyia* Tessier et al., 1999		
Pseudodaranyia carinata Tessier et al., 1999	M. Eocene	Italy

bartonensis Quayle and Collins, 1981, *P. depressus* Quayle and Collins, 1981, *P. guerini* Via, 1959, *P. inflatus* Bittner, 1875 (type species), *P. loczyanus* Lőrenthey, 1898 and *P. parvus* Müller and Collins, 1991 from the Eocene of Europe; *P. bittneri* Morris and Collins, 1991 from the Pliocene of Brunei. Among these, Schweitzer and Feldmann (2001) moved three species, *P. bartonensis, P. bittneri* and *P. depressus*, to the chasmocarcine genus *Orthakrolophos* Schweitzer and Feldmann, 2001, within the Goneplacidae. *Palaeograpsus guerini* is similar to members of *Orthakrolophos*, but is characterized by having transverse ridges on the dorsal carapace which are lacking in *Orthakrolophos*; therefore, Schweitzer and Feldmann (2001) did not include the species in *Orthakrolophos*. The species remains doubtfully placed within *Palaeograpsus*.

In his original description of the genus, Bittner (1875) indicated that *Palaeograpsus* had a close affinity with *Varuna* and *Pseudograpsus* within the Varuninae. Via (1959) suggested that *P. loczyanus* closely resembles members of *Carcinoplax* H. Milne Edwards, 1852 within the Goneplacidae. Beschin *et al.* (1994) reported well preserved carapaces associated with chelipeds and pereiopods of *P. loczyanus*. De Angeli (1995) also described carapaces, abdominal sternites, chelipeds and pereiopods of *P. inflatus*, the type species of the genus. We agree with the opinion of Via (1959). Examination of their specimens and the type specimen of *P. loczyanus* by one of us (Karasawa) strongly suggests that *Palaeograpsus* should be placed within the Goneplacidae. In *P. inflatus* and *P. loczyanus* the infraorbital ridge is absent; a median depression on thoracic sternite 3 is present, and a groove between sternites 3 and 4 is deep and well defined. However, in members of the Grapsidae sternite 3 usually lacks a median depression and a well defined groove between sternites 3 and 4 is absent. *Varuna* and *Pseudograpsus* possess the infraorbital ridge which *Palaeograpsus* lacks, a unique character of the Varuninae. *Palaeograpsus inflatus* and *P. loczyanus* have slender meri of the pereiopods while genera within the Grapsidae usually possess broad, flattened meri. *Palaeograpsus inflatus* and *P. loczyanus* possess carapace and cheliped characters most like those of *Carcinoplax*. However, the male abdominal somites 3 and 4 of *P. inflatus* are fused, while members of *Carcinoplax* have seven free abdominal somites in males.

The genus *Daranyia* Lőrenthey, 1901 was found in the Eocene of Hungary (Lőrenthey, 1901; Lőrenthey and Beurlen, 1929) and Italy (Di Salvo, 1933). Lőrenthey (1901) and Lőrenthey and Beurlen (1929) compared *Daranyia* with the extant genus *Euchirograpsus*, but the genus differs from *Euchirograpsus* by having a wide, sinuous frontal margin and well separated anterolateral teeth. Glaessner (1969) did not classify the genus in a known subfamily. We agree with Glaessner's opinion. Only the dorsal carapace of the genus is yet known. The subfamilial arrangement of the genus must await discovery of a ventral carapace and thoracic sternites.

Müller and Collins (1991) erected two monotypic genera, *Daragrapsus* and *Sculptoplax*, within the Grapsidae, based on material from the Hungarian Eocene. *Sculptoplax* does not appear to be a member of the Grapsidae. *Sculptoplax* resembles the xanthid genus *Carpilodes* Dana, 1851(= *Liomera* Dana, 1851; ICZN Opinion 73) (Müller and Collins,1991: 90); therefore, the genus is referred to the Xanthidae s.l. Müller and Collins (1991) indicated that *Daragrapsus* resembled *Daranyia*, but because the genus is represented by only a dorsal carapace specimen, subfamilial placement remains obscure.

Tessier *et al.* (1999) described two new grapsid genera, *Maingrapsus* and *Pseudodaranyia*, from the Eocene of Italy. Although Tessier *et al.* (1999) compared *Maingrapsus* with *Palaeograpsus*, the systematic position of the genus is doubtful. *Maingrapsus* is characterized by having a strongly inflated carapace with three transverse ridges and a wide, anteriorly protruded front, and lacking the infraorbital ridge and anterolateral teeth. There is no similarity between *Maingrapsus* and any known extant members of the Grapsidae. The genus has a resemblance to *Paracorallicarcinus* Tessier *et al.*,1999, but differs in having a longer carapace without anterolateral teeth. *Paracorallicarcinus* possesses carapace characters like those of the extant *Georgeoplax* Türkay,1983 of the family Goneplacidae; however, the carapace in *Paracorallicarcinus* is more inflated with weak transverse ridges and bears well defined anterolateral teeth. Therefore, *Maingrapsus* is placed within the family Goneplacidae. The subfamilial placement of *Pseudodaranyia* awaits the discovery of better material.

Thus 25 species in 17 genera of the family Grapsidae are recognized as fossils (Table 4). Three species in three extinct genera are not referred to any known subfamilies. Only the Plagusiinae lacks fossil records.

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Age calibration of megafossil biochronology based on Early Campanian planktonic foraminifera from Hokkaido, Japan

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Abstract. The occurrence of an Early Campanian planktonic foraminiferal assemblage consisting of *Globotruncana arca*, *G. linneiana*, *Rosita fornicata* and *R. patelliformis* is first reported from the Upper Haborogawa Formation exposed in the Haboro area, northwestern Hokkaido, Japan. This finding supports the previous interpretation that the Santonian/Campanian boundary can be placed at the basal part of *Inoceramus* (*Platyceramus*) *japonicus* Zone of the inoceramid biostratigraphy.

Key words: biostratigraphy, Hokkaido, planktonic foraminifera, Santonian/Campanian boundary

Introduction

The Late Cretaceous ammonoid and inoceramid zonal schemes in Japan have been progressively improved by several recent biostratigraphic studies (e.g. Toshimitsu and Maiya, 1986; Toshimitsu *et al*., 1995a, b; Toshimitsu *et al*., 1998). Five standard inoceramid zones, i.e. *Inoceramus* (*I.*) *uwajimensis, I.* (*I.*) *mihoensis, I.* (*I.*) *amakusensis, I.* (*Platyceramus*) *japonicus* and *Sphenoceramus schmidti - S. orientalis* in ascending order have been proposed by Toshimitsu *et al.* (1995b) for the Coniacian to middle Campanian sequence in the Haboro area, northwestern Hokkaido.

The megafossil assemblages in northwestern Hokkaido, however, lack frequently the Tethyan zonal markers, particularly during the Santonian to Maastrichtian intervals. This scarcity of marker species causes the international correlation difficult between the Tethyan and the Northwestern Pacific bioprovinces including Japan.

We here report the occurrence of the Tethyan planktonic foraminiferal species *Rosita patelliformis* (Gandolfi) from the Cretaceous Upper Yezo Group in the Haboro area and discuss age calibration of megafossil biochronology.

Geological setting and lithostratigraphy

The Upper Cretaceous strata exposed in the Haboro area are lithostratigraphically divided into three units, namely the Middle Yezo, Upper Yezo, and Hakobuchi Groups in ascending order (Figure 1). The Middle Yezo Group is composed of the Shirochi Formation. The Upper Yezo Group is subdivided into the Lower, Middle and Upper Haborogawa Formations. The Hakobuchi Group consists of the Pankezawa Formation. The Shirochi Formation is composed of alternating beds of sandstone and mudstone, and the Lower and Middle Haborogawa Formations consist of mudstone. The Upper Haborogawa Formation is characterized by two coarsening upward sequences, each of which begins with mudstones, graded to bioturbated muddy sandstones and ends with thick-bedded sandstones (Moriya and Hirano, 2001). The Pankezawa Formation is mainly composed of sandstone.

As concerns the Upper Haborogawa Formation in the study area (Figures 1, 2), the thickness of the first sequence is about 550 m, while the second one is approximately about 530 m. The mudstones in the lower part of the first sequence are intercalated with 4 to 5 cm thick, medium-bedded, fine- to medium-grained sandstones (Figure 3). The sandstone intercalations tend to be more frequent toward the top of the sequence. The uppermost part of the sequence represents a 10 m thick sandstone unit, named UHs1 (Toshimitsu, 1985), which is pale-green-colored, parallel- and cross-laminated, frequently interbedded with thin mudstone of a few cm thick (Figure 3). This unit can be traced laterally as a marker horizon in the investigated area (Figure 2). The weakly laminated mudstones of the second

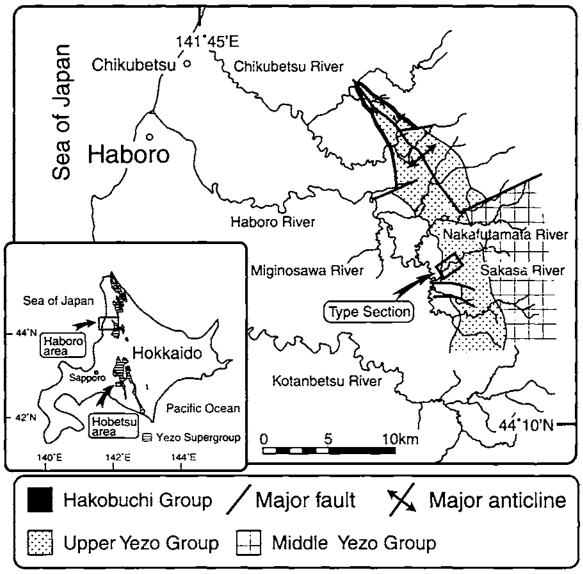


Figure 1. Index map and geological outline of the study area. The rectangle shows the investigated area where the type section of the Upper Haborogawa Formation is exposed.

cycle overlie the unit UHs1, but the upper part of this cycle is not exposed in the investigated section (Figures 2, 3).

Material and methods

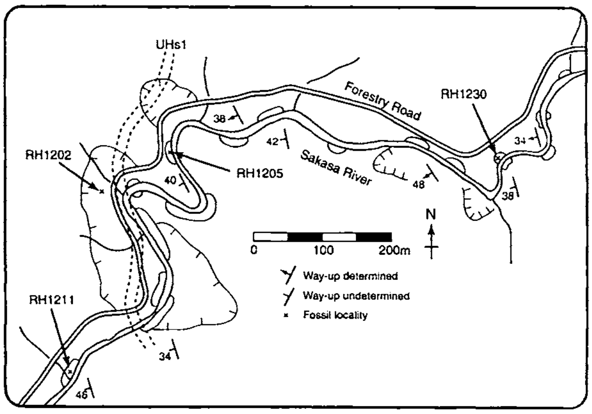


Figure 2. Route map of the type section of the Upper Haborogawa Formation along the Sakasa River in the Haboro area, showing the mega- and microfossil localities. For RH numbers, refer Toshimitsu (1985).

We collected three sediment samples from mudstones or sandy mudstones of the upper part of the Upper Haborogawa Formation at locs. RH1202 (along the Sakasagawa Forestry Road in the Haboro area), RH2530 and RH2531 (along the Nakafutamata River) (for RH1202 refer Figures 2, 3; for RH2530 and 2531 refer Toshimitsu, 1985, fig. 5a).

In a laboratory, each sample, 1.5 kg in weight was disaggregated with hydrogen peroxide and sodium tetraphenylborate (Hanken, 1979) to extract foraminiferal specimens. The disaggregated residues were washed using 75 μm sieve. All specimens larger than 125 μm were identified. The illustrated planktonic foraminifera (Figure 4) yielded from loc. RH1202 are housed in the University Museum of the University of Tokyo (UMUT).

Planktonic foraminiferal assemblages

The following species were recognized from the upper

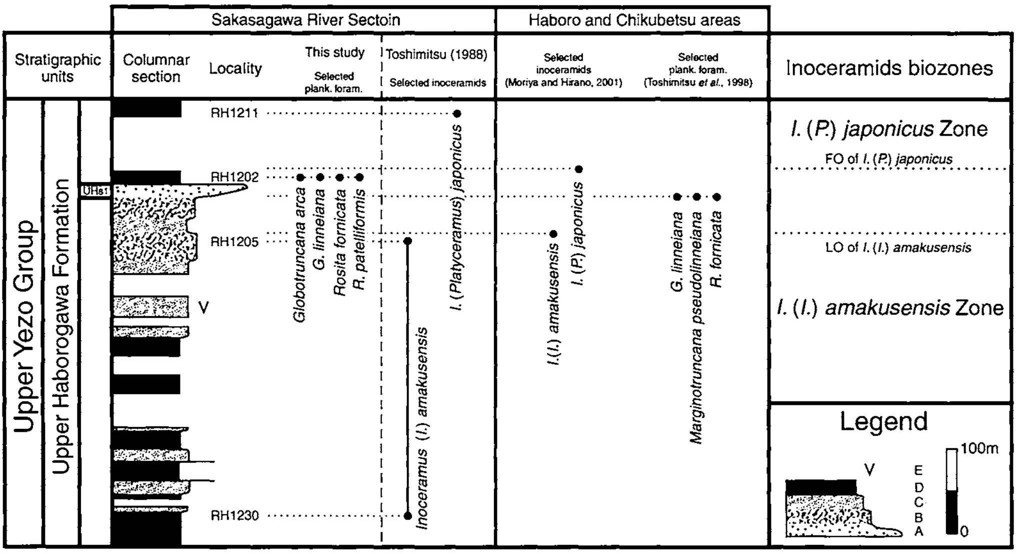


Figure 3. Biostratigraphic summary of selected mega- and microfossils in the Upper Haborogawa Formation along the Sakasa River and adjacent areas. The stratigraphic horizons of bioevents are compiled from Toshimitsu (1988), Toshimitsu *et al.* (1998) and Moriya and Hirano (2001; Chikubetsu area). A, sandstone; B, muddy sandstone; C, sandy mudstone; D, mudstone; E, acidic tuff.

Table 1. List and the number of specimens of the planktonic foraminiferal specimens occurred from the upper part of the Upper Haborogawa Formation. For the localities of RH2530 and RH2531, see Toshimitsu (1985, fig. 5a).

Species	Locality		
	RH 2531	RH 2530	RH 1202
Archaeoglobigerina blowi		17	
A. bosquensis		14	
A. cretacea		8	1
Dicarinella sp.		3	
Globigerinelloides asper		3	
Globotruncana arca		6	4
Globo. cf. *arca*		10	
Globo. bulloides		40	15
Globo. lapparenti			1
Globo. linneiana	16	125	38
Hedbergella aff. *planispira*	1		
Heterohelix reussi		1	
Marginotruncana pseudolinneiana	1	9	
Rosita fornicata		8	1
Rosita patelliformis			1

part of the Upper Haborogawa Formation: *Archaeoglobigerina blowi* Pessagno, *A. bosquensis* Pessagno, *A. cretacea* (d'Orbigny), *Dicarinella* sp., *Globigerinelloides asper* (Ehrenberg), *Globotruncana arca* (Cushman), *Globo. bulloides* Vogler, *Globo. lapparenti* Brotzen, *Globo. linneiana* (d'Orbigny), *Hedbergella* aff. *planispira* (Tappan), *Heterohelix reussi* (Cushman), *Marginotruncana pseudolinneiana* Pessagno, *Rosita fornicata* (Plummer), and *R. patelliformis* (Table 1). In the assemblages, *Globotruncana linneiana* is the most abundant species at all localities, and *Globotruncana bulloides* is subordinate at locs. RH1202 and 2530. The mudstone sample from loc. RH1202 yielded a total of 61 well-preserved specimens of planktonic foraminifers. Some of them identified as *Globotruncana arca, G. linneiana, Rosita fornicata,* and *R. patelliformis,* are shown in Figure 4. Among the assemblage, *R. patelliformis* is represented by a single specimen (Table 1), but this is the first report of the species from Japan. This specimen is not so large, having a circular peripheral outline and less convex spiral (Figure 4.1). Although the last chamber is somewhat deformed, chambers in the final whorl are crescentic and narrow, and the surface of the test is not so undulated. Judging from these characters, the specimen is undoubtedly identified as *R. patelliformis.*

Correlation

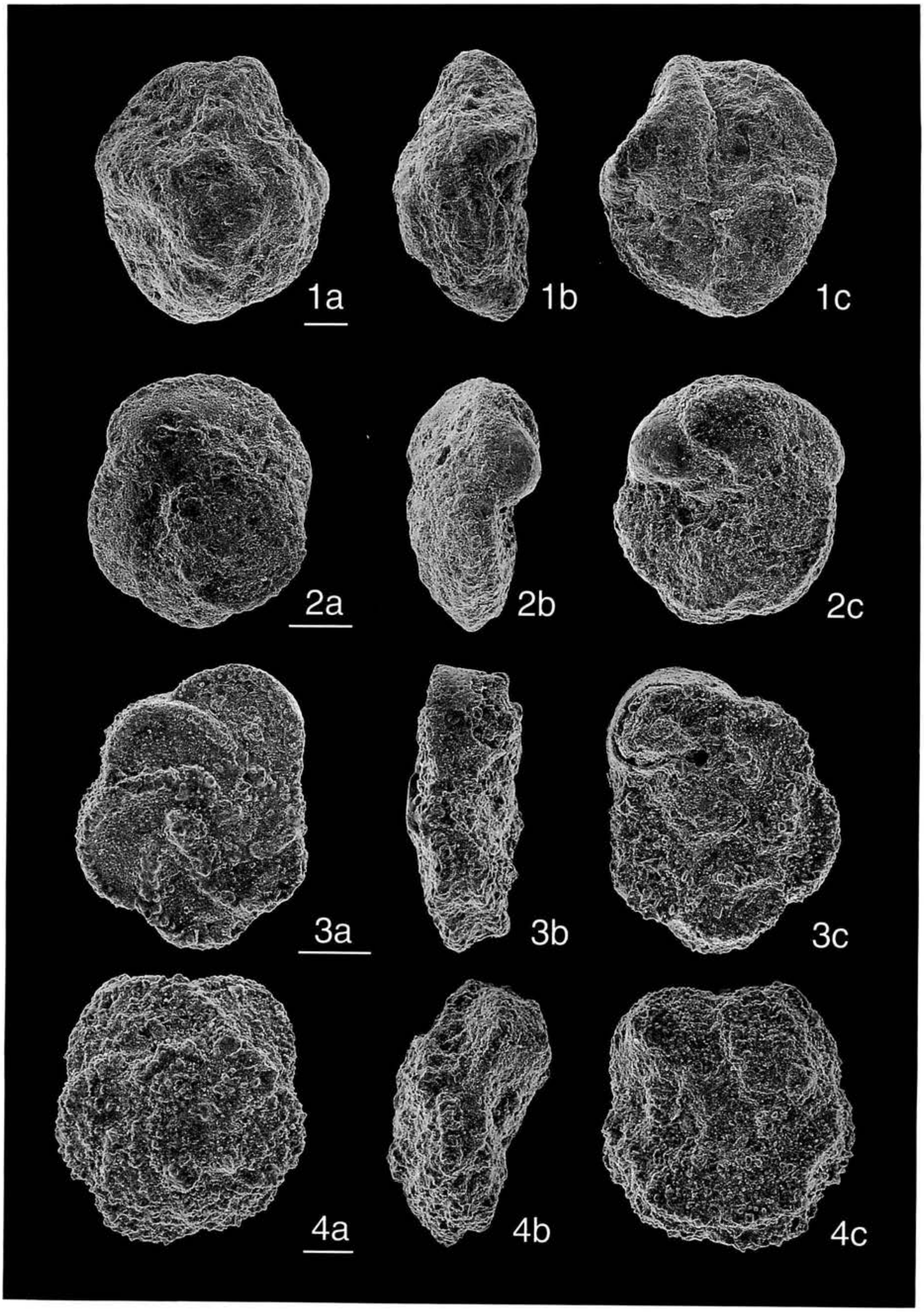
Sliter (1989) proposed a scheme of Cretaceous planktonic foraminiferal biostratigraphy, showing the stratigraphic ranges of selected species. The planktonic foraminiferal zonation applied here is based on that study. The first occurrence (FO) of *R. fornicata* is placed closed to the Coniacian/Santonian boundary. Although there are a few objections for the age of FO of *Globotruncana arca* (Kopaevich and Salaj *in* Hancock and Gale, 1996), *G. arca* and *G. linneiana* should appear within the uppermost Santonian *Dicarinella asymetrica* Zone (Caron, 1985; Sliter, 1989). The FO of *R. patelliformis* is placed within the *Globotruncanita elevata* Zone of the upper part of the Lower Campanian. The assemblage from the mudstone sample at loc. RH1202 is, therefore, assigned an age of Early Campanian, probably the *G. elevata* Zone.

Discussion

Inoceramus (*Inoceramus*) *amakusensis* Nagao and Matsumoto was obtained from bioturbated muddy sandstones at locs. RH1205 and RH1230 (Toshimitsu, 1985; Figures 2, 3). *I.* (*Platyceramus*) *japonicus* Nagao and Matsumoto occurs from the mudstones above the UHs1 sandstones (Toshimitsu, 1988; loc. RH 1211 in Figures 2, 3). The last occurrence (LO) of *I* (*I.*) *amakusensis* is recognized at about 50 m below the unit UHs1, whereas *I.* (*P.*) *japonicus* first appears at about 20 m above UHs1 (Toshimitsu, 1998; Moriya and Hirano, 2001). Hence, the Upper Haborogawa Formation can be biosratigraphically divided into the *I.* (*I.*) *amakusensis* and *I.* (*P.*) *japonicus* Zones, with a boundary within the UHs1 sandstones (Figure 3).

Toshimitsu *et al.* (1998) defined the Santonian/Campanian boundary by the FOs of the ammonoid *Submortoniceras* cf. *condamyi* (Collignon) and a planktonic foraminifer *Globotruncana arca* in the Haboro area, and placed the boundary just above the UHs1 of the Upper Haborogawa Formation.

Hancock (1991) initially stated that the FO of *Submortoniceras* might coincide with the Santonian/Campanian boundary. The evolution of *Submortoniceras* from *Texanites* was, however, later inferred to have occurred during the late Santonian (Gale *et al.*, 1995; Hancock and Gale, 1996). Furthermore, although Kopaevich and Salaj (*in* Hancock and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Gale, 1996) emphasized that the "*G. arca*" which occurred from the Upper Santonian is an ancestral form of the true "*G. arca*", the FO of *G. arca* should be placed within the upper Santonian *D. asymetrica* Zone (e.g., Caron, 1985; Sliter, 1989; Hancock and Gale, 1996). Therefore, the FOs of *Submortoniceras* and *G. arca* are inappropriate as the boundary markers, and these bioevents have not been adopted as Santonian/Campanian boundary criteria (Hancock and Gale, 1996).

We found an Early Campanian planktonic foraminiferal assemblage consisting of *Globotruncana arca*, *G. linneiana*, *Rosita fornicata* and *R. patelliformis* from just above the unit UHs1 of the upper part of the Upper Haborogawa Formation in the Haboro area (Figures 2, 33; loc. RH1202 along the Sakasagawa Forestry Road in the Haboro area). Toshimitsu *et al.* (1998) found a Late Santonian planktonic foraminiferal assemblage consisting of *Globotruncana linneiana*, *Marginotruncana pseudolinneiana* and *Rosita fornicata* from mudstones just below the UHs1 unit along the Miginosawa Creek. Toshimitsu *et al.* (1998) also described the occurrence of *Globigerinelloides prairiehillensis* Pessagno from about 200 m above the UHs1 unit along the Kotanbetsu River. Therefore, in the Haboro area, the Santonian/Campanian boundary can be temporally placed at the top of the unit UHs1.

This level is very close to the boundary between the *Inoceramus* (*I.*) *amakusensis* Zone and the *I.* (*Platyceramus*) *japonicus* Zone of the inoceramid biostratigraphy (Figure 3). Toshimitsu *et al.* (1998) expected to place the Santonian/Campanian boundary at the basal part of the *I.* (*P.*) *japonicus* Zone and our finding substantiates this idea.

The K-Ar dating, furthermore, revealed that in the Horosari-zawa section of the Hobetsu area, a white acid tuff intercalated with mudstones of the lower part of the *I.* (*P.*) *japonicus* Zone is dated at 82.2 ± 0.6 Ma (Shibata and Uchiumi, 1995; Toshimitsu *et al.*, 1998). The K-Ar age supports the idea that the age of the *I.* (*P.*) *japonicus* Zone is Early Campanian.

Concluding remarks

In this paper, we have reported the FO of *Rosita patelliformis* at about 10 m above the sandstone beds UHs1 (Figures 2, 3; loc. RH1202 along the Sakasagawa Forestry Road in the Haboro area). Our new finding of this planktonic foraminifera suggests that the Santonian/Campanian boundary should be drawn around the horizon of the sandstone beds UHs1, probably close to the boundary between the *I. amakusensis* and *I.* (*P.*) *japonicus* Zones as proposed by Toshimitsu *et al.* (1998).

Hancock and Gale (1996) proposed the following Santonian/Campanian boundary criteria: (1) the lowest occurrence of the ammonoid *Placenticeras bidorsatum* (Roemer), (2) the extinction level of the crinoid *Marsupites testudinarius* (Schlotheim), (3) the extinction in the planktonic foraminifers of *Dicarinella concavata* group, (4) the first occurrence (FO) of nannofossil *Broinsonia parca* (Stradner), and (5) the basal part of the paleomagnetic the Chron C33r. To set the Santonian/Campanian boundary precisely in Japan, we need to inspect these boundary criteria for further study.

Acknowledgments

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← **Figure 4.** Planktonic foraminifera from the loc. RH1202 along the Sakasagawa forestry road in the Haboro area. **1a-c.** *Rosita patelliformis* (Gandolfi), UMUT MF 27977. **2a-c.** *Rosita fornicata* (Plummer), UMUT MF 27978. **3a-c.** *Globotruncana linneiana* (dOrbigny), UMUT MF 27979. **4a-c.** *Globotruncana arca* Cushman, UMUT MF 27980. 1-3, Scale bars are 100 μm; 4, Scale bar is 50 μm.

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Middle Permian brachiopods from the Moribu area, Hida Gaien Belt, central Japan

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Abstract. A Middle Permian (Murgabian) brachiopod fauna is described from the lower Moribu Formation in the Moribu area, Hida Gaien Belt, central Japan. This fauna consists of 29 species, of which 2 are new, in 27 genera. The new species are *Fallaxoproductus moribuensis* and *Alispiriferella japonica*. The Moribu fauna is a Boreal-Tethyan mixed fauna and allied with the Middle Permian brachiopod faunas of central Japan (Ise in the Hida Gaien Belt), northeast Japan (South Kitakami Belt), eastern Russia (South Primorye), northeast China (Jilin) and north China (Inner Mongolia). These regions were probably a continental shelf bordering the northeastern margin of the Sino-Korean block, which was present at a middle northern palaeolatitude in the Middle Permian time.

Key words: Boreal-Tethyan mixed fauna, brachiopods, Hida Gaien Belt, Middle Permian, Moribu

Introduction

The brachiopod fauna that is the subject of this paper was recovered from the lower member of the Moribu Formation in the Moribu area, about 10 km NE of Takayama, Hida Gaien Belt, central Japan (Figure 1). The Moribu Formation was named by Isomi and Nozawa (1957) for a Permian succession of the Hongo-Arakigawa area including the Moribu area. Since then the stratigraphy of the Moribu Formation has been discussed by Fujimoto *et al.* (1962), Yamada and Yamano (1980), Horikoshi *et al.* (1987), Tanase and Kasahara (1988), Tazawa (1996), and Yoshida and Tazawa (2000).

Faunal data for the Moribu Formation are included in several papers, fusulinaceans by Yamada and Yamano (1980) and Tazawa *et al.* (1993), radiolarians by Umeda and Ezaki (1997), corals by Yamada and Yamano (1980), and brachiopods by Horikoshi *et al.* (1987), Tazawa (1999a, b), and Shi and Tazawa (2001). To date, 5 fusulinacean and 3 brachiopod species have been described. Permian brachiopods of the Hida Gaien Belt are poorly known. Only one fauna, consisting of 13 species in 12 genera, was described by Tazawa and Matsumoto (1998) from the Oguradani Formation in the Ise area, about 80 km SW of Moribu. Thus, the Moribu fauna is the second-described but more plentiful Permian brachiopod fauna in the Hida Gaien Belt.

The purpose of the present study is to describe all available brachiopod elements of the Moribu fauna, and to discuss the age and palaeobiogeography of this fauna. The brachiopod fossils were collected from 10 localities in the Moribu area by E. Horikoshi (and his students), K. Tsushima, Y. Miyake and by myself in 1985-1999. All specimens described in this paper are housed in the Department of Geology, Faculty of Science, Niigata University.

Stratigraphy

Fossil localities, geological map and columnar sections of the Moribu Formation are shown in Figures 2–4, respectively. The Moribu Formation is distributed in the northwestern part of the Moribu area, having a general trend of NE-SW, and dipping towards the NW, although there are beds striking N-S or NW-SE and dipping W to SW in the eastern part. The Moribu Formation is composed of shallow marine continental shelf sediments and lithologically subdivided into three members, the lower shale-sandstone member (550 m thick) with some conglomerate and limestone beds, the middle sandstone member (230 m thick) with some tuffaceous sandstone beds, and the upper shale member (more than 650 m thick) with numerous, thin sandstone layers. The total thickness of this formation is more than 1,430 m. The Moribu Formation covers the Lower to Upper Carboniferous Arakigawa Formation with an unconformity, and is in turn unconformably overlain by the Upper Cretaceous-Palaeo gene volcanic rocks (Nohi rhyolites). In general the Moribu Formation is sparsely fossiliferous. The lower member contains various marine invertebrate fossils, such as fusulinaceans, corals, bryozoans, brachiopods, bivalves, gastropods and crinoids. The middle member lacks macrofossils, but

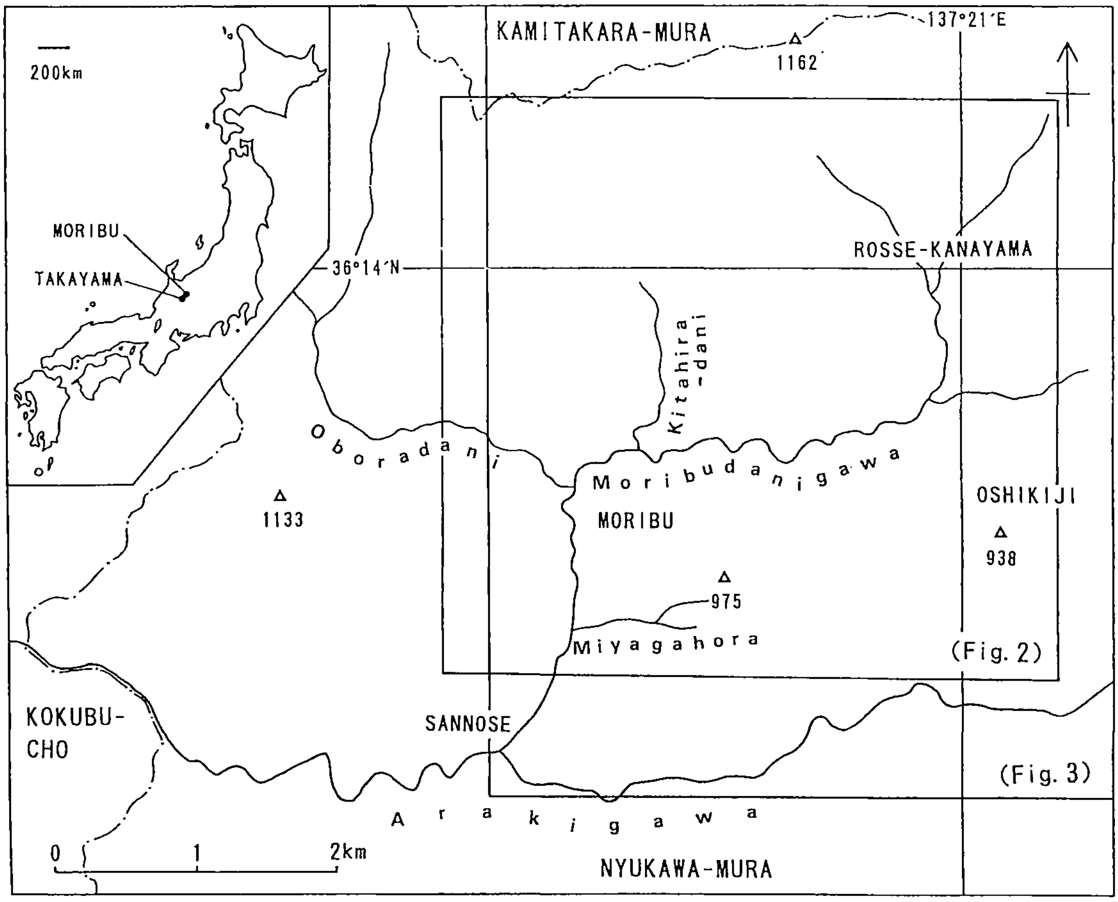

Figure 1. Index map showing the study area.

contains fusulinaceans and radiolarians in some horizons. The upper member is barren of fossils.

Brachiopods are the most common macrofossils. The brachiopod fossils treated in this paper were collected from the shale, sandstone and argillaceous impure limestone of the lower member at 10 localities (HMF1, 2, 3, 5, 8, 12, 13, 14, 16 and 25) (Figure 2). The topographical and stratigraphical positions, rock types and brachiopod lists of the collecting localities are as follows (see also Figure 4):

HMF1: Black shale, 10 m below the limestone of the lower member, at the left (east) bank of the lower Moribudanigawa River, 200 m S of a bridge in Moribu Village (Lat. 36° 12′ 41″ N, Long. 137° 19′ 10″ E); *Enteletes* sp., *Rhynchopora* sp., *Hustedia ratburiensis* Waterhouse and Piyasin, *Martiniopsis* sp., *Blasispirifer* cf. *reedi* (Licharew), and *Alispiriferella japonica* sp. nov.

HMF2: Dark grey argillaceous impure limestone, 4 m above the base of the limestone of the lower member, at the right (west) bank of the lower Moribudanigawa River, 30 m SW of HMF1; *Capillomesolobus* sp., *Transennatia gratiosa* (Waagen), *Reticulatia* sp., *Linoproductus lineatus* (Waagen), *Megousia* sp., *Cancrinella* cf. *spinosa* Hayasaka and Minato, *Urushtenoidea crenulata* (Ting), *Leptodus nobilis* (Waagen), *Derbyia* sp., *Stenoscisma margaritovi* (Tschernyschew), *Hustedia ratburiensis* Waterhouse and Piyasin, *Spiriferella lita* (Fredericks), and *Alispiriferella japonica* sp. nov.

HMF3: Black shale, 10 m above the calcareous conglomerate of the lower member, at the left bank of the middle Moribudanigawa River, 130 m W of the junction of the Kuragatani Valley and the Moribudanigawa River (Lat. 36° 13′ 24″ N, Long. 137° 20′ 42″ E); *Orbiculoidea* cf. *jangarensis* Ustritsky, *Stenoscisma margaritovi* (Tschernyschew), *Hustedia ratburiensis* Waterhouse and Piyasin, *Martinia* sp., *Blasispirifer* cf. *reedi* (Licharew), and *Dielasma* sp.

HMF5: Grey fine-grained sandstone, 65 m below the sandstone of the middle member, at the left bank of the upper Moribudanigawa River, 250 m NW of the junction of the Suganotani Valley and the Moribudanigawa River (Lat. 36° 14′ 17″ N, Long. 137° 20′ 29″ E); *Yakovlevia kaluzinensis* Fredericks, *Juresania* cf. *juresanensis* (Tschernyschew), *Hustedia ratburiensis* Waterhouse and Piyasin, *Gypospirifer volatilis* Duan and Li, and *Alispiriferella japonica* sp. nov.

HMF8: Black shale, 20 m below the limestone of the lower member, at 75 m upper from the entrance of a small tributary in the middle Moribudanigawa River, 250 m NE of HMF12; *Linoproductus lineatus* (Waagen), *Neospirifer* cf. *fasciger* (Keyserling), and *Alispiriferella japonica* sp. nov.

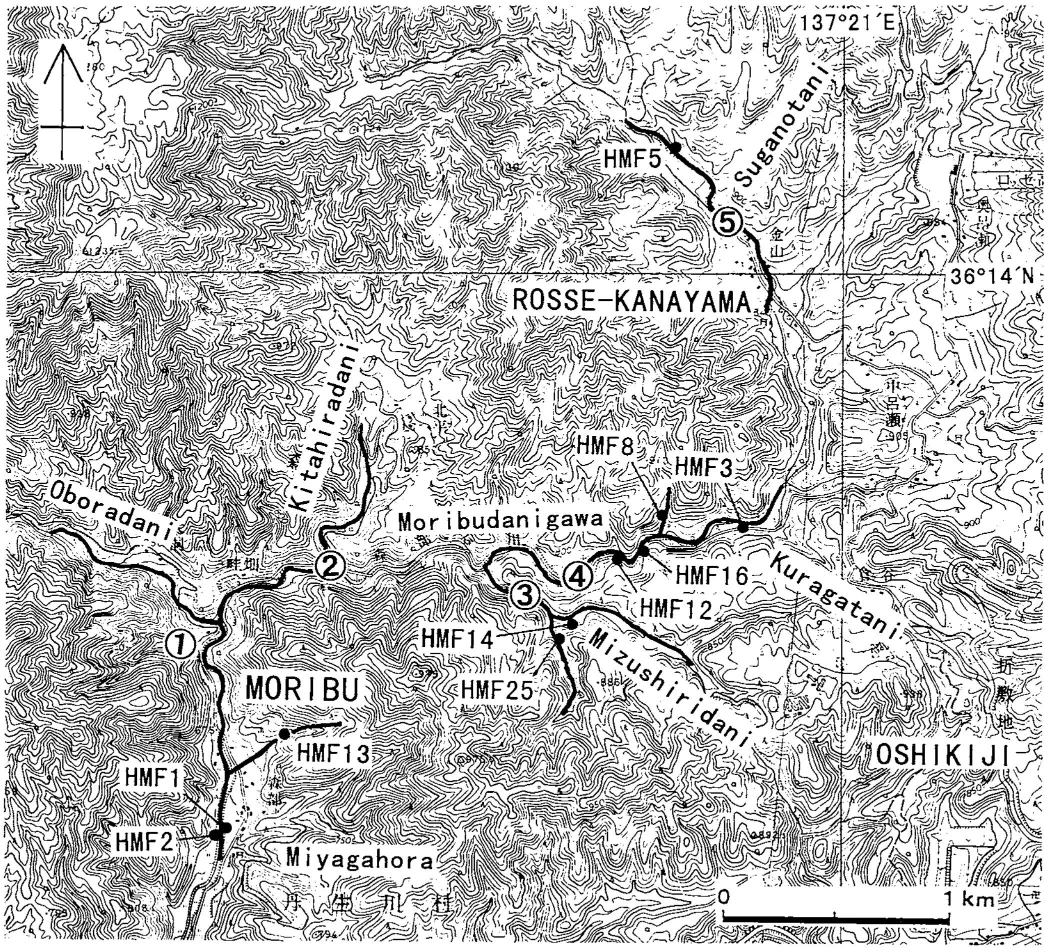

Figure 2. Index map showing the fossil localities (HMF1–3, 5, 8, 12–14, 16, 25) and the studied sections (①–⑤).

HMF12: Black shale, 5 m below the limestone of the lower member, at the left (south) bank of the middle Moribudanigawa River, 625 m E of the junction of the Mizuyagadani Valley and the Moribudanigawa River (Lat. 36° 13′ 20″ N, Long. 137° 20′ 21″ E); *Yakovlevia kaluzinensis* Fredericks, *Waagenoconcha permocarbonica* Ustritsky, *Waagenoconcha* cf. *imperfecta* Prendergast, *Fallaxoproductus moribuensis* sp. nov., *Permundaria asiatica* Nakamura, Kato and Choi, *Gypospirifer volatilis* Duan and Li, and *Alispiriferella ordinaria* (Einor).

HMF13: Black shale of the same horizon as HMF1, at the eastern slope facing the lower Moribudanigawa River, 500 m NNE of HMF1; *Transennatia gratiosa* (Waagen).

HMF14: Black shale, 10 m below the limestone of the lower member, at the middle Mizushiridani Valley, 500 m SE of the junction of the Mizushiridani Valley and the Moribudanigawa River (Lat. 36° 13′ 10″ N, Long. 137° 20′ 12″ E); *Yakovlevia kaluzinensis* Fredericks and *Alispiriferella japonica* sp. nov.

HMF16: Black shale of the same horizon of HMF8, at the left (east) bank of the middle Moribudanigawa River, 125 m NE of HMF12; *Alispiriferella japonica* sp. nov.

HMF25: Black shale, 30m below the limestone of the lower member, at 100 m SW of HMF14; *Yakovlevia kaluzinensis* Fredericks and *Gypospirifer volatilis* Duan and Li.

The Moribu fauna

Age and Correlation

The brachiopod fauna described here includes the following 29 species assigned to 27 genera: *Orbiculoidea* cf. *jangarensis* Ustritsky, *Capillomesolobus* sp., *Transennatia gratiosa* (Waagen), *Yakovlevia kaluzinensis* Fredericks, *Reticulatia* sp., *Juresania* cf. *juresanensis* (Tschernyschew), *Waagenoconcha permocarbonica* Ustritsky, *Waagenoconcha* cf. *imperfecta* Prendergast, *Linoproductus lineatus* (Waagen), *Megousia* sp., *Cancrinella* cf. *spinosa* Hayasaka and Minato, *Fallaxoproductus moribuensis* sp. nov., *Permundaria asiatica* Nakamura, Kato and Choi, *Urushtenoidea crenulata* (Ting), *Leptodus nobilis* (Waagen), *Derbyia* sp., *Enteletes* sp., *Stenoscisma margaritovi* (Tschernyschew), *Rhynchopora* sp., *Hustedia ratburiensis* Waterhouse and Piyasin, *Martinia* sp., *Martiniopsis* sp., *Neospirifer* cf. *fasciger* (Keyserling), *Blasispirifer* cf. *reedi* (Licharew), *Gypospirifer volatilis* Duan and Li, *Spiriferella lita* (Fredericks), *Alispiriferella ordinaria* (Einor), *Alispiriferella japonica* sp. nov. and *Dielasma* sp.

The list suggests a Middle Permian age, and certain taxa further suggest a narrower age ranging from the Murgabian

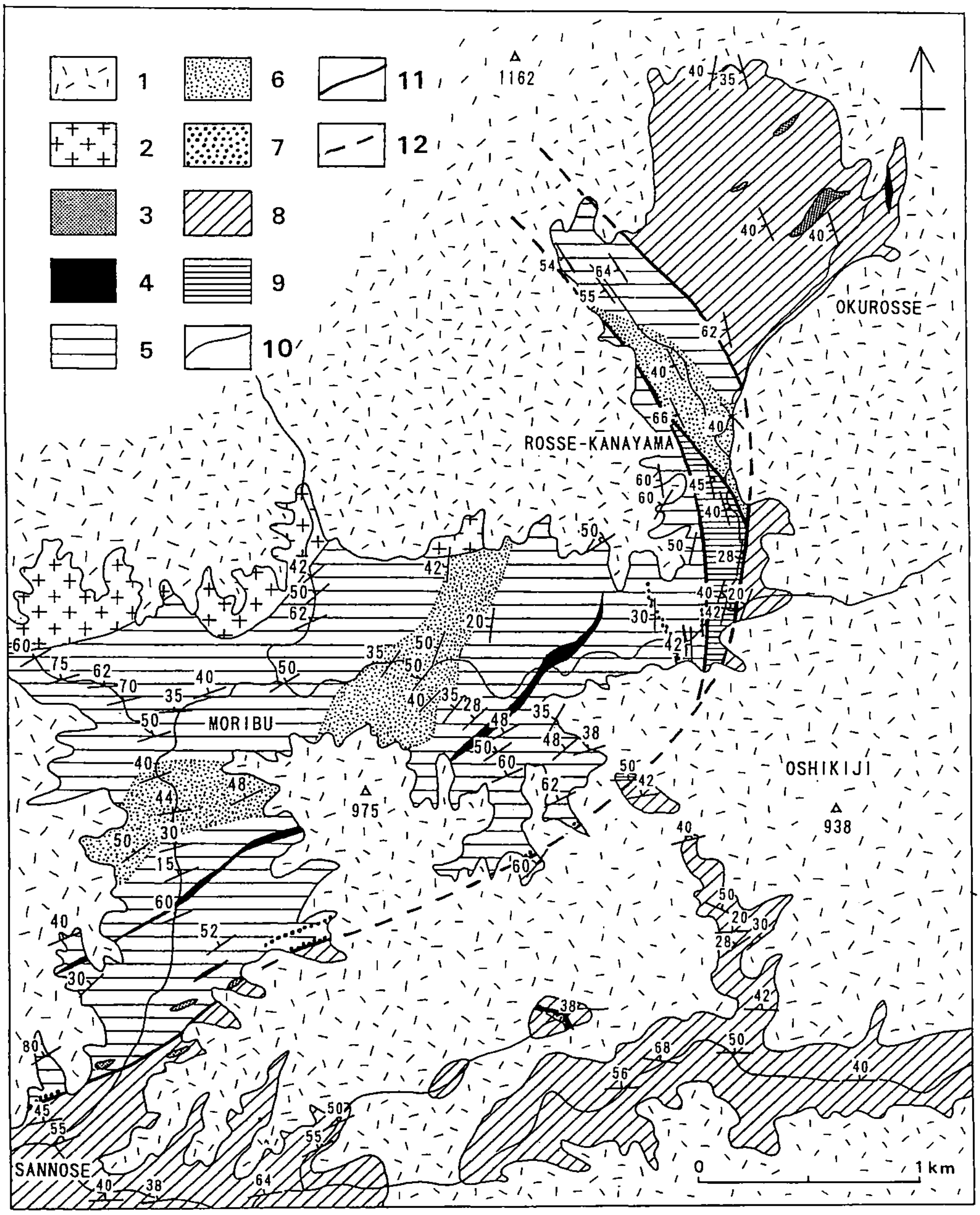

Figure 3. Geological map of the Moribu area (after Tazawa, Hasegawa and Yoshida, 2000). 1: Late Cretaceous and Palaeogene volcanic rocks, 2: Jurassic granitic rocks, 3: Dyke rocks, 4: Limestone of the Arakigawa and Moribu Formations, 5: Shale-dominant facies of the Moribu Formation, 6: Sandstone of the Moribu Formation, 7: Conglomerate of the Moribu Formation, 8: Arakigawa Formation (Carboniferous), 9: Rosse Formation (Devonian), 10: Unconformity, 11: Fault, 12: Concealed fault.

to the Midian. *Gypospirifer volatilis* has been known only from the Murgabian of Inner Mongolia. *Cancrinella* cf. *spinosa*, *Rhynchopora* sp. and *Blasispirifer* cf. *reedi* are similar to the Murgabian species. *Permundaria asiatica*, *Urushtenoidea crenulata*, *Stenoscisma margaritovi* and *Spiriferella lita* are elsewhere known from the Murgabian-Midian. *Yakovlevia kaluzinensis* is known from the Kubergandian-Midian. *Transennatia gratiosa* occurs in the Murgabian-Dzhulfian. *Waagenoconcha permocarbonica* has a long range from the Middle Carboniferous to the Middle Permian, but the lineage is restricted up to the Murgabian. *Linoproductus lineatus* is a long ranging species from the Middle Carboniferous to the Upper Permian, but most common in the Middle Permian. *Leptodus nobilis* ranges into the Kubergandian-Dorashamian. *Hustedia ratburiensis* is recorded from the Yakhtashian-Dzhulfian.

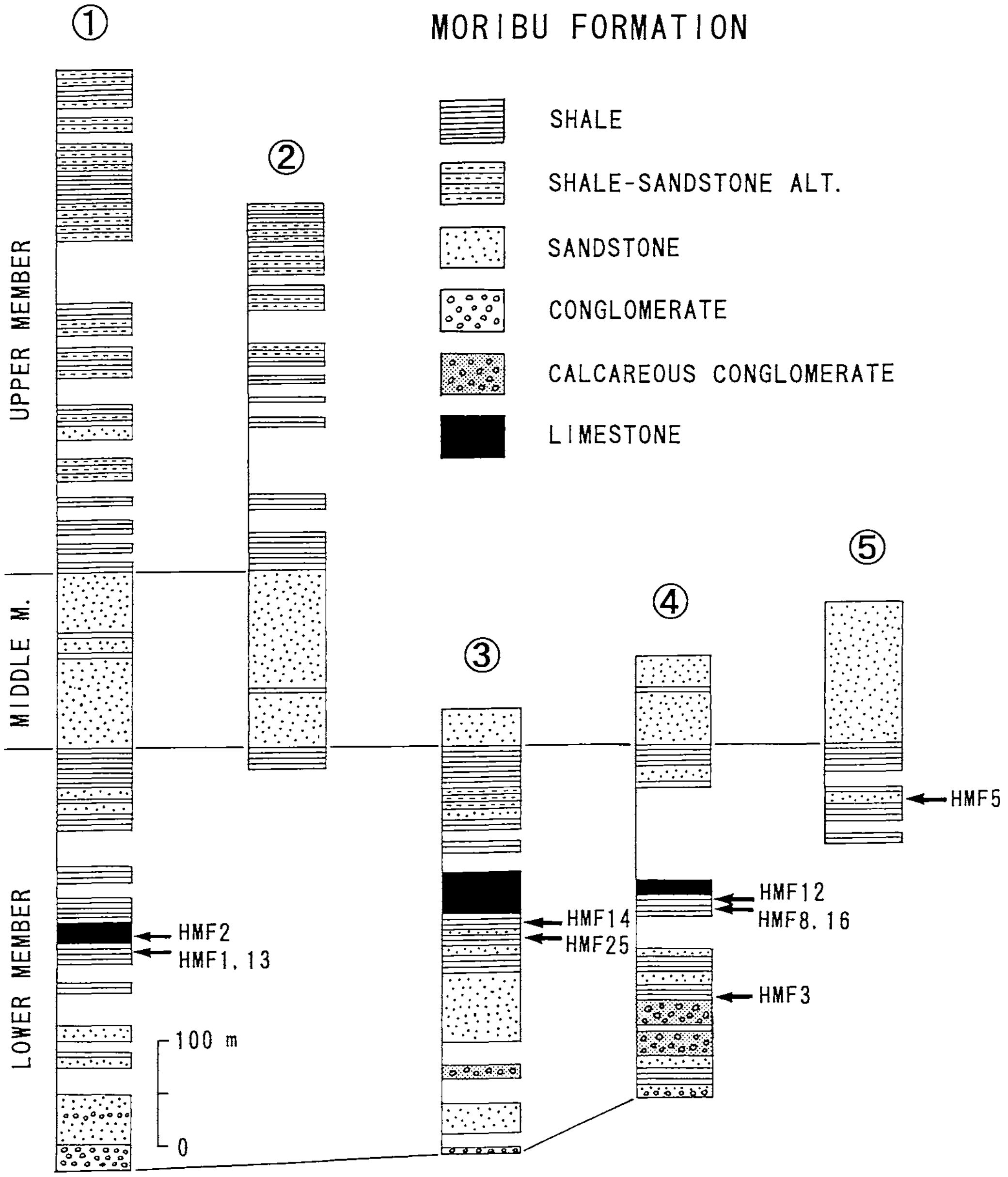

Figure 4. Columnar sections of the Moribu Formation, showing the stratigraphic positions of the fossil localities (HMF1-3, 5, 8, 12-14, 16, 25).

From this evidence, the Moribu fauna can be regarded as Murgabian in age. The Murgabian age assignment does not conflict with data from other fossils of the Moribu Formation.

Published data on fusulinaceans indicate similar age to that shown by brachiopods. The brachiopods occur from the middle and upper parts of the lower member of the Moribu Formation, i.e., the horizons between the calcareous conglomerate of the lower member, with *Pseudofusulina fusiformis* (Schellwien and Dyhrenfurth) and *Misellina* sp., described by Yamada and Yamano (1980), and the sandstone of the middle member, with *Monodiexodina* cf. *matsubaishi* (Fujimoto), described by Tazawa *et al.* (1993). These fusulinaceans confine the age of the brachiopod fauna between the Kubergandian and Murgabian. Consequently the age of the Moribu fauna is judged to be the Murgabian.

In generic and specific composition, the Moribu fauna is most similar to the Middle Permian brachiopod faunas from the Oguradani Formation of the Ise area, Hida Gaien Belt, central Japan (Tazawa and Matsumoto, 1998), and the Barabash and Chandalaz Formations of South Primorye, eastern Russia (Fredericks, 1924, 1925; Licharew and Kotlyar, 1978; Koczyrkevicz, 1979a, b). Furthermore, the

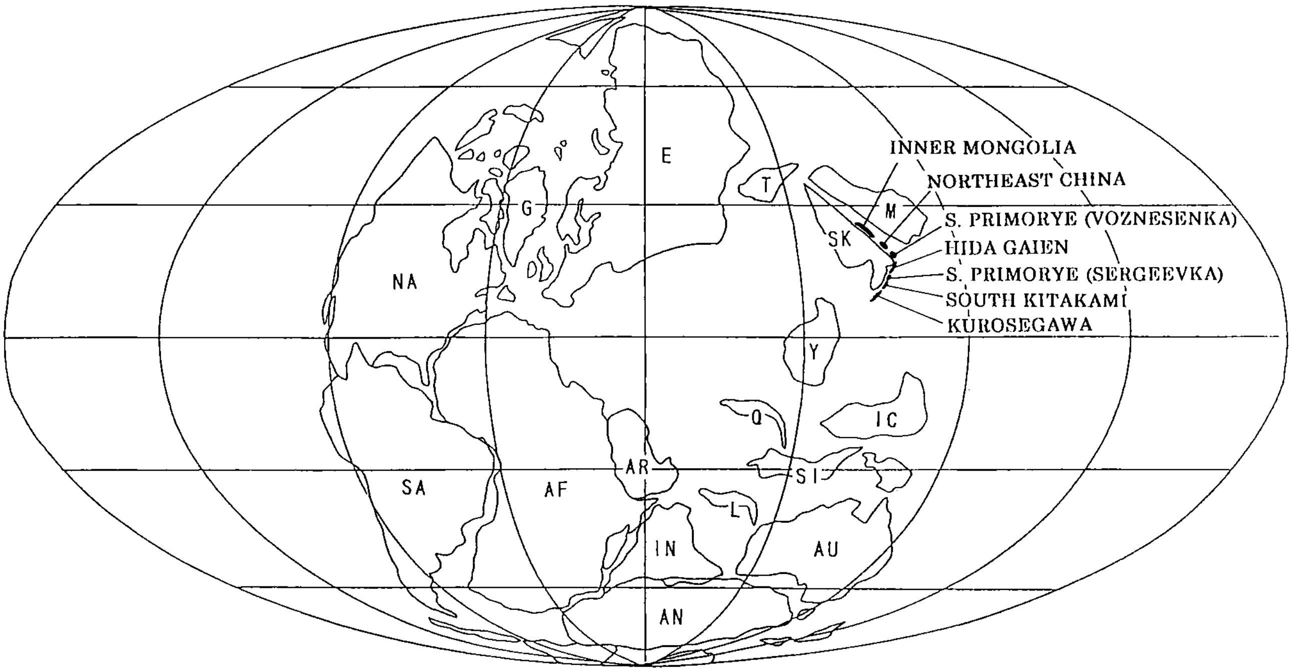

Figure 5. Palaeogeographical map in the Middle Permian time (adapted from Ziegler *et al.*, 1996). Black areas are continental shelf. AF: Africa, AN: Antarctica, AR: Arabia, AU: Australia, E: Eurasia, G: Greenland, IC: Indochina, IN: India, L: Lhasa, M: Mongolia, NA: North America, Q: Qiangtang, SA: South America, SI: Sibumasu, SK: Sino-Korea, T: Tarim, Y: Yangtze.

Middle Permian brachiopod faunas from the South Kitakami Belt (Hayasaka, 1925, 1960; Hayasaka and Minato, 1956; Nakamura *et al.*, 1970; Nakamura, 1979; Tazawa, 1979; Tazawa *et al.*, 2000), Jilin, northeast China (Lee *et al.*, 1980) and Inner Mongolia, north China (Grabau, 1931; Lee and Gu, 1976; Lee *et al.*, 1982; Duan and Li, 1985) also closely resembles the Moribu fauna in species composition.

Palaeobiogeography of the fauna

Palaeobiogeographically, the Moribu fauna contains rather numerous Boreal or bipolar (anti-tropical) elements, *Yakovlevia kaluzinensis, Waagenoconcha permocarbonica, Waagenoconcha* cf. *imperfecta, Megousia* sp., *Cancrinella* cf. *spinosa, Fallaxoproductus moribuensis, Stenoscisma margaritovi, Rhynchopora* sp., *Hustedia ratburiensis, Blasispirifer* cf. *reedi, Gypospirifer volatilis, Spiriferella lita, Alispiriferella ordinaria*, and *Alispiriferella japonica*. The Tethyan elements are also present but not abundant in this fauna. The Tethyan-type species in this fauna are *Transennatia gratiosa, Permundaria asiatica, Urushtenoidea crenulata, Leptodus nobilis*, and *Enteletes* sp. Consequently, the Moribu fauna is a mixture of the Boreal (bipolar or anti-tropical) and Tethyan elements, although the Boreal elements are predominant.

The Hida Gaien Belt with the Moribu fauna is restricted geographically to a continental shelf in the transitional zone between the Boreal and Tethyan Realms in east Asia, i.e., the Inner Mongolian-Japanese Transition Zone of Tazawa (1991, 1998), which includes Inner Mongolia, northeast China, South Primorye, Hida Gaien and South Kitakami, and placed on the northeastern margin of the Sino-Korean block in the middle palaeolatitude of the Northern Hemisphere during the Permian (Figure 5). The Hida Gaien Belt was probably located between the Voznesenka Belt (Barabash-Vladivostok area) and the Sergeevka Belt (Nakhodka-Paltizansk area), and more northerly than the South Kitakami, as mentioned by Tazawa (2001).

Systematic descriptions

Order Lingulida Waagen, 1885
Superfamily Discinoidea Gray, 1840
Family Discinidae Gray, 1840
Genus ***Orbiculoidea*** d'Orbigny, 1847

Type species.—*Orbicula forbesii* Davidson, 1848.

Orbiculoidea cf. *jangarensis* Ustritsky, 1960

Figure 6.11

Compare.—

Orbiculoidea jangarensis Ustritsky, 1960, p. 98, pl. 1, figs. 10-12; Ustritsky and Tschernjak, 1963, p. 68, pl. 1, figs. 5-9; Ifanova, 1972, p. 84, pl. 1, figs. 26-27; Kalashnikov, 1983, p. 204, pl. 45, figs. 3, 4; Kalashnikov, 1993, p. 14, pl. 2, fig. 13; pl. 3, figs. 5a, b; pl. 4, figs. 3a, b.

Material.—One specimen, from locality HMF3, external mould of a ventral valve, NU-B370.

Remarks.—This specimen is assigned to the genus *Orbiculoidea* due to its elliptical outline, short pedicle opening (7 mm long) and numerous, fine concentric lirae on the ventral valve. The Moribu species is a large *Orbiculoidea* of about 30 mm in diameter, and most resembles *Orbiculoidea jangarensis* Ustritsky, 1960, originally described by Ustritsky (1960) from the Talatin Formation of Pay Khoy, Pechora Basin, northern Russia in size and external ornament. *O. jangarensis* has been known from the Upper Artinskian to the Ufimian of the Pechora Basin and Taimyr Peninsula (Ustritsky, 1960; Ustritsky and Tschernjak, 1963; Ifanova, 1972; Kalashnikov, 1983, 1993).

Orbiculoidea sp. Hayasaka (1963, p. 479, figs. 1a, b), from the lower Kanokura Formation of the southern Kitakami Mountains (South Kitakami Belt), northeast Japan, is also close to the present species in size and external ornament of the ventral valve. But accurate comparison is difficult for the fragmentary specimen.

Order Productida Sarytcheva and Sokolskaya, 1959
Suborder Chonetidina Muir-Wood, 1955
Superfamily Chonetoidea Bronn, 1862
Family Rugosochonetidae Muir-Wood, 1962
Subfamily Capillomesolobinae Pecar, 1986
Genus **Capillomesolobus** Pecar, 1986

Type species.—*Capillomesolobus karavankensis* Pecar, 1986.

Capillomesolobus sp.

Figure 6.8a-6.10

Material.—Three specimens, from locality HMF2: (1) external and internal moulds of two ventral valves, NU-B371, 372; (2) external mould of a ventral valve, NU-B373.

Description.—Shell medium size for genus, transverse outline; length about 12 mm, width 14 mm+ in the best preserved specimen (NU-B371). Ventral valve gently and evenly convex in lateral profile; sulcus with median fold occupying whole length of sulcus. External surface of ventral valve ornamented by numerous capillae, having a density of 6 per 1 mm near anterior margin.

Remarks.—This species resembles the shells, described as *Mesolobus sinuosa* (Schellwien, 1898) by Hayasaka (1925, p. 93, pl. 5, figs. 5, 6) and *Mesolobus* sp. by Tazawa (1979, p. 25, pl. 4, figs. 2a, b), from the lower Kanokura Formation of the southern Kitakami Mountains, in size of ventral valve and characters of sulcus. But the Moribu specimens are inadequate for detailed comparison.

Suborder Productidina Waagen, 1883
Superfamily Productoidea Gray, 1840
Family Productellidae Schuchert, 1929
Subfamily Marginiferinae Stehli, 1954
Tribe Paucispiniferini Muir-Wood and Cooper, 1960
Genus **Transennatia** Waterhouse, 1975

Type species.—*Productus gratiosus* Waagen, 1884.

Transennatia gratiosa (Waagen, 1884)

Figure 6.1-6.7

Productus gratiosus Waagen, 1884, p. 691, pl. 72, figs. 3-7; Diener, 1897, p. 23, pl. 3, figs. 3-7; Mansuy, 1913, p. 115, pl. 13, figs. 1a, b; Colani, 1919, p. 10, pl. 1, figs. 2a-c; Chao, 1927, p. 44, pl. 4, figs. 6-10; Chi-Thuan, 1962, p. 491, pl. 2, figs. 5-7.
Productus (*Dictyoclostus*) *gratiosus* Waagen. Huang, 1933, p. 88, pl. 11, figs. 14a, b; Hayasaka, 1960, p. 49, pl. 1, fig. 8.
Marginifera gratiosa (Waagen). Reed, 1944, p. 98, pl. 19, figs. 6-7.
Dictyoclostus gratiosus (Waagen). Zhang and Ching, 1961, p. 411, pl. 4, figs. 12-18; Wang *et al.*, 1964, p. 291, pl. 45, figs. 14-19.
Gratiosina gratiosa (Waagen). Grant, 1976, pl. 33, figs. 19-26; Licharew and Kotlyar, 1978, pl. 12, figs. 5, 6; pl. 20, figs. 1a, b; Minato *et al.*, 1979, pl. 61, figs. 11-13.
Asioproductus gratiosus (Waagen). Yang *et al.*, 1977, p. 350, pl. 140, figs. 5a-c; Feng and Jiang, 1978, p. 254, pl. 90, figs. 1-2; Tong, 1978, p. 228, pl. 80, figs. 7a, b; Lee *et al.*, 1980, p. 373, pl. 164, figs. 14a-c; pl. 166, figs. 5-6.
Asioproductus bellus Chan (Zhan), 1979, p. 85, pl. 6, figs. 7-13; pl. 9, figs. 8-10; text-fig. 18.
Gratiosina sp. Minato *et al.*, 1979, pl. 61, fig. 14; Tazawa, 1991, p. 215.
Transennatia gratiosus (Waagen). Liu *et al.*, 1982, p. 185, pl. 132, figs. 9a-d; Wang et al., 1982, p. 214, pl. 92, figs. 6-8; pl. 102, figs. 4-9; Ding and Qi, 1983, p. 280, pl. 95, figs. 14a, b.
Transennatia gratiosa (Waagen). Yang, 1984, p. 219, pl. 33, figs. 7a-c; Jin, 1985, pl. 4, figs. 33, 34, 45, 46; Tazawa and Matsumoto, 1998, p. 6, pl. 1, figs. 4-8; Tazawa, Takizawa and Kamada, 2000, p. 7, pl. 1, figs. 3-5; Tazawa, 2000, figs. 3.6, 3.7; Tazawa and Ibaraki, 2001, p. 7, pl. 1, figs. 1-3.

Material.—Ten specimens, from localities HMF2, 13: (1) external and internal moulds of two ventral valves, NU-B374, 375; (2) external casts of two ventral valves, NU-B376, 377; (3) external mould of a ventral valve, NU-B378; (4) internal moulds of two ventral valves, NU-B379, 380; (5) external moulds of three dorsal valves, NU-B381-383.

Description.—Shell small for genus, transversely subquadrate in outline, widest at hinge; length 9 mm, width 11 mm in the best preserved ventral valve specimen (NU-B374); length 11 mm+, width 21 mm in the largest dorsal valve specimen (NU-B382). Ventral valve strongly and unevenly convex in lateral profile, most convex at umbonal region, slightly geniculated at anterior margin of visceral disc, with long trail; umbo small, slightly incurved; ears small, distinct and pointed; sulcus narrow and deep; lateral slopes steep. Dorsal valve almost flat on visceral disc, slightly geniculated at anterior margin of visceral disc, followed by short trail; fold narrow and low. External surface of ventral valve reticulate on visceral disc, costate on trail; costae converging into sulcus anteriorly, having a density of 7-8 per 5 mm at midtrail; spines or spine bases not observed. External ornament of dorsal valve similar to that of opposite valve.

Remarks.—*Transennatia gratiosa* (Waagen, 1884) was originally described by Waagen (1884) from the Wargal and Chhidru Formations of the Salt Range. The Moribu specimens are smaller than the Salt Range specimens, and most resemble the smaller shells of *T. gratiosa,* from the Middle


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8 a


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8 b


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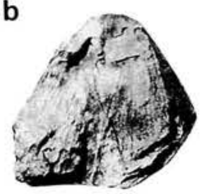
14 b


14 a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15 a


15 b


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18 b


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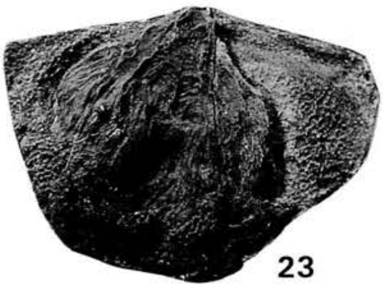
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Permian (Murgabian-Midian) of the southern Kitakami Mountains (Hayasaka, 1960, p. 49, pl. 1, fig. 8), South Primorye, eastern Russia (Licharew and Kotlyar, 1978, pl. 12, figs. 5, 6; pl. 20, figs. 1a, b) and Heilongjiang and Jilin, northeast China (Lee *et al.*, 1980, p. 373, pl. 164, figs. 14 a-c; pl. 166, figs. 5, 6).

Transennatia insculpta (Grant, 1976, p. 135, pl. 32, figs. 1-37; pl. 33, figs. 1-16) from the Rat Buri Limestone of Ko Muk, southern Thailand, is close to *T. gratiosa* in general appearance, but has wider shell and more prominent ears.

Transennatia huananensis (Zhan, 1979, p. 86, pl. 6, figs. 14-16) from the Longtan Formation of Guangdong, south China, is also a small *Transennatia*, but the Chinese species differs from *T. gratiosa* in having finer costae on the ventral valve.

Distribution. — Middle Permian (Murgabian-Midian) of Nepal (Kumaon Himalayas), Cambodia (Sisophon), Vietnam (Quang Tri), south China (Guangxi, Hubei and Shaanxi), northeast China (Jilin and Heilongjiang), eastern Russia (South Primorye) and Japan (Hida Gaien and South Kitakami Belts); Middle Permian (Murgabian) to Upper Permian (Dzhulfian) of Pakistan (Salt Range); Upper Permian (Dzhulfian) of south China (Sichuan, Guizhou, Guangdong, Hunan, Hubei, Jiangxi, Zhejiang and Anhui).

Subfamily Plicatiferinae Muir-Wood and Cooper, 1960
Tribe Yakovleviini Waterhouse, 1975
Genus **Yakovlevia** Fredericks, 1925

Type species.—Yakovlevia kaluzinensis Fredericks, 1925.

Yakovlevia kaluzinensis Fredericks, 1925

Figure 6.20-6.25

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; Kotlyar, 1961, figs. 1-3; Licharew and Kotlyar, 1978, pl. 14, figs. 1, 2; Manankov, 1998, pl. 8, figs. 18, 19; Tazawa, 1999a, figs. 2.4-6; Tazawa, 1999b, p. 90, figs. 3.7-15; Tazawa, 2000, fig. 3.18.

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

Material.—Fourteen specimens, from localities HMF5, 12, 14, 25: (1) external mould of a dorsal valve and associated internal mould of the conjoined valve, NU-B192; (2) external and internal moulds of a ventral valve, NU-B157; (3) internal moulds of seven ventral valves, NU-B158-160, 193-196; (4) external moulds of three dorsal valves, NU-B163, 164, 191; (5) internal moulds of two dorsal valves, NU-B161, 162.

Description.—Shell large for genus, transversely rectangular in outline, with greatest width at hinge; length about 37 mm, width about 44 mm in the smaller, but well preserved ventral valve specimen (NU-B157); length about 47mm, width about 64 mm in the largest dorsal valve specimen (NU-B191).

Ventral valve gently convex on venter, strongly geniculated and followed by 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 ventral valve invisible except for a row of oblique spines just anterior to posterior margin. Dorsal valve almost flat on venter and strongly geniculated; fold narrow and low on anterior half of valve. External surface of dorsal valve ornamented by numerous fine costellae, with a density of 11-13 per 5 mm at midvalve.

Ventral valve interior with a pair of small, elongate subtrigonal adductor scars and two large diductor scars; diductor scars striated anteriorly and demarcated by a strong ridge posterolaterally. Internal structures of dorsal valve obscure in the present material.

Remarks. — The Moribu specimens are referred to *Yakovlevia kaluzinensis* Fredericks, 1925, originally described by Fredericks (1925) from the Chandalaz Formation of the Vladivostok area, South Primorye in size and shape of the shells, in particular, the transversely rectangular 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.

Distribution.—Middle Permian (Kubergandian-Midian) of southeastern Mongolia (near Mt. Dzhirem-Ula), eastern Russia (South Primorye) and central Japan (Hida Gaien Belt).

Family Productidae Gray, 1840
Subfamily Dictyoclostinae Stehli, 1954
Genus **Reticulatia** Muir-Wood and Cooper, 1960

Type species.—Productus huecoensis King, 1931.

← **Figure 6.** 1-7. *Transennatia gratiosa* (Waagen), 1: Internal mould of a ventral valve, NU-B375, 2: Internal mould of a ventral valve, NU-B374, 3: External cast of a ventral valve, NU-B377, 4: External cast of a ventral valve, NU-B376, 5: External mould of a dorsal valve, NU-B382, 6: External mould of a dorsal valve, NU-B383, 7: External mould of a dorsal valve, NU-B381, **8a-10.** *Capillomesolobus* sp., 8a, 8b: External latex cast of ventral valve, NU-B373, (8b ×2), 9: External latex cast of a ventral valve, NU-B372, (×2), 10: Internal mould of a ventral valve, NU-B371, (×2), **11.** *Orbiculoidea* cf. *jangarensis* Ustritsky, external mould of a ventral valve, NU-B370, **12, 13.** *Reticulatia* sp., 12: External mould of a dorsal valve, NU-B477, 13: External mould of a dorsal valve, NU-B476, **14a-15b.** *Juresania* cf. *juresanensis* (Tschernyschew), 14a, 14b: Internal mould and external latex cast of a ventral valve, NU-B384, 15a, 15b: Internal mould and lateral view of external latex cast of a ventral valve, NU-B385, **16.** *Megousia* sp., external mould of a dorsal valve, NU-B404, **17.** *Cancrinella* cf. *spinosa* Hayasaka and Minato, external cast of a ventral valve, NU-B397, **18a-19.** *Linoproductus lineatus* (Waagen), 18a, 18b: External mould and external latex cast of a dorsal valve, NU-B396, 19: External cast of a ventral valve, NU-B395, **20-25.** *Yakovlevia kaluzinensis* Fredericks, 20: Internal mould of a ventral valve, NU-B158, 21: Internal mould of a ventral valve, NU-B159, 22: Internal mould of a ventral valve, NU-B160, 23: Internal mould of a ventral valve, NU-B193, 24: Internal mould of a dorsal valve, NU-B161, 25: External mould of a dorsal valve, NU-B163. (Natural size unless otherwise indicated).

Reticulatia sp.

Figure 6.12, 6.13

Material.—Two specimens, from locality HMF2, external moulds of two dorsal valves, NU-B476, 477.

Description.—Shell small for genus, slightly transverse subquadrate in outline; length about 29 mm, width about 34 mm in the larger specimen (NU-B476). Dorsal valve flat on disk, strongly geniculated and followed by short trail. External surface of dorsal valve ornamented by regular numerous rugae and costae on disc, costae only on trail; costae numbering 5 in 5 mm at anterior margin of disc. Internally, dorsal valve having strong cardinal process; other details not observed.

Remarks.—These specimens are safely assigned to the genus *Reticulatia* by its shape and external ornament of the dorsal valve. However, the specific identification is difficult because of the poor preservation.

Superfamily Echinoconchoidea Stehli, 1954
Family Echinoconchidae Stehli, 1954
Subfamily Juresaniinae Muir-Wood and Cooper, 1960
Tribe Juresaniini Muir-Wood and Cooper, 1960
Genus ***Juresania*** Fredericks, 1928

Type species.—*Productus juresanensis* Tschernyschew, 1902.

Juresania cf. ***juresanensis*** (Tschernyschew, 1902)

Figure 6.14a-6.15b

Compare.—

Productus juresanensis Tschernyschew, 1902, p. 276, 620, pl. 29, figs. 1-2; pl. 47, figs. 1-2; pl. 53, figs. 4a, b; Fredericks, 1925, p. 27, pl. 4, figs. 118, 119.

Buxtonia juresanensis (Tschernyschew). Chao, 1927, p. 81, pl. 8, figs. 4-8; Czarniecki, 1969, p. 282, pl. 7, figs. 1-10; pl. 8, figs. 1-5; pl. 9, figs. 1-5; Sarytcheva and Sokolskaya, 1952, p. 102, pl. 17, fig. 117.

Productus (*Juresania*) *juresanensis* (Tschernyschew). Ozaki, 1931, p. 107, pl. 10, figs. 5a-c.

Productus juresanensis typicus Miloradovich, 1935, p. 79, 140, pl. 5, figs. 22-26; text-fig. 29.

Juresania juresanensis (Tschernyschew). Grabau, 1936, p. 140, pl. 13, figs. 5-6; Gobbett, 1963, p. 82, pl. 4, figs. 34-37; Nakamura, 1959, p. 203, pl. 2, figs. 1a-c; Yanagida, 1967, p. 52, pl. 15, figs. 1-7; text-fig. 4; Kalashnikov, 1980, p. 40, pl. 8, figs. 10a-v; Lazarev, 1982, p. 70, pl. 8, figs. 8-11; Liu *et al.*, 1982, p. 207, pl. 79, figs. 10a-c; Zhang *et al.*, 1983, p. 293, pl. 131, figs. 2a, b; Zeng, 1990, p. 217, pl. 4, figs. 9a-c; Fan and He, 1999, p. 119, pl.10, figs. 9-10.

Material.—Two specimens, from locality HMF5, external and internal moulds of two ventral valves, NU-B384, 385.

Description.—Shell medium size for genus, longer than wide; length about 26 mm, width about 22 mm in the smaller but better preserved specimen (NU-B385). Ventral valve strongly convex in both lateral and anterior profiles, with small, convex ears, shallow sulcus and very steep lateral slopes. External ornament of ventral valve consisting of regular concentric bands and numerous spine bases of two sizes on them; smaller spine bases sometimes occur between larger ones on anterior half of valve.

Remarks.—In external character the Moribu specimens resemble well the ventral valves of *Juresania juresanensis* (Tschernyschew, 1902), from the Lower Permian Indiga Horizon of Timan (Tschernyschew, 1902, pl. 29, figs. 1a-c) and from the Maping Limestone of Yunnan Province, south China (Grabau, 1936, pl. 13, figs. 5-6). But the poor preservation of this material makes accurate comparison difficult. *J. juresanensis* has been described from the Middle Carboniferous (Moscovian) to the Middle Permian (Midian) of Spitsbergen, northern Russia (Novaya Zemlya, Urals, Timan, Kanin Peninsula and Moscow Basin), northern Thailand, south China (Yunnan), northwest China (Xinjiang and Gansu), north China (Inner Mongolia, Shanxi and Shandong), eastern Russia (South Primorye), and northeast Japan (South Kitakami Belt).

Tribe Waagenoconchini Muir-Wood and Cooper, 1960
Genus ***Waagenoconcha*** Chao, 1927

Type species.—*Productus humboldtii* d'Orbigny, 1842.

Waagenoconcha permocarbonica Ustritsky, in Ustritsky and Tschernjak, 1963

Figure 7.20-7.23

Waagenoconcha permocarbonica Ustritsky, in Ustritsky and Tschernjak, 1963, p. 79, pl. 7, fig. 6; pl. 8, figs. 1-3; Lee *et al.*, 1980, p. 364, pl. 168, figs. 1, 6; pl. 169, figs. 3, 4; Duan and Li, 1985, p. 107, pl. 37, figs. 3-5; Shi and Waterhouse, 1996, p. 77, pl. 9, figs. 4-15; pl. 10, figs. 1-4; Tazawa, 2000, figs. 3.16, 3.17.

Material.—Eight specimens, from locality HMF12: (1) external and internal moulds of a conjoined valve, NU-B386; (2) internal moulds of a conjoined valve, NU-B387; (3) external moulds of two ventral valves, NU-B388, 389; (4) external and internal moulds of two dorsal valves, NU-B390, 391; (5) external moulds of two dorsal valves, NU-B392, 393.

Description. — Shell large for genus, transverse, subrectangular in outline, with greatest width slightly anterior to midvalve; length 49 mm, width 51 mm in a ventral valve specimen (NU-B388). Ventral valve strongly convex in both lateral and anterior profiles, with steep lateral slopes; sulcus moderately developed, originating at about 8-10 mm from umbo, deepest at midvalve, and shallowing and widening anteriorly. Dorsal valve with low fold, flat on visceral disc, moderately geniculated, and followed by short trail. External surface of ventral valve ornamented by irregular concentric rugae and numerous, quincuncially arranged spine bases; spine bases becoming fine at anterolateral parts; numbering 5-6 in 5 mm at midvalve, 15-17 in 5 mm near anterior margin. External ornament of dorsal valve similar to that of opposite valve. Internal structures of both valves obscure.

Remarks.—These specimens are referred to *Waagenoconcha permocarbonica* Ustritsky, 1963, originally described by Ustritsky (in Ustritsky and Tschernjak, 1963) from the Bashkirian to the Sakmarian of Taimyr, on account of size, shape and external ornament of both valves.

Waagenoconcha sp. B, described and figured by Liu and Waterhouse (1985, p. 15, pl. 2, figs. 3, 4) from the Middle Permian Zhesi (Jisu) Formation of Xiujimqinqi, Inner Mongolia, differs from the present species in its less transverse outline.

Waagenoconcha waageni (Rothpletz, 1892) from the Middle Permian of Timor is close in general outline, but it has more numerous and stronger concentric bands and coarser spine bases on the ventral valve (see Archbold and Bird, 1989, figs. 3C, D).

Distribution.—Middle Carboniferous (Bashkirian) to Lower Permian (Sakmarian) of northern Russia (Taimyr); Lower Permian (Sakmarian) of western Canada (Yukon Territory); Middle Permian (Kubergandian-Murgabian) of north China (Inner Mongolia), northeast China (Jilin and Heilongjiang) and central Japan (Hida Gaien Belt).

***Waagenoconcha* cf. *imperfecta* Prendergast, 1935**

Figure 7.24a, 7.24b

Compare.—

Waagenoconcha imperfecta Prendergast, 1935, p. 15, pl. 4, figs. 1-3; Prendergast, 1943, p. 25, pl. 3, figs. 7-9; Coleman, 1957, p. 82, pl. 10, figs. 8-14; pl. 11, figs. 1-6; Tazawa, 1974b, p. 127, pl. 1, figs. 4-6; pl. 2, figs. 2-7; pl. 3, figs. 1-3; pl. 4, figs. 1-4, 7.

Waagenoconcha (*Wimanoconcha*) *imperfecta* Prendergast. Archbold, 1993, p. 20, figs. 11A-H, 12A-K, 13A-G.

Material.—One specimen, from locality HMF2, external and internal moulds of a dorsal valve, NU-B394.

Remarks.—The single dorsal valve specimen from Moribu is small in size (length 27 mm, width 29 mm), almost flat on venter, with a low and wide fold on the anterior half of the valve, weakly geniculated, and ornamented by numerous, fine, quincuncially arranged spine bases, having a density of 8 per 5 mm at the midvalve. This specimen may be a young shell of *Waagenoconcha imperfecta* Prendergast, 1935, which has been described from the Upper Permian (Dzhulfian) Hardman Formation of the Canning Basin, western Australia (Prendergast, 1935, 1943; Coleman, 1957; Archbold, 1993) and the Middle Permian (Murgabian) lower Kanokura Formation of the southern Kitakami Mountains, northeast Japan (Tazawa, 1974b). *W. imperfecta* is distinguished from any other waagenoconchids by its very fine and closely arranged spine bases on both the ventral and dorsal valves.

Superfamily Linoproductoidea Stehli, 1954
Family Linoproductidae Stehli, 1954
Subfamily Linoproductinae Stehli, 1954
Genus **Linoproductus** Chao, 1927

Type species.—Productus cora d'Orbigny, 1842.

***Linoproductus lineatus* (Waagen, 1884)**

Figure 6.18a-6.19

Productus lineatus Waagen, 1884, p. 673, pl. 66, figs. 1-2; pl. 67, fig. 3; text-figs. 21a-d; Diener, 1903, p. 138, pl. 7, figs. 1a-c; Tschernyschew, 1914, p. 30, 63, pl. 10, figs. 1a-c.

Productus (*Linoproductus*) *lineatus* (Waagen). Grabau, 1931, p. 293, pl. 29, figs. 25-27.

Linoproductus lineatus (Waagen). Chao, 1927, p. 129, pl. 15, figs. 25-27; Ivanov, 1935, p. 105, pl. 5, fig. 6; pl. 6, figs. 1-4; Minato, 1943, p. 54, pl. 2, figs. 2-5; Sarytcheva and Sokolskaya, 1952, p. 115, pl. 21, fig. 149; Volgin, 1960, p. 70, pl. 7, figs. 2a-v; Lee and Gu, 1976, p. 259, pl. 162, fig. 10; Feng and Jiang, 1978, p. 260, pl. 92, figs. 4a, b; Licharew and Kotlyar, 1978, pl. 13, fig. 1; Tong, 1978, p. 231, pl. 81, figs. 7a, b; Lee *et al.*, 1980, p. 376, pl. 152, fig. 13; Yang, 1984, p. 222, pl. 34, figs. 14a, b; Sremac, 1986, p. 28, pl. 9, figs. 9a-c; Wang and Yang, 1998, p. 100, pl. 16, figs. 1, 3-6.

Linoproductus lineatus lineatus (Waagen). Ramovs, 1958, p. 515, 592, pl. 6, figs. 1a-c; pl. 7, figs. 1a-c; pl. 8, figs. 1a, b.

Linoproductus cf. *lineatus* (Waagen). Yanagida, 1963, p. 74, pl. 10, figs. 8-14.

Linoproductus lineata (Waagen). Ding and Qi, 1983, p. 291, pl. 99, figs. 3a-c.

Material.—Two specimens, from localities HMF2, 8: (1) external cast of a ventral valve, NU-B395; (2) external mould of a dorsal valve, NU-B396.

Remarks.—The specimens from Moribu are referred to *Linoproductus lineatus* (Waagen, 1884), originally described by Waagen (1884) from the Amb, Wargal and Chhidru Formations of the Salt Range, because of similarities in size, shape and external ornament. The ventral valve specimen (NU-B395) is elongate in outline (length 44 mm, width 40 mm), and has small ears and a shallow sulcus. The dorsal valve specimen (NU-B396) is also longer than wide, with a rather short hinge line, and ornamented by numerous costellae (8-10 per 5 mm at the midvalve) and irregular, strong concentric rugae.

The type species, *Linoproductus cora* (d'Orbigny, 1842), from the Lower Permian of Bolivia, differs from *L. lineatus* in its larger, transverse shell and in having much larger ears and lacking a ventral sulcus (see Muir-Wood and Cooper, 1960, pl. 111, figs. 3-6).

Distribution.—Middle Carboniferous (Moscovian) of northeast China (Jilin); Upper Carboniferous (Kasimovian-Gzhelian) of Russia (Moscow Basin and southern Fergana); Lower Permian of northwest China (Xinjiang); Lower Permian (Asselian) to Upper Permian (Dzhulfian) of Croatia, Pakistan (Salt Range), India (Spiti, Punjab Himalayas), Fergana, south China (Guizhou, Sichuan and Hubei), northwest China (Gansu), north China (Inner Mongolia), northeast China (Jilin), eastern Russia (South Primorye) and Japan (Mizukoshi in Kyushu Island and Moribu in the Hida Mountains).

Subfamily Anidanthinae Waterhouse, 1968
Genus **Megousia** Muir-Wood and Cooper, 1960

Type species. — *Megousia auriculata* Muir-Wood and Cooper, 1960.

***Megousia* sp.**

Figure 6.16


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10b


5a


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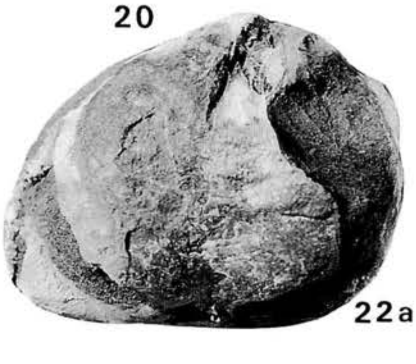
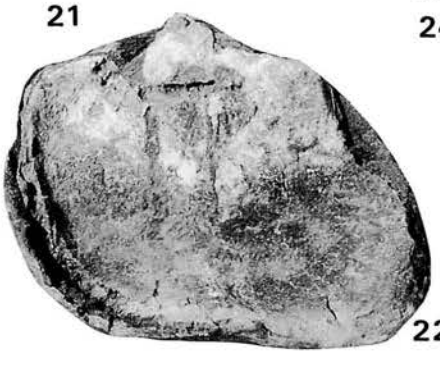
24a


24b


22a


22b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Megousia sp. Tazawa, 2000, fig. 3.3.

Material.—One specimen, from locality HMF2, external mould of a dorsal valve, NU-B404.

Remarks.—This specimen is safely assigned to the genus *Megousia* on the basis of its small size, transversely elliptical outline (length 11 mm, width 26 mm), and in having greatly developed ears with radial ornament. The Moribu species superficially resembles *Megousia solita* Waterhouse (1968, p. 1172, pl. 154, figs. 1-6, 8-10), from the Middle Permian Ulladulla Formation of New South Wales, eastern Australia, but the material is too poor for comparison.

Megousia koizumii Nakamura (1972, p. 438, pl. 2, figs. 1, 4, 5), from the Middle Permian Kashiwadaira Formation of the Takakurayama area, Abukuma Mountains, northeast Japan, is clearly distinguished from the present species by its larger, recurved and hung down ears.

Subfamily Grandaurispininae Lazarev, 1986
Genus **Cancrinella** Fredericks, 1928

Type species.—*Productus cancrini* de Verneuil, 1845.

Cancrinella cf. **spinosa** Hayasaka and Minato, 1956

Figure 6.17

Comapare.—

Productus villiersi kozlowskianus Fredericks. Hayasaka, 1925, p. 96, pl. 5, figs. 10, 11.

Cancrinella cancriniformis spinosa Hayasaka and Minato, 1956, p. 144, pl. 23, figs. 4a, b.

Cancrinella spinosa Hayasaka and Minato. Tazawa, 1976, pl. 2, fig. 5; Minato *et al.*, 1979, pl. 62, figs. 5-8, 11.

Material.—One specimen, from locality HMF2, external cast of a ventral valve, NU-B397.

Remarks.—The fragmentarily preserved specimen is assigned to the genus *Cancrinella* on the basis of its small sized ventral valve (length 18 mm+, width 16 mm+), lacking sulcus, and ornamented by fine concentric rugae and numerous, quincuncially arranged spine bases on the venter.

This specimen can be safely assigned to the *Cancrinella cancriniformis* group of Grigoreva *et al.* (1977) by having distinct rugae on the ventral valve. Within the group, the Moribu species is closely allied to *Cancrinella spinosa* Hayasaka and Minato, 1956, described from the Middle Permian (Murgabian) lower Kanokura Formation of the southern Kitakami Mountains (Hayasaka, 1925; Hayasaka and Minato, 1956; Tazawa, 1976; Minato *et al.*, 1979) in size, shape and external ornament of the ventral valve.

Family Monticuliferidae Muir-Wood and Cooper, 1960
Subfamily Compressoproductinae Jin and Hu, 1978
Genus **Fallaxoproductus** Lee, Gu and Li, 1982

Type species.—*Fallaxoproductus sutungensis* Lee, Gu and Li, 1982.

Fallaxoproductus moribuensis sp. nov.

Figure 7.12a, 7.12b

Material.—Two specimens, from locality HMF12: (1) external and internal moulds of a ventral valve (holotype), NU-B398; (2) external mould of a ventral valve, NU-B399.

Diagnosis.—Shell medium size for genus, slightly elongate trigonal, with very fine costellae on ventral valve, having a density of 12-14 in 5 mm near anterior margin.

Description.—Shell small to medium for genus, slightly elongate trigonal in outline, with short hinge, greatest width near anterior margin; length about 39 mm, width about 32 mm in the holotype (NU-B398). Ventral valve strongly convex on umbonal slope and slightly convex to nearly flat on anterior half of valve; beak prominent, strongly incurved, but not overhanging hinge line; without ears and sulcus. External surface of ventral valve ornamented by regular, numerous, fine costellae, numbering 12-14 in 5 mm near anterior margin; spines clustering along lateral margins; rugae completely absent. Internal structures of ventral valve obscure in the present material.

Remarks.—*Fallaxoproductus moribuensis* sp. nov. can be differentiated from the type and two other described species, *F. dedorus* Lee, Gu and Li, 1982 and *F. plenus* Lee, Gu and Li, 1982, both from the Lower Permian of the Xiujimqinqi area, Inner Mongolia, by its fine costellae on the ventral valve.

The type species, *Fallaxoproductus sutungensis* Lee, Gu and Li, 1982, is much closer to *F. moribuensis* in size and outline of shell, but it differs from the latter in having fewer and more strong costellae on the ventral valve.

← **Figure 7. 1-9.** *Urushtenoidea crenulata* (Ting), 1: Internal mould of a ventral valve, NU-B407, 2: Internal mould of a ventral valve, NU-B411, 3: Internal mould of a ventral valve, NU-B409, 4: Anterior view of internal mould of a ventral valve, NU-B405, 5a, 5b: Ventral and dorsal views of internal mould of a conjoined valve, NU-B406, 6: External mould of a dorsal valve, NU-B416, 7: External mould of a dorsal valve, NU-B415, 8: Internal mould of a dorsal valve, NU-B418, 9: Internal mould of a dorsal valve, NU-B417, **10a, 10b.** *Enteletes* sp., internal mould of a ventral valve, NU-B430, (10b ×2), **11.** *Derbyia* sp., internal mould of a ventral valve, NU-B429, **12a, 12b.** *Fallaxoproductus moribuensis* sp. nov., internal mould and external latex cast of a ventral valve, NU-B398 (holotype), **13-16.** *Leptodus nobilis* (Waagen), 13: Internal mould of a ventral valve, NU-B424, 14: Internal mould of a ventral valve, NU-B427, 15: Internal mould of a ventral valve, NU-B421, 16: Internal mould of a ventral valve, NU-B426, **17a-19.** *Permundaria asiatica* Nakamura, Kato and Choi, 17a, 17b: External latex cast and internal mould of a ventral valve, NU-B400, 18: External latex cast of a ventral valve, NU-B402, 19: External latex cast of a ventral valve, NU-B403, **20-23.** *Waagenoconcha permocarbonica* Ustritsky, 20: External latex cast of a ventral valve, NU-B388, 21: External mould of a dorsal valve, NU-B392, 22a, 22b: Ventral and dorsal views of internal mould of a conjoined valve, NU-B387, 23: Internal mould of a dorsal valve, NU-B390, **24a, 24b.** *Waagenoconcha* cf. *imperfecta* Prendergast, internal and external moulds of a dorsal valve, NU-B394. (Natural size unless otherwise indicated).

Subfamily Schrenkiellinae Lazarev, 1986
Genus **Permundaria** Nakamura, Kato and Choi, 1970

Type species.— Permundaria asiatica Nakamura, Kato and Choi, 1970.

Permundaria asiatica Nakamura, Kato and Choi, 1970

Figure 7.17a-7.19

Striatifera? sp. Hayasaka and Minato, 1956, p. 144, pl. 23, figs. 6, 7.

Permundaria asiatica Nakamura, Kato and Choi, 1970, p. 296, pl. 2, figs. 1, 2; Tazawa, 1974a, p. 315, pl. 43, figs. 3-4; Minato *et al.*, 1979, pl. 62, figs. 12, 13; Tazawa, 2000, fig. 3.4.

Material.—Four specimens, from locality HMF12, external and internal moulds of four ventral valves, NU-B400-403.

Remarks.—Among the specimens from Moribu, the largest ventral valve specimen (NU-B400) may have originally been about 45 mm long, and about 70 mm wide, although both the anterior portion and left half of the valve have been broken off. The valve is slightly convex in the lateral and anterior profiles, and is ornamented by irregularly developed and somewhat flexuous concentric rugae and numerous costellae, numbering 11-12 in 5 mm near the anteror margin. Another specimen (NU-B403) is also an imperfect ventral valve, but the posterior part is well preserved. The ventral valve has a straight hinge, large and flattened ears, and a small, pointed and slightly elevated umbo.

These specimens can be identified with *Permundaria asiatica* Nakamura, Kato and Choi, 1970 by having a small and pointed umbo, irregular and slightly flexuous rugae, and relatively coarse costellae on the ventral valves. *P. asiatica* was originally described by Nakamura *et al.* (1970, p. 296) based on two specimens, the holotype from the lower Kanokura Formation of the southern Kitakami Mountains, northeast Japan, and the paratype from the Sisophon Limestone (*Yabeina* Zone) of Sisophon, Cambodia. The present species is easily distinguished from the following three *Permundaria* species in having coarser costellae on both valves: *P. sisophonensis* Nakamura, Kato and Choi (1970, p. 297, pl. 2, figs. 3a, b) from the Sisophon Limestone of Cambodia, *P. tenuistriata* Tazawa (1974a, p. 317, pl. 43, figs. 1, 2) from the lower Kanokura Formation of the southern Kitakami Mountains, and *P. liaoningensis* Lee and Gu (in Lee *et al.*, 1980, p. 385, pl. 172, figs. 5-8) from the Lower Permian of Liaoning and Heilongjiang, northeast China.

Permundaria shizipuensis Jin, Liao and Fang (1974, p. 310, pl. 162, fig. 18) from the Maokou Formation of Guizhou, south China, differs from *P. asiatica* in having a massive and rounded umbo on the ventral valve.

Distribution. — Middle Permian (Murgabian-Midian) of Cambodia and Japan (South Kitakami and Hida Gaien Belts).

Suborder Strophalosiidina Schuchert, 1913
Superfamily Aulostegoidea Muir-Wood and Cooper, 1960
Family Aulostegidae Muir-Wood and Cooper, 1960
Subfamily Chonosteginae Muir-Wood and Cooper, 1960
Genus **Urushtenoidea** Jin and Hu, 1978

Type species.—Urushtenia chaoi Jin, 1963.

Urushtenoidea crenulata (Ting, in Yang *et al.*, 1962)

Figure 7.1-7.9

Eomarginifera crenulata Ting, in Yang *et al.*, 1962, p. 85, pl. 37, figs. 6 right-8.

Urushtenia costata Ting, in Yang *et al.*, 1962, p. 87, pl. 25, figs. 5-7; pl. 37, fig. 6 left.

Urushtenia chenanensis Chan, in Chan (Zhan) and Lee, 1962, p. 478, 488, pl. 3, figs. 4-6; Tong, 1978, p. 218, pl. 78, figs. 16a-c.

Urushtenia crenulata (Ting). Jin, 1963, p. 20, pl. 1, figs. 17-24; pl. 2, figs. 9, 10, 18-20; text-fig. 5; Yang *et al.*, 1977, p. 335, pl. 136, figs. 11a-c; Feng and Jiang, 1978, p. 246, pl. 89, figs. 11a, b; Tong, 1978, p. 218, pl. 78, figs. 17a-c; Yang and Gao, 1996, pl. 34, figs. 7-8.

Urushtenoidea chenanensis (Chan). Jin and Hu, 1978, p. 117, pl. 2, fig. 9; Hu, 1983, pl. 3, figs. 4-5.

Urushtenoidea maceus (Ching). Nakamura, 1979, p. 227, pl. 1, figs. 1-4; pl. 2, figs. 1-3; Minato *et al.*, 1979, pl. 65, figs. 8-11.

Urushtenoidea crenulata (Ting). Nakamura, 1979, p. 228, pl. 1, figs. 5-9; pl. 3, figs. 1-2; Tazawa, 2000, figs. 3.10, 3.11.

Uncisteges crenulata (Ting). Liu *et al.*, 1982, p. 178, pl. 129, figs. 1a-d; Jin, 1985, pl. 6, fig. 41; Zhu, 1990, p. 74, pl. 14, figs. 4-14; pl. 17, figs. 12, 12a.

Material.—Fifteen specimens, from locality HMF2; (1) external mould of a ventral valve and associated internal mould of conjoined valve, NU-B405; (2) internal mould of a conjoined valve, NU-B406; (3) internal moulds of six ventral valves, NU-B407-412; (4) external and internal moulds of a dorsal valve, NU-B413; (5) external moulds of three dorsal valves, NU-B414-416; (6) internal moulds of three dorsal valves, NU-B417-419.

Description.—Shell medium size for genus, transversely subquadrate in outline; hinge straight, a little less than greatest width; the latter occurring at about midvalve; length 12 mm, width 19 mm in a smaller ventral valve specimen (NU-B406); length 12 mm, width 20 mm in a larger dorsal valve specimen (NU-B415).

Ventral valve strongly geniculated at right angle and followed by long trail; umbo small; lateral slopes steep; ears small; sulcus low and wide, originating at midvisceral disc. External ornament of ventral valve consisting of few weak concentric rugae and costae on visceral disc, numerous costae on trail; costae regular, straight and strong on trail, with a density of 6 per 5 mm at middle of trail; anterior half of ventral trail having some concentric rugae and row of spines on costae. Dorsal valve almost flat on visceral disc, strongly geniculated, and followed by short trail; fold low and wide. External ornament of brachial valve similar to that of opposite valve, but more distinct and regular reticulate ornament on visceral disc.

Interior of dorsal valve with a median septum, extending to midvalve, a pair of elongate muscle scars on both sides of median septum. Other internal structures not observed in the present specimens.

Remarks.—These specimens are identical with *Urushtenoidea crenulata* (Ting, in Yang *et al.*, 1962) in size, shape and external ornament of shell, especially the density of costae on the ventral trail. *Urushtenoidea chenanensis* (Chan, in Chan and Lee, 1962) is a synonym of the present species.

Urushtenoidea maceus (Jin, 1963), originally described and figured as *Urushtenia maceus* from the Middle Permian of Hubei, Anhui, Zhejiang and Jiangsu, south China (Jin, 1963, p. 19, pl. 2, figs. 1-6) somewhat resembles *U. crenulata* in size and outline, but the former differs from the latter in having much finer costae on the ventral valve.

Distribution. — Middle Permian (Murgabian-Midian) of Cambodia (Sisophon), south China (Guizhou, Sichuan, Hunan, Guangdong, Jiangxi, Fujian, Jiangsu, Hubei and Shaanxi), northwest China (Qinghai and Gansu), and Japan (South Kitakami and Hida Gaien Belts).

Superfamily Lyttonioidea Waagen, 1883
Family Lyttoniidae Waagen, 1883
Subfamily Lyttoniinae Waagen, 1883
Genus **Leptodus** Kayser, 1883

Type species.—Leptodus richthofeni Kayser, 1883.

Leptodus nobilis (Waagen, 1883)

Figure 7.13-7.16

Lyttonia nobilis Waagen, 1883, p. 398, pl. 29, figs. 1-3; pl. 30, figs. 1, 2, 5, 6, 8, 10, 11; Diener,1897, p. 37, pl. 1, figs. 5-7; Noetling, 1904, p. 112, text-figs. 4-7; Noetling, 1905, p. 140, pl. 17, figs. 1, 2; pl. 18, figs. 1-11, text-fig. 2; Mansuy, 1913, p. 123, pl. 13, fig. 10; Mansuy, 1914, p. 32, pl. 6, figs. 7a-d; pl. 7, figs. 1a-e; Diener, 1915, p. 99, pl. 10, fig. 15; Albrecht, 1924, p. 289, figs. 1a, b; Grabau, 1931, p. 285, pl. 28, figs. 3-6; Huang, 1932, p. 89, pl. 7, figs. 9, 10; pl. 8, figs. 8, 9; pl. 9, figs. 1-8, text-figs. 8-11; Simic, 1933, p. 49, pl. 4, fig. 1.

Lyttonia tenuis Waagen, 1883, p. 401, pl. 30, figs. 3, 4, 7, 9.

Lyttonia sp. Yabe, 1900, p. 2, text-figs. 1, 2.

Lyttonia cf. *tenuis* Waagen. Mansuy, 1912, p. 19, pl. 4, fig. 4; pl. 5, figs. 1a-e; Huang, 1936, p. 493, pl. 1, fig. 6.

Oldhamina (*Lyttonia*) *richthofeni* var. *nobilis* Waagen. Fredericks, 1916, p. 76, pl. 4, fig. 2, text-fig. 22.

Lyttonia richthofeni (Kayser). Hayasaka, 1917, p. 43, pl. 18, figs. 1-8; Hayasaka, 1922a, p. 62, pl. 11, figs. 1-6; Hayasaka, 1922b, p. 103, pl. 4, figs. 12, 13; Fredericks, 1925, p. 14, pl. 3, figs. 105-107; Licharew, 1932, p. 56, 86, pl. 1, figs. 1-16; pl. 2, figs. 1, 2, 5, 7, 10, 12; pl. 3, figs. 2-7; pl. 4, figs. 1-17; pl. 5, figs. 1-4, 6; Mashiko, 1934, p. 182, text-fig.

Lyttonia (*Leptodus*) *richthofeni* Kayser. Hamlet, 1928, p. 31, pl. 6, figs. 1-4.

Lyttonia richthofeni forma *nobilis* Waagen. Licharew, 1932, p. 69, 96, pl. 2, figs. 13, 14; pl. 5, figs. 1-4, 6; text-fig. 3.

Lyttonia cf. *richthofeni* (Kayser). Huang, 1932, p. 87, pl. 8, figs. 4a, b.

Leptodus nobilis (Waagen). Wanner and Sieverts, 1935, p. 249, pl. 9, figs. 27, 28; text-figs. 16-18; Termier and Termier, 1960, p. 241, text-pl. 3, figs. 1-10; Chi-Thuan, 1961, p. 274, pl. 1, figs. 1a, b; Schréter, 1963, p. 107, pl. 3, figs. 5-8; Sarytcheva, 1964, p. 65, pl. 7, figs. 5-8; text-fig. 1; Ruzhentsev and Sarytcheva, 1965, pl. 39, figs. 6-8; Cooper and Grant, 1974, pl. 191, figs. 8, 9; Grant, 1976, pl. 43, figs. 18, 19; Lee and Gu, 1976, p. 267, pl. 162, figs. 1, 2; Tazawa, 1976, pl. 2, fig. 8; Yang *et al.*, 1977, p. 371, pl. 147, fig. 5; Feng and Jiang, 1978, p. 269, pl. 100, fig. 2; Licharew and Kotlyar, 1978, pl. 14, figs. 13-15; Jin *et al.*, 1979, p. 82, pl. 23, fig. 15; Minato *et al.*, 1979, pl. 66, figs. 1, 4, 5; Zhan, 1979, p. 93, pl. 9, fig. 12; Lee *et al.*, 1980, p. 389, pl. 172, figs. 15, 16; Wang *et al.*, 1982, p. 229, pl. 95, fig. 20; Zhan and Wu, 1982, pl. 4, fig. 4; Ding and Qi, 1983, p. 297, pl. 102, figs. 7, 8; Yang, 1984, p. 226, pl. 35, fig. 12; Gu and Zhu, 1985, pl. 1, figs. 31, 33, 34; Liao and Meng, 1986, p. 81, pl. 2, figs. 24, 25; Sremac, 1986, p. 30, pl. 10, figs. 1-2; Tazawa, 1987, fig. 1.11; Kotlyar, in Kotlyar and Zakharov, 1989, pl. 20, fig. 6; pl. 23, fig. 12; Liang, 1990, p. 225, pl. 40, figs. 1, 5; Tazawa and Matsumoto, 1998, p. 7, pl. 2, figs. 7-12; Tazawa *et al.*, 1998, p. 241, figs. 2.1, 2.2; Kato *et al.*, 1999, p. 47, figs. 4a, b; Tazawa, 2000, figs. 3.14, 3.15, 7.1a, 7.1b; Tazawa and Ibaraki, 2001, p. 11, pl. 1, figs. 7-10.

Lyttonia cf. *nobilis* Waagen. Huang, 1936, p. 493, pl. 1, fig. 5.

Leptodus cf. *nobilis* (Waagen). Thomas, 1957, p. 177, pl. 20, figs. 1-6.

Leptodus richthofeni Kayser. Shimizu, 1961, pl. 18, figs. 14, 15; Schréter, 1963, p. 106, pl. 3, fig. 4; Sarytcheva, 1964, p. 65, pl. 7, figs. 2-4; Yang *et al.*, 1977, p. 372, pl. 147, fig. 10; Yang, 1984, p. 226, pl. 35, fig. 11; Duan and Li, 1985, p. 119, pl. 35, figs. 17-19.

Leptodus ivanovi Frederiks. Minato *et al.*, 1979, pl. 66, fig. 3.

Leptodus sp. Minato *et al.*, 1979, pl. 66, fig. 2.

Leptodus tenuis (Waagen). Yang, 1984, p. 226, pl. 35, fig. 13; Duan and Li, 1985, p. 119, pl. 35, figs. 14-16; Liang, 1990, p. 226, pl. 40, fig. 9; Zhu, 1990, p. 79, pl. 18, figs. 19-21.

Leptodus sp. Tazawa, 1987, fig. 1.10.

Gubleria sp. Zhu, 1990, p. 80, pl. 16, fig. 24.

Material.—Nine specimens, from locality HMF2: (1) external and internal moulds of three ventral valves, NU-B420-422; (2) external mould of a ventral valve, NU-B423; (3) internal moulds of five ventral valves, NU-B424-428.

Description.—Shell small to medium size for genus, elongate subtrigonal in outline, with greatest width near anterior margin; length 40 mm, width 32 mm in the largest specimen (NU-B424). Ventral valve almost flat, slightly convex in lateral and anterior profiles. Ventral valve interior with regularly and synmmetrically arranged lateral septa on both sides of mediam septum; lateral septa broad and solid (solidiseptate), straight to slightly arched toward front, numbering 12 pairs in the largest specimen; interseptal spaces 2.0-2.5 mm in width; median septum highly developed.

Remarks.—These specimens are relatively small in size, and seem to be immature shells of *Leptodus nobilis* (Waagen, 1883), originally described by Waagen (1883, p. 398) from the Wargal and Chhidru Formations of the Salt Range. The Moribu specimens externally most resemble the shells, described as *Lyttonia richthofeni* (Kayser) by Hayasaka (1917, p. 43, pl. 18, figs. 1-6; Hayasaka, 1922a, p. 62, pl. 11, figs. 2, 3) from the lower Kanokura Formation of the southern Kitakami Mountains.

The type species, *Leptodus richthofeni* Kayser, 1883 from the Permian of Loping, Jiangxi Province, south China (Kayser, 1883, p. 161, pl. 21,figs.9-11; Cooper and Grant, 1974, p. 411, pl. 191, figs. 11-15) differs from *L. nobilis* in having a more strongly convex ventral valve, with sharp lateral septa and much broader interseptal spaces.

Distribution.—Middle Permian (Kubergandian) to Upper Permian (Dorashamian) of Hungary, Croatia, Serbia, western Russia (Caucasus Mountains), Pakistan (Salt Range and Khisor Range), India (Kashmir), Nepal (Kumaon Himalayas), Cambodia, Laos, Timor, northern Australia (Port Keats), northwest China (Tibet and Qinghai), south China (Yunnan, Guangxi, Guizhou, Sichuan, Hubei, Hunan, Guangdong, Jiangxi, Fujian and Zhejiang), north China (Inner Mongolia), northeast China (Jilin and Heilongjiang), eastern Russia (South Primorye), and Japan (Imo, Kamiyasse, Matsukawa and Ogatsu in the South Kitakami Belt, Moribu and Ise in the Hida Gaien Belt, Takauchi in the Maizuru Belt and Akasaka in the Mino Belt).

Order Orthotetida Waagen, 1884
Suborder Orthotetidina Waagen, 1884
Superfamily Orthotetoidea Wagen, 1884
Family Derbyiidae Stehli, 1954
Genus **Derbyia** Waagen, 1884

Type species.—Derbyia regularis Waagen, 1884.

Derbyia sp.

Figure 7.11

Derbyia sp. Tazawa, 2000, fig. 3.2.

Material.—One specimen, from locality HMF2, internal mould of a ventral valve, NU-B429.

Remarks.—This specimen is safely assigned to the genus *Derbyia* by its almost flat ventral valve, ornamented by numerous fine costellae and having a strong median septum 10 mm long. However, the single imperfect specimen does not allow specific assignment.

Order Orthida Schuchert and Cooper, 1932
Suborder Dalmanellidina Moore, 1952
Superfamily Enteletoidea Waagen, 1884
Family Enteletidae Waagen, 1884
Genus **Enteletes** Fischer de Waldheim, 1825

Type species.—Enteletes glabra Fischer de Waldheim, 1830.

Enteletes sp.

Figure 7.10a, 7.10b

Enteletes sp. Tazawa, 2000, figs. 3.1a, 3.1b.

Material.—One specimen, from locality HMF1, internal mould of a ventral valve, NU-B430.

Remarks.—The single ventral valve specimen of Moribu is safely assigned to the genus *Enteletes* by its small size (length about 10 mm, width about 11 mm), rounded elliptical outline, and having a long median septum and a pair of thin, long, subparallel dental plates, both of them extending to the midvalve. Specific identification remains difficult due to the poor preservation of the specimen.

Order Rhynchonellida Kuhn, 1949
Superfamily Stenoscismatoidea Oehlert, 1887
Family Stenoscismatidae Oehlert, 1887
Genus **Stenoscisma** Conrad, 1839

Type species.—Terebratula schlotheimii von Buch, 1835.

Stenoscisma margaritovi (Tschernyschew, 1888)

Figure 8.1a-8.4

Camarophoria margaritovi Tschernyschew, 1888, p. 355, figs. 1-3; Fredericks, 1924, p. 48, pl. 1, figs. 32-42; text-fig. 4.

Camarophoria humbletonensis Howse. Hayasaka, 1922a, p. 62, pl. 9, figs. 10-12; pl. 10, fig. 9; Hayasaka, 1966, p. 1226, text-figs. 6-8.

Stenoscisma humbletonensis (Howse). Tazawa, 1976, pl. 2, figs. 9, 10; Minato *et al.*, 1979, pl. 66, figs. 6-8.

Stenoscisma gigantea (Diener). Lee and Gu, 1976, p. 272, pl. 176, fig. 3; pl. 177, fig. 18; Lee *et al.*, 1980, p. 395, pl. 173, figs. 6, 8.

Stenoscisma margaritovi (Tschernyschew). Licharew and Kotlyar, 1978, pl. 17, figs.7a, b; Koczyrkevicz, 1979b, p. 50, pl. 11, figs. 5, 6; Duan and Li, 1985, p. 120, pl. 43, figs. 5-8; Tazawa and Matsumoto, 1998, p. 9, pl. 2, figs. 1-5; Tazawa, 2000, fig. 3.5; Tazawa, Takizawa and Kamada, 2000, p. 10, pl. 1, figs. 7-11.

Stenoscisma gigantea elongatum Lee and Su, in Lee *et al.*, 1980, p. 395, pl. 173, figs. 1, 2.

Stenoscisma purdoni (Davidson). Lee *et al.*, 1980, p. 395, pl. 173, figs. 4, 5, 7.

Material.—Five specimens, from localities HMF2, 3: (1) external cast of a conjoined valve, NU-B431; (2) external casts of three ventral valves, NU-B432-434; (3) external cast of a dorsal valve, NU-B435.

Description.—Shell medium size for genus, longer than wide, with greatest width slightly anterior to midvalve; length 21 mm, width about 18 mm in the best preserved specimen (NU-B434). Ventral valve gently convex in lateral profile; umbo small; sulcus shallow; costae often bifurcating or intercalating anteriorly, numbering 7-9 on sulcus and 6-7 on each flank. Dorsal valve moderately convex in lateral profile, with low fold; costae numbering 8 on fold and 6-7 on each flank.

Remarks.—These specimens are poorly preserved but can be referred to *Stenoscisma margaritovi* (Tschernyschew, 1888) by their narrow and elongate outline, shallow ventral sulcus and low dorsal fold, and rather numerous costae on both valves.

The shells, described and figured as *Stenoscisma humbletonensis* (Howse, 1848) from the lower Kanokura Formation of the southern Kitakami Mountains (Hayasaka, 1922a, 1966; Tazawa, 1976; Minato *et al.*, 1979), are referred to *S. margaritovi* on the basis of their shallow sulcus, low fold, and many costae on both valves.

An elongate species, described as *Stenoscisma gigantea* (Diener, 1897), *S. gigantea elongatum* Lee and Su, in Lee *et al.*, 1980, and *S. purdoni* (Davidson, 1862) from the Middle Permian of Jilin and Heilongjiang, northeast China and Jisu (Zhesi), Inner Mongolia (Lee and Gu, 1976; Lee *et al.*, 1980), may be conspecific with *S. margaritovi*.

Stenoscisma tetricum Grant (1976, p. 185, pl. 50, figs. 9-28) from the Rat Buri Limestone of Ko Muk, southern Thailand is also close to *S. margaritovi* in size and outline, but the Thailand species is distinguished from the present species by its strong concentric laminae on both valves.

Distribution. — Middle Permian (Murgabian-Midian) of north China (Inner Mongolia), northeast China (Heilongjiang and Jilin), eastern Russia (South Primorye), and Japan (South Kitakami and Hida Gaien Belts).

Superfmily Rhynchoporoidea Muir-Wood, 1955
Family Rhynchoporidae Muir-Wood, 1955
Genus **Rhynchopora** King, 1865

Type species. — *Terebratula geinitziana* de Verneuil, in Murchison *et al.*, 1845.

Rhynchopora sp.

Figure 8.5a-8.5c

Rhynchopora sp. Shi and Tazawa, 2001, p. 756, figs. 2.2a, b.

Material. — One specimen, from locality HMF1, internal mould of a conjoined valve, NU-B478.

Remarks.—This specimen is safely assigned to the genus *Rhynchopora* by its small size (length 10 mm, width 9 mm), pentagonal outline, fine simple costae and, in particular, the high dorsal fold which originates from midvalve, has 5 costae and is sharply incurved ventrally to form almost a square-shaped, flat anterior surface at the anterior margin. The Moribu specimen well resembles *Rhynchopora tchernyshae* Koczyrkevicz (1979a, p. 47, pl. 11, figs. 1-4), originally described from the lower Barabash Formation of South Primorye, in size and outline of the shell, and the number of costae on the dorsal fold. But accurate comparison is difficult for the poorly preserved specimen.

Order Athyridida Boucot, Johnson and Staton, 1964
Suborder Retziidina Boucot, Johnson and Staton, 1964
Superfmily Retzioidea Waagen, 1883
Family Neoretziidae Dagis, 1972
Subfamily Hustediinae Grunt, 1986
Genus **Hustedia** Hall and Clarke, 1893

Type species.—*Terebratula mormonii* Marcou, 1858.

Hustedia ratburiensis Waterhouse and Piyasin, 1970

Figure 8.6a-8.6c

Hustedia ratburiensis Waterhouse and Piyasin, 1970, p. 138, pl. 23, figs. 15-30; Grant, 1976, p. 241, pl. 66, figs. 1-69; pl. 67, figs. 51-58; Sun, 1991, p. 254, pl. 6, figs. 5-8; Yanagida and Nakornsri, 1999, p. 118, pl. 32, figs.11-16.
Hustedia thailandica Waterhouse and Piyasin, 1970, text-figs. 12, 13.
Hustedia nakornsrii Yanagida, 1970, p. 79, pl. 14, figs. 9a-d.

Material.—Four specimens, from localities HMF1, 2, 5: (1) external moulds of two ventral valves, NU-B436, 437; (2) external mould of a dorsal valve, NU-B438; (3) internal mould of a dorsal valve, NU-B439.

Description.—Shell small to medium for genus, suboval in outline, with greatest width slightly anterior to midvalve; length 9 mm, width 8 mm in the larger ventral valve specimen (NU-B436). Ventral valve moderately convex in both lateral and anterior profiles, without sulcus. External surface of ventral valve ornamented by simple, broad and rounded costae; 2 close-set costae medially and 3 pairs of costae laterally. Dorsal valve moderately convex in both profiles, having no fold, and ornamented by 3 costae medially and 3 pairs of costae laterally; costae originating at umbo except median costa, which commences a little below umbo; outer 2 pairs of costae curved towards posterolateral margins. Internal structure of dorsal valve obscure in the present material.

Remarks. — The Moribu specimens can be referred to *Hustedia ratburiensis* Waterhouse and Piyasin, 1970 by their external ornament, 2 close-set costae on median part of the ventral valve and 3 costae on median part of the dorsal valve, especially the median costa of the dorsal valve originating a short distance below umbo. This species was described and compared in detail by Waterhouse and Piyasin (1970), Yanagida (1970) and Grant (1976).

A single dorsal valve specimen, figured by Koizumi (1979, pl. 1, fig. 5) as *Hustedia indica* (Waagen, 1883) from the Kashiwadaira Formation of the Takakurayama area, Abukuma Mountains, northeast Japan, resembles closely *H. ratburiensis* in having a median costa originating slightly anterior to umbo.

Distribution. — Lower Permian (Artinskian) to Upper Permian (Dzhulfian) of north-central Thailand (Khao Hin King), southern Thailand (Khao Phrik, Khao Tok Nam and Ko Muk), and central Japan (Hida Gaien Belt).

Order Spiriferida Waagen, 1883
Suborder Spiriferidina Waagen, 1883
Superfamily Martinioidea Waagen, 1883
Family Martiniidae Waagen, 1883
Subfamily Martiniinae Waagen, 1883
Genus **Martinia** M'Coy, 1844

Type species.—*Spirifer glaber* Sowerby, 1820.

Martinia sp.

Figure 8.7a, 8.7b

Material. — One specimen, from locality HMF3, internal mould of a ventral valve, NU-B440.

Remarks.—This specimen is safely assigned to the genus *Martinia* by its transversely subelliptical ventral valve with several vascular markings radially branching out from umbonal region and extending two-thirds of the length of the valve. However, the poor preservation of this specimen prevents accurate specific identification.

Family Martiniopsidae Kotlyar and Popeko, 1967
Genus **Martiniopsis** Waagen, 1883

Type species.—*Martiniopsis inflata* Waagen, 1883.


1a


1b


2


3


4


5a


5b


5c


6a


6b


6c


7a


7b


8


9


10a


10c


11a


10b


14b


11b


12a


12b


13


14a


16a


17


15


14c

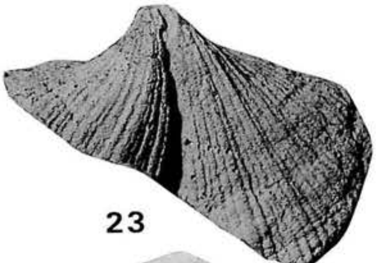

16b


18


19


20


21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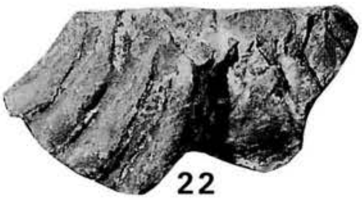
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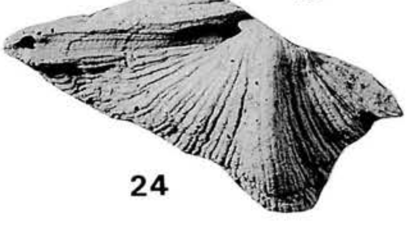
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Martiniopsis sp.

Figure 8.8, 8.9

Material.—Two specimens, from locality HMF1, internal moulds of two ventral valves, NU-B441, 442.

Remarks. — These specimens are fragmentarily preserved, but safely assigned to the genus *Martiniopsis* by their transversely oval outline and a pair of long adminicula reaching to the midlength of the ventral valves. The Moribu species is a medium, transverse *Martiniopsis*; length about 21 mm, width about 28 mm in the lager specimen (NU-B441), and most resembles *Martiniopsis cathaysiensis* Grabau (1936, p. 242, pl. 21, figs. 7, 8; pl. 24, figs. 9a-e), from the Maping Limestone of Guangxi and Guizhou, south China, in size and shape of the ventral valve.

The single ventral valve specimen, described as *M. cathaysiensis* by Hayasaka (1967, p. 254, figs. 2a, b) from the lower Kanokura Formation of the southern Kitakami Mountains, is poorly preserved, and inadequate for comparison.

Superfamily Spiriferoidea King, 1846
Family Trigonotretidae Schuchert, 1893
Subfamily Neospiriferinae Waterhouse, 1968
Genus **Neospirifer** Fredericks, 1919

Type species.—Spirifer fasciger Keyserling, 1846.

Neospirifer cf. ***fasciger*** (Keyserling, 1846)

Figure 8.10a-8.10c

Compare.—

Spirifer fasciger Keyserling, 1846 pars, p. 231, pl. 8, fig. 3b only; Chao, 1925, p. 236, pl. 3, figs. 1-2.

Spirifer (*Neospirifer*) *fasciger* Keyserling. Ozaki, 1931, p. 28, pl. 1, figs. 3-6.

Neospirifer fasciger (Keyserling). Archbold and Thomas, 1984 pars, figs. 1F, H, I, 2C only; Poletaev, 1997, pl. 4, figs. 2-7.

Material.—One specimen, from locality HMF8, external mould of a conjoined valve, NU-B443.

Remarks.—The material available is a single imperfect shell lacking the anterior and lateral parts. This specimen is safely assigned to the genus *Neospirifer* because of its distinct fasciculate costae on the lateral slopes of both valves. Externally the Moribu specimen most resembles the shells of *Neospirifer fasciger* (Keyserling, 1846), described from the Upper Carboniferous of Gansu and Shanxi, north China and Jilin and Liaoning, northeast China (Chao, 1925; Ozaki, 1931). The lectotype of *N. fasciger*, designated by Cooper and Grant (1976, p. 2173) and refigured by Archbold and Thomas (1984, figs. 1F-I, 2C) and Poletaev (1997, pl. 4, figs. 3b-3d) is also close to the present specimen in size, outline and ornament of the brachial valve. The present material is, however, too imperfect for comparison.

Genus ***Blasispirifer*** Kulikov, 1950

Type species.—Spirifer blasii de Verneuil, 1845.

Blasispirifer cf. ***reedi***
(Licharew, in Licharew and Kotlyar, 1978)

Figure 8.11a-8.13

Spirifer cf. *reedi* Licharew. Shi and Tazawa, 2001, p. 756, figs. 2.4-6.

Material.— Three specimens, from localities HMF1, 3: (1) internal mould of a conjoined valve, NU-B479; (2) internal mould of a ventral valve, NU-B480; (3) internal mould of a dorsal valve, NU-B481.

Description.—Shell small for genus, slightly transverse, rounded rhomboidal in outline, with narrow hinge; length 13 mm, width 14 mm in a dorsal valve specimen (NU-B481). Ventral valve with a narrow and deep sulcus. Dorsal valve having a narrow but distinct fold; costae mostly simple, but weakly bundled in the innermost pair bounding fold; numbering 9-12 on each slope, 5-6 on fold in dorsal valve. Internally ventral valve lacking dental plates. Dorsal valve with no crural plates.

Remarks.—These specimens are safely assigned to the genus *Blasispirifer* by their small, rounded rhomboidal shell, fine, weakly bundled costae on dorsal valve, and lacking both dental plates and crural plates. In size and shape, the Moribu specimens most resemble *Blasispirifer reedi*

← **Figure 8. 1a-4.** *Stenoscisma margaritovi* (Tschernyschew), 1a, 1b: Ventral and dorsal views of external cast of a conjoined valve, NU-B431, 2: External cast of a ventral valve, NU-B434, 3: External cast of a ventral valve, NU-B433, 4: External cast of a ventral valve, NU-B432, **5a-5c.** *Rhynchopora* sp., dorsal and anterior views of internal mould of a conjoined valve, NU-B478, (5b, 5c ×2), **6a-6c.** *Hustedia ratburiensis* Waterhouse and Piyasin, 6a, 6b: External latex cast of a dorsal valve, NU-B438, (6b ×2), 6c: External cast of a ventral valve, NU-B436, (×2), **7a, 7b.** *Martinia* sp., internal mould of a ventral valve, NU-B440, (7b ×2), **8, 9.** *Martiniopsis* sp., internal moulds of two ventral valves, NU-B442, 441, **10a-10c.** *Neospirifer* cf. *fasciger* (Keyserling), ventral, posterior and dorsal views of external latex cast of a conjoined valve, NU-B443, **11a-13.** *Blasispirifer* cf. *reedi* (Licharew), 11a, 11b: Internal mould of a dorsal valve, NU-B481, (11b ×2), 12a, 12b: Ventral and dorsal views of internal mould of a conjoined valve, NU-B479, 13: Internal mould of a ventral valve, NU-B480, **14a-14c.** *Alispiriferella ordinaria* (Einor), external and internal latex casts and internal mould of a ventral valve, NU-B458, **15-18.** *Alispiriferella japonica* sp. nov., 15: Internal mould of a ventral valve, NU-B462, 16a, 16b: External and internal latex casts of a ventral valve, NU-B461 (holotype), 17: Posterior view of external latex cast of a conjoined valve, NU-B460, 18: External latex cast of a ventral valve, NU-B465, **19-22.** *Spiriferella lita* (Fredericks), 19: External cast of a dorsal valve, NU-B455, 20: External cast of a dorsal valve, NU-B452, 21: External cast of a dorsal valve, NU-B456, 22: External cast of a ventral valve, NU-B451, **23-26.** *Gypospirifer volatilis* Duan and Li, 23: External latex cast of a ventral valve, NU-B444, 24: External latex cast of a dorsal valve, NU-B449, 25: Internal mould of a ventral valve, NU-B448, 26: External latex cast of a ventral valve, NU-B445, **27, 28.** *Dielasma* sp., external latex casts of two ventral valves, NU-B475, 474. (Natural size unless otherwise indicated).

(Licharew, 1978), originally described by Licharew (in Licharew and Kotlyar, 1978, p. 73, pl. 21, figs. 13a, b, v) from the Chandalaz Formation of South Primorye. Accurate comparison is difficult due to the lack of clear external information in the present material.

Genus ***Gypospirifer*** Cooper and Grant, 1976

Type species.—*Gypospirifer nelsoni* Cooper and Grant, 1976.

Gypospirifer volatilis Duan and Li, 1985

Figure 8.23-8.26

Gypospirifer volatilis Duan and Li, 1985, p. 127, 207, pl. 48, figs. 1-2; pl. 49, figs. 1-2.
Gypospirifer sp. Tazawa, 2000, figs. 3.12, 3.13.

Material.—Seven specimens, from localities HMF5, 12, 25: (1) external moulds of a conjoined valve, NU-B444; (2) external moulds of three ventral valves, NU-B445-447; (3) internal mould of a ventral valve, NU-B448; (4) external and internal moulds of a dorsal valve, NU-B449; (5) external mould of a dorsal valve, NU-B450.

Description.—Shell medium to large for genus, transversely semielliptical in outline, with greatest width at hinge, and slightly alate; length 42 mm, width about 73 mm in the best preserved specimen (NU-B445).

Ventral valve gently convex in lateral and anterior profiles, most convex at umbonal region; umbo slightly extended and strongly incurved; sulcus very deep and rapidly widening anteriorly, with U-shaped bottom. External surface of ventral valve ornamented by numerous fine costae and concentric ornament of some rugae and numerous fine growth lines; costae subridged, added by bifurcation, and weakly fasciculated, numbering 9-10 in 10 mm at about midvalve, 7-8 in 10 mm at anterior margin. Dorsal valve gently convex in both profiles, having a high and narrow fold. External ornament of dorsal valve identical to opposite valve.

Ventral interior with a pair of thick, short dental plates and a deeply impressed, large, heart-shaped muscle field. Other internal structures not preserved.

Remarks.—These specimens are referred to *Gypospirifer volatilis* Duan and Li, 1985, originally described from the Middle Permian Zhesi (Jisu) Formation of the Zhesi area, Inner Mongolia, by their size, outline and surface ornament of shells, especially the deep ventral sulcus and high dorsal fold.

Gypospirifer marcoui (Waagen, 1883, p. 510, pl. 47, figs. 1-3) from the Amb and Wargal Formations of the Salt Range most resembles *G. volatilis*, but differs from the latter in having a shallower ventral sulcus and a lower dorsal fold.

The type species, *G. nelsoni* Cooper and Grant (1976, p. 2214, pl. 591, figs. 8-9) from the Hueco Formation of west Texas is clearly distinguished from *G. volatilis* by its more transverse shell, shallower ventral sulcus and lower dorsal fold.

Distribution.—Middle Permian (Murgabian) of north China (Inner Mongolia) and central Japan (Hida Gaien Belt).

Family Spiriferellidae Waterhouse, 1968
Subfamily Spiriferellinae Waterhouse, 1968
Genus ***Spiriferella*** Tschernyschew, 1902

Type species.—*Spirifer saranae* de Verneuil, 1845.

Spiriferella lita (Fredericks, 1924)

Figure 8.19-8.22

Spirifer saranae mut. *lita* Fredericks, 1924, p. 36, pl. 1, figs. 16-27; Hayasaka, 1925, p. 98, pl. 5, fig. 14.
Spiriferella lita (Fredericks). Tazawa, 1979, p. 28, pl. 4, figs. 12-13; pl. 5, figs. 1-4, 6; Tazawa, 2000, fig. 3.9.

Material.—Seven specimens, from locality HMF2: (1) external cast of a ventral valve, NU-B451; (2) external mould and casts of three dorsal valves, NU-B452-454; (3) external casts of three dorsal valves, NU-B455-457.

Description.—Shell medium size for genus, transversely trapezoidal in outline; cardinal extremities blunt, produced; hinge straight, equal to widest part; length about 40 mm, width 68 mm+ in a dorsal valve specimen (NU-B457); length about 27 mm, width 43 mm in the best preserved dorsal valve specimen (NU-B452). Ventral valve having a deep, wide, V-shaped and smooth-bottomed sulcus and 5 strong, simple costae on each side of sulcus. Dorsal valve moderately convex in both lateral and anterior profiles, with a high fold and 5-6 simple or slightly bifurcated costae on each side of fold; fold having a median groove.

Remarks.—*Spiriferella lita* (Fredericks, 1924), originally described from the Middle Permian of Ussuri, South Primorye, is characterized by its strong and simple costae on the ventral valve, especially the enormously large costae on both sides of the sulcus. The material available consists of a fragmentarily preserved ventral valve and six incomplete dorsal valves. These specimens can be assigned to *S. lita* on account of their large, transverse shells with strong and simple costae on the ventral valve.

Spiriferella keilhavii (von Buch, 1846), from the Middle Permian of Bear Island, is also a large, transverse *Spiriferella*, but it differs from *S. lita* by its weakly fasciculate costae on both valves.

Distribution. — Middle Permian (Murgabian-Midian) of eastern Russia (South Primorye) and Japan (South Kitakami and Hida Gaien Belts).

Genus ***Alispiriferella*** Waterhouse and Waddington, 1982

Type species.—*Spiriferella ordinaria* Einor, 1939.

Alispiriferella ordinaria
(Einor, in Licharew and Einor, 1939)

Figure 8.14a-8.14c

Spirifer (*Spiriferella*) *keilhavi* var. *ordinaria* Einor, in Licharew and Einor, 1939, p. 140, pl. 23, figs. 6, 7; pl. 24, figs. 1a-d.
Spiriferella ordinaria Einor. Nelson and Johnson, 1968, p. 738, pl. 95, figs. 5, 6; pl. 96, figs. 4-6; text-figs. 10, 13a; Bamber and Waterhouse, 1971, pl. 15, figs. 10, 12-14; Waterhouse *et al.*, 1978, pl. 2, figs. 6-8.

Alispiriferella ordinaria (Einor). Waterhouse and Waddington, 1982, p. 30, pl. 2, figs. 7-13; text-figs. 11i, j, 20; Abramov and Grigorjeva, 1988, p. 158, pl. 22, figs. 7a-g; pl. 25, figs. 4, 5; Shi and Waterhouse, 1996, p. 133, pl. 25, figs. 11-15; text-fig. 46.

Material.—Two specimens, from locality HMF12: (1) external and internal moulds of a ventral valve, NU-B458; (2) external mould of a dorsal valve with internal moulds of a conjoined valve, NU-B459.

Description.—Shell small to medium for genus, slightly wider than long, subpentagonal in outline, with greatest width at hinge; length about 31 mm, width about 37 mm in the better preserved specimen (NU-B458).

Ventral valve moderately convex in lateral profile, most convex at posterior third of shell length; cardinal extremities blunt, produced; interarea moderately high, triangular in shape and slightly concave; sulcus deep and having smooth, broad, V-shaped bottom; 4 pairs of broad, rounded, simple or bifurcated costae on ventral valve. Dorsal valve having a low fold, with a deep, wide, flat-bottomed median groove for almost entire length; 4 pairs of bifurcated or trifurcated costae on dorsal valve.

Ventral valve interior with a pair of high dental plates and a deeply impressed heart-shaped muscle field. Other internal structures not observed in the present material.

Remarks.—The Moribu specimens are not so well preserved but they can be identified with *Alispiriferella ordinaria* (Einor, 1939) by their small, slightly wider subpentagonal shell, with weakly bundled costae on both ventral and dorsal valves. This species was originally described by Einor (in Licharew and Einor, 1939) from the Lower Permian of Novaya Zemlya, and afterwards redescribed by Waterhouse and Waddington (1982) as the type species of the genus *Alispiriferella.*

Distribution. — Lower Permian (Asselian) to Middle Permian (Murgabian) of the Arctic Russia (Novaya Zemlya, western Verkhoyansk Range), northern Canada (Yukon Territory) and central Japan (Hida Gaien Belt).

Alispiriferella japonica sp. nov.

Figure 8.15-8.18

Spiriferella sp. Horikoshi *et al.*, 1987, p. 142; Tazawa, 1987, text-figs. 1.1, 1.3.

Alispiriferella sp. Tazawa, 2000, fig. 3.8.

Material.—Fourteen specimens, from localities HMF1, 2, 5, 8, 14, 16: (1) external mould of a conjoined valve, NU-B460; (2) external and internal moulds of three ventral valves, NU-B461 (holotype), 462, 463; (3) external moulds of eight ventral valves, NU-B464-471; (4) internal moulds of two dorsal valves, NU-B472, 473.

Diagnosis.—Small, transversely much wider *Alispiriferella* with alate cardinal extremities, smooth ventral sulcus and coarse, simple and rounded costae on both valves.

Description.—Shell small for genus, alate, transversely subquadrate in outline, with greatest width at hinge; length 21 mm, width 39 mm in the largest specimen (NU-B465); length 18 mm, width about 32 mm in the holotype (NU-B461).

Ventral valve strongly convex in lateral profile, most convex at umbonal region; umbo well extended and strongly incurved; interarea moderately high, nearly triangular in shape; cardinal extremities slightly produced; sulcus deep and wide, having smooth, rounded bottom; costae broad and simple with rounded crest, numbering 4-5 on each flank of ventral valve. Dorsal valve moderately convex in lateral profile; fold originating at beak and having a narrow but distinct median groove, which extends from umbo to anterior margin; each flank having 3-4 coarse, simple and rounded costae.

Ventral valve interior with high dental plates and a deeply impressed heart-shaped muscle field; the latter is longitudinally striated and divided into two parts by a low ridge with a median narrow groove. Dorsal valve interior obscure in the present material.

Remarks. — *Alispiriferella japonica* sp. nov. is distinguished from *Alispiriferella ordinaria* (Einor, 1939) by its more alate and wider outline, smooth noncostate ventral sulcus and coarse, simple costae on both valves.

The present species somewhat resembles *Alispiriferella* sp. Yanagida (1996, figs. 2.2, 2.4) from the Middle Permian Tsunemori Formation of Akiyoshi, southwest Japan in having transverse shell, broad, simple costae on both valves, and dorsal fold with a narrow median groove. The Akiyoshi species is unfortunately represented by only two incomplete specimens, and an accurate comparison is therefore hampered.

Alispiriferella gydalensis (Zavodowsky, 1968, p. 159, pl. 46, fig. 1) from the Middle Permian Omolon Horizon (correlated with the Kungurian) of the Kolyma River region, northeastern Siberia, differs from *A. japonica* in having a much larger shell and dorsal fold with a wide, shallow median groove.

Order Terebratulida Waagen, 1883
Suborder Terebratulidina Waagen, 1883
Superfamily Dielasmatoidea Schuchert, 1913
Family Dielasmatidae Schuchert, 1913
Subfamily Dielasmatinae Schuchert, 1913
Genus **Dielasma** King, 1859

Type species. — *Terebratulites elongatus* Schlotheim, 1816.

Dielasma sp.

Figure 8.27, 8.28

Material.—Two specimens, from locality HMF3, external moulds of two ventral valves, NU-B474, 475.

Description. — Shell medium size for genus, elongate subpentagonal in outline, almost flat to slightly concave in both lateral and anterior profiles; length 29 mm, width 15 mm in the larger specimen (NU-B474). Ventral valve with narrow but distinct median fold, originating slightly anterior to umbo and extending to anterior margin. External surface of ventral valve smooth.

Remarks. — This species may be a new species of *Dielasma*. The Moribu species resembles *Dielasma* sp. B, described by Yang *et al.* (1962, p. 118, pl. 46, figs. 8a-c) from the Middle (?) Permian of Qilianshan Mountains, Qinghai, northwest China, in size and shape of the ventral valve and in having a narrow, distinct median fold on the ventral valve.

Dielasma biplex Waagen (1882, p. 349, pl. 25, figs. 3-5) from the Wargal Formation of the Salt Range also has a narrow median ventral fold, but it is clearly distinguished from the Moribu species by its strongly convex ventral valve.

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A phosphatized cephalopod mouthpart from the Upper Pennsylvanian of Oklahoma, U.S.A.

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Abstract. An exceptionally well-preserved cephalopod mouthpart was discovered in a phosphate concretion from the lower Missourian (Upper Pennsylvanian) in Tulsa, Oklahoma, U. S. A. It consists of an almost complete jaw apparatus and a radula, both of which are in the living orientation. The black upper and lower jaws, preserved as phosphate, were probably chitinous. The lower jaw is slightly larger than the upper and is characterized by a widely open outer lamella. The upper jaw is built up of a large outer lamella and a short, scallop-shaped inner lamella; the former is distinctly divided into two portions in the posterior region. The radula is preserved in the anterior portion of the buccal cavity; it is made of more than ten rows of teeth, each consisting of seven tooth elements with a pair of marginal plates. The overall features of the jaws and radula are essentially similar to those described in association with ammonoids rather than nautiloids and coleoids, suggesting that this mouthpart can be referred to the Ammonoidea. However, the lower jaw in our specimen differs from previously described mandibles of Carboniferous Gastrioceratoidea, Neoglyphioceratoidea, Goniolobоceratoidea, and Dimorphoceratoidea in its less elongate outline. For this reason, we refer the cephalopod mouthpart to the Ammonoidea other than the above superfamilies with reservation.

Key words: Ammonoidea, cephalopod mouthpart, Oklahoma, Upper Pennsylvanian

Introduction

All exatnt cephalopods possess a well-developed buccal mass in the proximal portion of the digestive system. The organic hard tissues of the cephalopod buccal mass consist of upper and lower jaws (beaks or mandibles) and a radula, all of which are surrounded by well-developed jaw-radular musculature. Fossilized remains of jaws and radula are rarely found in body chambers of ectocochliate cephalopod shells, especially of ammonoids and in the soft tissue remains of coleoids (see Tanabe and Fukuda, 1999, for a recent review). As Mapes (1987) has briefly documented, the marine Carboniferous in the U.S. Midcontinent occasionally yields goniatite conchs preserving jaws and a radula within their body chambers (Saunders and Richardson, 1979; Tanabe and Mapes, 1995; Doguzhaeva *et al.*, 1997). These goniatites occur in carbonate and phosphate concretions, together with occasional isolated cephalopod jaws and even more rarely radulae. In this article, an exceptionally preserved cephalopod mouthpart from the Upper Pennsylvanian of Oklahoma is described and its possible taxonomic relationship is discussed on the basis of comparison with the jaws and radulae of extant and fossil cephalopods.

Material and its geologic setting

The cephalopod mouthpart examined was preserved as a nucleus in a small spherical phosphate concretion (ca. 15 mm in diameter) that was recovered by one of us (RHM) from the Lower Missourian (Upper Pennsylvanian) on the southern side of Tulsa, Tulsa County, Oklahoma. The concretion came from an approximately 3 m thick stratigraphic sequence that consists of three distinct black platy shales that were exposed at the northeast corner of the junction of the 71st Street and the U.S. Highway 75 in the southern part of Tulsa, Tulsa County, Oklahoma (SW1/4, SW1/4, sec. 2, T. 18 N., R. 12E.: Supulpa 71/2 minute quadrangle; Figure 1). These shales were deposited in marine water under oxygen-stressed conditions that occurred during three distinct times of marine transgression and regression (Boardman, personal commun., 2001). The stratigraphic

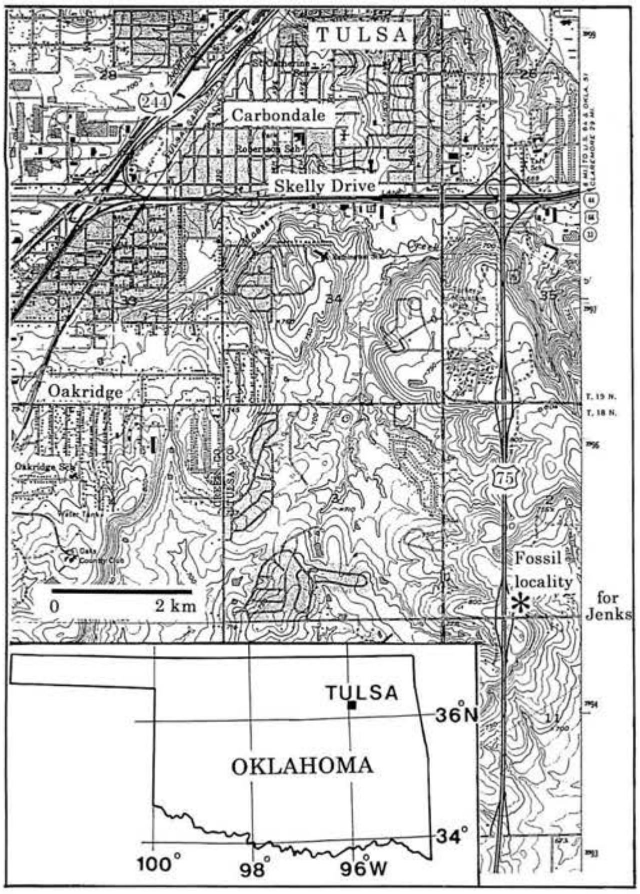


Figure 1. Index map of the southern part of Tulsa, Oklahoma, showing the locality of the cephalopod mouthpart remain examined.

assignment by Boardman *et al.* (1995, see localities OKM-28 and 56, p.86, although the reported coordinates they provide are incorrect) places these shale units in the lowest three cycles of the basal Missourian in the northern Midcontinent. All of the shales belong to the Coffeyville Formation, and the stratigraphic assignments for the three shale beds from oldest to youngest are the basal Tacket Shale, the lower Tacket Shale (= Mound City Member, Hertha Formation of Kansas) and the upper Tacket Shale (= Huspuckney Member, Swope Limestone of Kansas).

The exposure originally extended laterally for about 100 m and was covered by thousands of phosphate concretions that were eroding from the three black platy shales. Initial collections were made of the loose specimens on the surface without regard to stratigraphic position. In about 1990, prior to a field expedition to recollect and sample the exposure stratigraphically, the Oklahoma Highway Department of Transportation grassed the exposure, and it is not collectable at this time.

The cephalopod mouthpart specimen examined is housed in the Zoological Collection of Ohio University (OUZC).

Notes on preservational conditions

It has been reported that some phosphate concretions from some Carboniferous Midcontinent black shales contain both mineralized skeletal material (bones and shells) and less commonly preserved softer organs (cephalopod mouthparts) of invertebrates (for mouthpart reports see Closs, 1967; Mapes, 1987; Tanabe and Mapes, 1995; Dogushaeva *et al.*, 1997). The reasons why and how phosphate preserves the soft tissue remains in this geologic setting has not been addressed. Because of the lack of *in situ* phosphate concretions from this Oklahoma locality, a detailed study of these specimens to solve the above problems is not warranted at this time. However, it is possible to make some general exterior and internal observations about the concretions from this exposure to help explain the preservation.

There are five concretion types classified on the basis of shape (flat and spheroidal) and on surface texture (smooth, rough, and bioturbated). The five concretion types are: 1) spheroidal with a smooth exterior, 2) flat with a smooth exterior, 3) spheroidal with a rough exterior, 4) flat with a rough exterior, and 5) bioturbated nodules which bear no body fossils. The cephalopod mouthparts that form the basis of this paper and most of the fossil material from this locality are preserved in the type 1 concretions. Although no systematic characterization of the nodule types was linked to the outcrop stratigraphy during initial collections in the early 1990s, the lowest shale (basal Tacket Shale Member) appeared to contain the most fossiliferous concretions.

The internal fabric of the concretions probably controls the surface texture and one of these fabrics lent itself particularly well to fossil preservation. Fecal pellets are common in these coprolite-dominated phosphate nodules. Both of the smooth-surfaced concretions (types 1 and 2) have a tightly packed, pelletal fabric without interstitial calcite cement; whereas, the two rough-surfaced types contain loosely

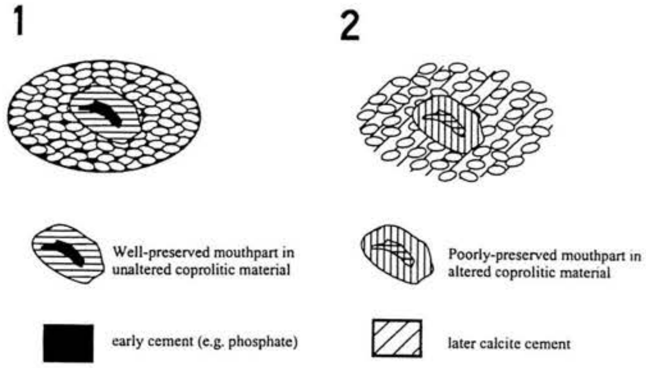


Figure 2. Schematic illustration of pelletal coprolites. **1.** Tightly packed pelletal fabric that was cemented early enough to favor high-quality fossil preservation. **2.** Calcite-cemented and loosely packed fabric that resulted in a rough surface exterior. Relatively poor fossil preservation characterizes these concretions probably because of later calcite cement that precipitated with infiltration of fluids that altered the coprolite and its enclosed fossils.

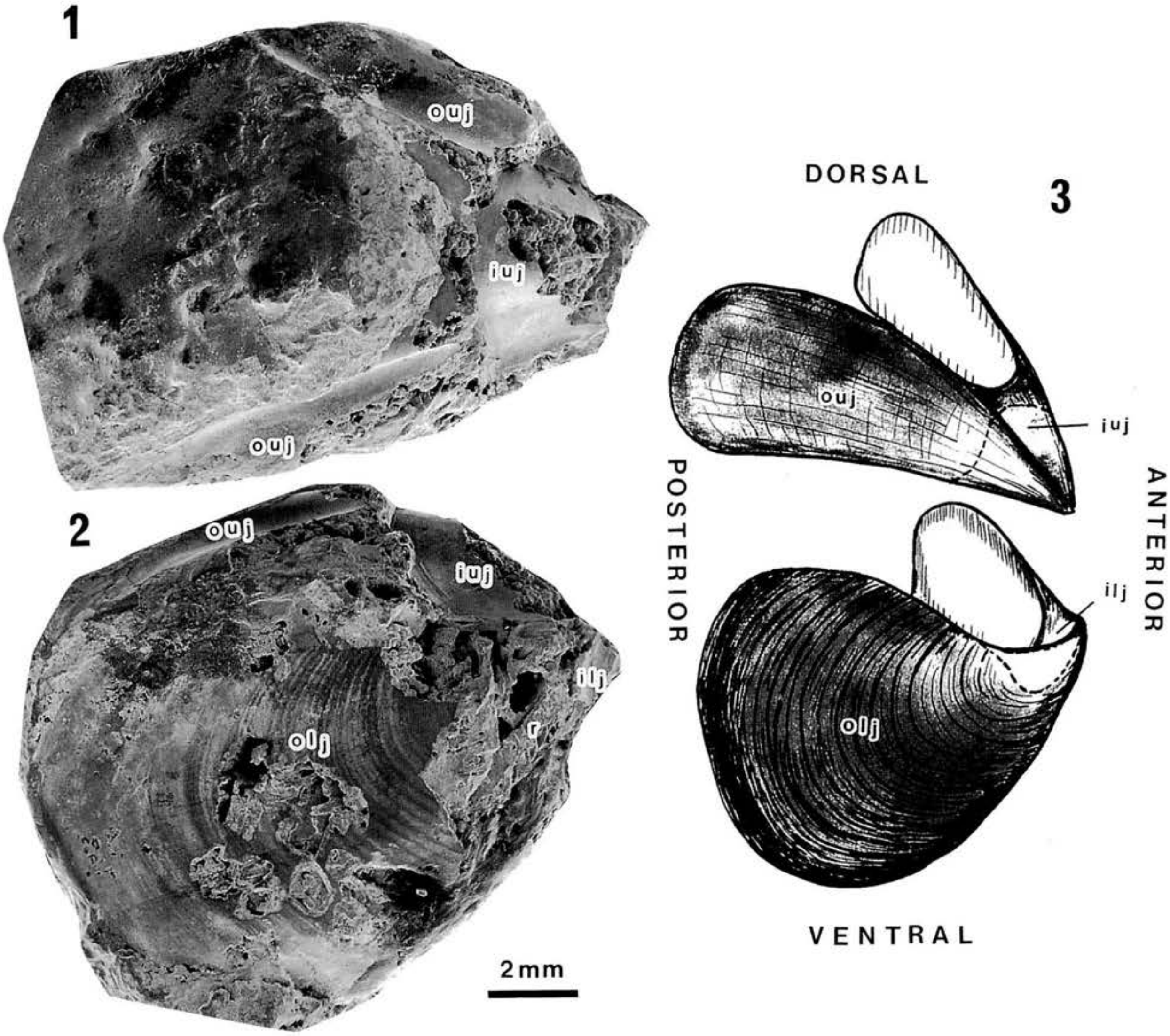


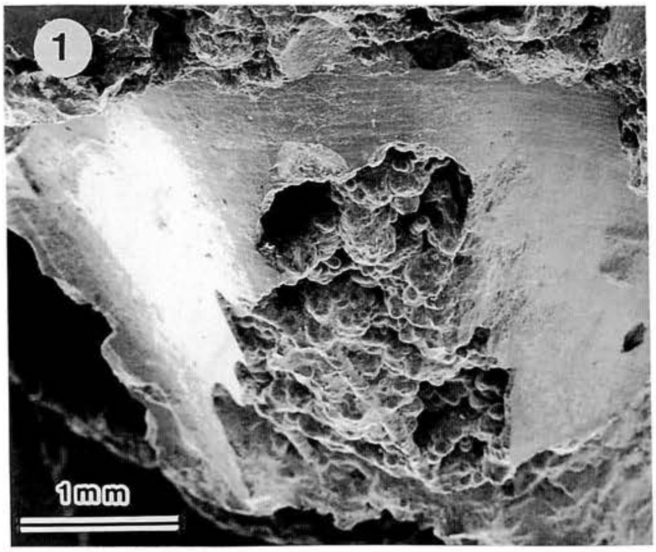
Figure 3. Dorsal (1) and left lateral (2) views of the phosphatized cephalopod mouthpart examined, and the reconstructed diagram of the jaw apparatus (anterolateral view) (3). Ohio University Zoological Collection, OUZC 4001. Abbreviations. ouj: outer lamella of upper jaw, iuj: inner lamella of upper jaw, olj: outer lamella of lower jaw, ilj: inner lamella of lower jaw, r: radula.

packed pellets and conspicuous interstitial calcite cement. The tight packing of pellets probably resulted in part from rapid, early diagenetic phosphate cementation of these concretions that sealed the concretions and favored high-quality fossil preservation by restricting entry of later pore fluids (Figure 2.1). Softness of pellets may also be a preservational factor, but analysis for that is beyond the scope of this report. The calcite cementation and loose packing of the rough concretions which contain poorly preserved fossils are interpreted as the result of infiltration of later diagenetic fossil-altering fluids (Figure 2.2).

Based on these observations, it seems apparent that the mode of phosphate and carbonate preservation will control some of the preservational potential of cephalopod mouthparts. However, detailed studies of carefully collected concretions will be required to resolve some of these preservational variables.

Description of the cephalopod mouthpart

Methods of observations.—The cephalopod mouthpart from the Tacket Shale (Tacket specimen) was coated with platinum and examined by means of a Hitachi model S2400 scanning electron microscope. SEM images of the jaws and radula were transferred to a desktop computer via a PCI interface, and different portions of them were reorganized into a few images using imaging software (Quartz PCI and Adobe Photoshop, Ver. 5). They were printed out using a high-resolution digital photo-printer (Fuji Film Pictrography, model 3500).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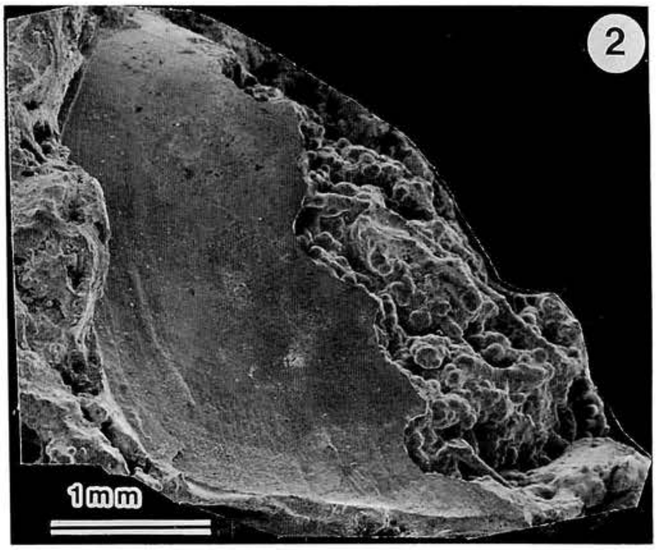
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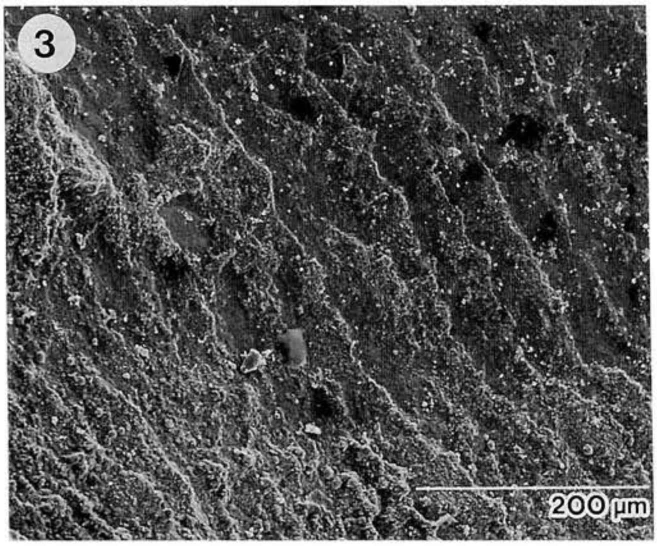
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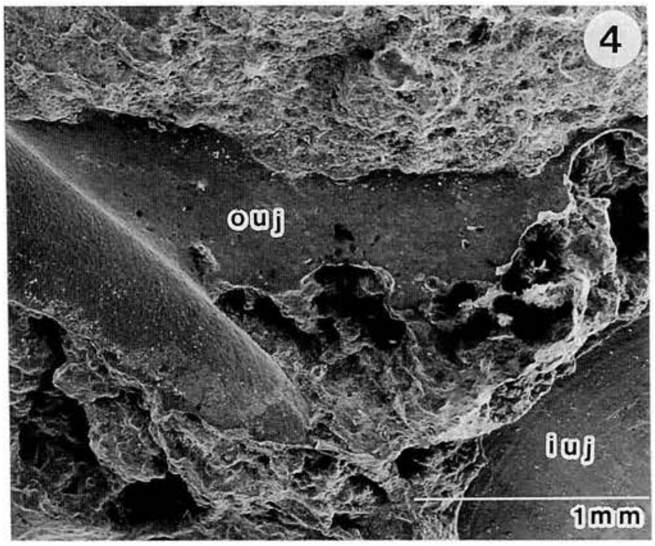
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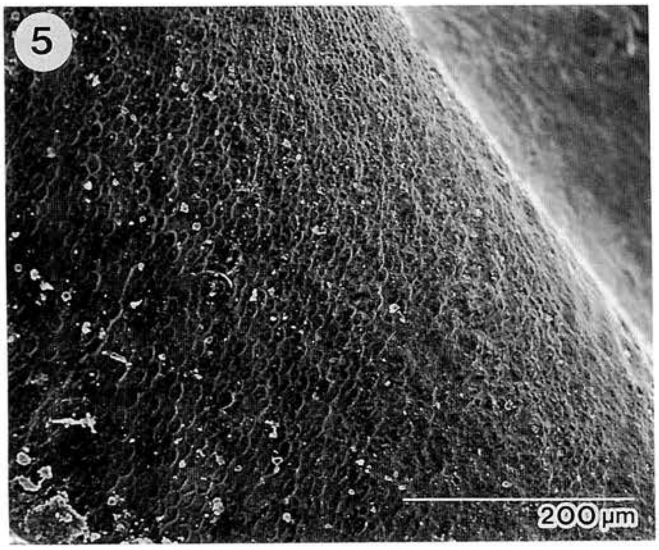
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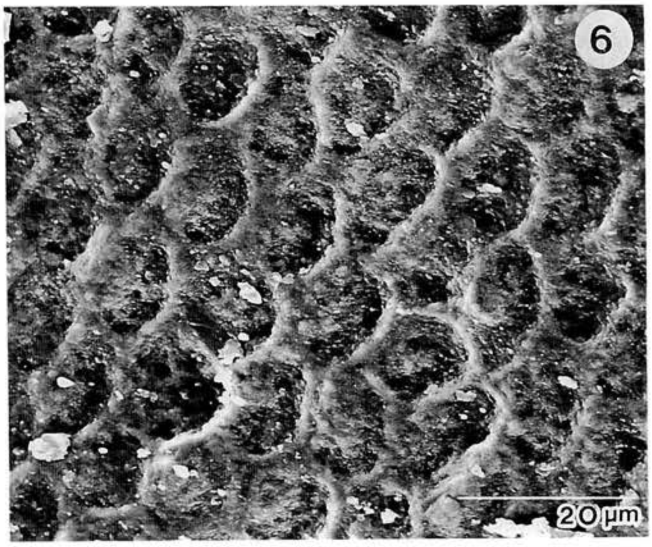
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For determination of upper and lower jaws, we follow the criteria described by Lehmann (1976, 1990), Nixon (1988a, 1996), and Tanabe and Fukuda (1999), who relied upon the comparison with the jaws of extant cephalopods.

Overall morphology.—The Tacket specimen, of about 11.5 mm maximum length and 7 mm width, consists of an almost complete jaw apparatus and a radula (Figure 3.1, 3.2). The ventral margin of the upper jaw fits well with the dorsal margin of the lower jaw. The anterior portion of the lower jaw is partly eroded and/or corroded, and where the mandible is missing, a radular ribbon is exposed in the buccal cavity between the jaws (**r** in Figure 3.2). These observations indicate that the jaws and radula have been fossilized by keeping their original life orientation as a complete buccal mass.

Upper jaw.—The upper jaw is made of a black material which was probably originally chitinous. It consists of a large outer lamella and a short inner lamella, which are joined in the anterior portion; the former, though the anterior portion is missing due to weathering, is distinctly divided into two wing portions in the posterior region (Figure 3.1). The open angle of the wings is about 45°. The dorsal margin of the paired wing portions exhibits a sharp ridge-like elevation. This elevation can be traced to the anterior portion where two wing portions are connected by a slightly concave outer lamellar element (Figure 4.4). The inner shorter lamella is scallop-shaped and is prominently convex dorsally (Figure 4.1, 4.2). The anterior portion is partly missing, but the reconstructed outline suggests that this portion appears to be sharply pointed (Figure 3.3). The inner lamella is ornamented with dense concentric lirae (Figure 4.1-4.3). The outer lamella lacks growth lines and instead retains a delicate pattern represented by numerous honeycomb-like polygonal pits (Figure 4.5, 4.6). Each pit, about 8-12 µm diameter, is surrounded by a sharp ridge (Figure 4.6). In view of their shape and distribution, these pits are undoubtedly comparable to the anchor-type polygonal imprints of columnar cells (becublasts) that are present on the outer side of the upper jaw and on the inner side of the lower jaw in extant coleoids (Dilley and Nixon, 1976).

Lower jaw.—As in the upper jaw, the lower jaw is made of a black, probably originally chitinous material without any trace of a calcareous element. It is slightly larger than the upper jaw (Figure 3.2), and consists of a large outer lamella and a short inner lamella, though the inner one is partly visible from outside in the eroded anterior buccal cavity (**ilj**; Figures 3.2, 3.3). The two lamellae are connected to each other in the anterior portion. The outer lamella is curved posteriorly, with an open angle of about 50 degrees. Its outer surface is sculptured by regular-spaced, concentric undulations, which become finer and denser toward the posterior margin (Figure 3.2).

Radula.—The exposed radula comprises a total of 13 rows of teeth, retaining their original orientation. Each transverse row, about 2.5 mm wide, consists of seven tooth elements (a central rhachidian tooth, two paired lateral teeth, and a pair of marginal teeth), with a pair of marginal plates (Figures 5.1, 5.2). The shape of the rhachidian tooth is unclear because it is hidden by lateral teeth. The paired inner and outer lateral teeth are unicuspid, asymmetrical in frontal view and project markedly toward the anterodorsal side; the former is much shorter than the latter. The paired marginal teeth are the longest in the tooth elements and unicuspid as are the lateral teeth. The marginal plate has an oval outline.

Taxonomic relationships

The isolated cephalopod mouthpart from the Tacket Shale exhibits several characteristic features including 1) a radula consisting of a total of seven tooth elements in each row, 2) an upper jaw being build up of a short, scallop-shaped inner lamella and a large outer lamella that is distinctly divided into two portions in the posterior region, 3) a lower jaw being made of a widely open outer lamella and a shortly reduced inner lamella, 4) absence of a calcareous jaw element, and 5) presence of coleoid-type polygonal imprints of beccublasts on the upper jaw lamella. These observations provide a reliable basis to infer the taxonomic relationship of the mouthpart owner by comparison with the radulae and jaws of extant and fossil cephalopods (Table 1). The upper jaw in our specimen is distinguished from those of extant coleoids and *Nautilus* in that the outer and inner lamellae of the latter are never divided into two wing portions (Clarke, 1986; Nixon, 1988a, b; Tanabe and Fukuda, 1999). Among the extant and fossil cephalopods, upper jaws with paired lamellae are only known from ammonoids (Tanabe and Fukuda, 1999, fig. 19.3). The three-dimensional architecture of the upper jaws of Goniatitina and Ceratitina is still unclear due to relatively poor fossil preservation. Bandel (1988, fig. 6) and Zakharov (1974, fig. 2B), respectively, reconstructed the upper jaws of the Upper Paleozoic goniatite (*Eoasianites*) and the early Triassic ceratite (*Olenekites)*, as consisting of a widely opened, well-developed outer lamella and a short, reduced inner lamella. Later, Doguzhaeva *et al.* (1997) interpreted that the upper jaw of *Girtyoceras* (Carboniferous Goniatitina) is made of a large inner lamella and a short outer lamella, though they did not present an illustration showing this construction. The structure of the upper jaw in the Tacket specimen correlates well with the reconstruction of the upper jaws of goniatites and ceratites by Bandel (1988) and Zakharov (1974). Unlike the upper jaws of Goniatitina and Ceratitina, those of most Jurassic and Cretaceous ammonoids consist of a large inner lamella with paired lateral walls and a short, reduced outer lamella, though the two lamellae appear to be united as a single lamella in Late Cretaceous Ancyloceratina (e. g. *Jeletzkytes*;

← **Figure 4.** Upper jaw of the phosphatized cephalopod mouthpart examined. 1, 2: Anterior (frontal) (1) and right lateral (2) views of the scallop-shaped short inner lamella with concentric fine lirae. 3: Closeup of 2, showing the fine concentric lirae. 4. Part of anterior portion showing the outer lamella (ouj) with a strong lateral ridge and marginal portion of the inner lamella (iuj). 5. Outer surface of the left lateral portion of the outer lamella ornamented with numerous honeycomb-like imprints of beccublasts. 6. Closeup of imprints of beccublasts on the jaw plate, each surrounded by a sharp ridge.

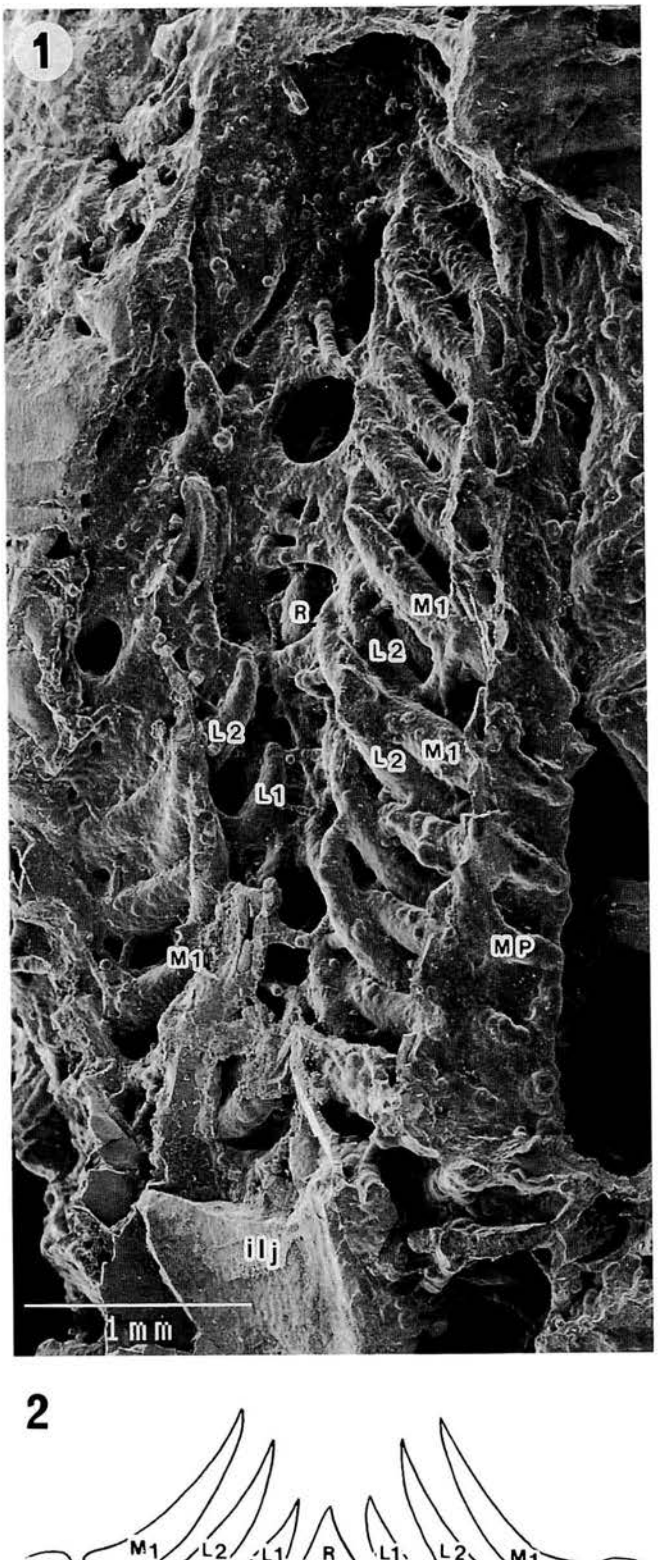

Figure 5. 1. Anterior view of the radular ribbon preserved in the buccal cavity which is partly covered with the inner lamella of the lower jaw (ilj). 2. Diagram showing the frontal view of a transverse row of the radula. Abbreviations. R: central rachidian tooth, L1: inner lateral tooth, L2: outer lateral tooth, M1: marginal tooth, MP: marginal plate.

Table 1. Comparison of the morphological features of buccal structure in extant and fossil cephalopods (modified from Tanabe and Fukuda, 1999).

	Upper jaw elements		Lower jaw elements			Beccublast imprints	Radular teeth in each row
Cephalopod taxa	Rostrum	Lamellae	Rostrum	Inner lamella	Calcite cover		
Recent *Nautilus*	calcified	non-divided	calcified	shortly reduced	partly present	micropores	9
Recent Coleoidea	non-calcified	non-divided	non-calcified	projected posteriorly	absent	polygonal pits	7
Ammonoidea							
Goniatitina	non-calcified	divided	calcified?	shortly reduced	absent	polygonal pits	7
Ceratitina	non-calcified	divided	non-calcified	shortly reduced	absent	unknown	unknown
Phylloceratina	unknown	unknown	calcified	shortly reduced	absent	unknown	unknown
Lytoceratina	unknown	unknown	calcified	shortly reduced	absent	polygonal pits	unknown
Ammonitina	non-calcified	non-calcified	non-calcified	shortly reduced	present or absent	polygonal pits	7
Ancyloceratina	non-calcified	non-calcified	non-calcified	shortly reduced	present	unknown	7
Present specimen	non-calcified	non-calcified	non-calcified	shortly reduced	absent	polygonal pits	7

Landman and Waage 1993, figs. 37, 39-41; *Subptychoceras;* Tanabe and Landman, 2001, text-fig. 2. 6).

The lower jaw of the Tacket specimen is similar in the development of a large outer lamella to those of Upper Paleozoic Goniatitina such as *Eoasianites* (Neoicoceratoidea, Neoicoceratidae; Closs, 1967, fig. 4; Bandel, 1988, fig. 6), *Cravenoceras* (Neoglyphioceratoidea, Cravenoceratidae; Mapes, 1987, fig. 3.3, 3.4; Tanabe and Mapes, 1995, figs. 2-2, 3), *Wiedeyoceras* (Gonioloboceratoidea, Wiedeyoceratidae; Saunders and Richardson, 1979, fig. 7), and *Girtyoceras* (Dimorphoceratoidea, Girtyoceratidae; Doguzhaeva *et al.*, 1997, fig. 4), but in the latter, the outer lamellae are much more elongated posteriorly than in the former (we follow Bogoslovskaya *et al.*, 1999 for higher taxonomy of each genus). The lower jaw of an indeterminate goniatite (not *Girtyoceras limatum* as reported in Doguzhaeva *et al.*, 1997, fig. 2C, D) possesses a calcified rostrum, but such calcification has not yet been observed in the lower jaws of other Goniatitina and the Tacket specimen.

The radula in the Tacket specimen is allied to those of Goniatitina (e.g. *Eoasianites;* Lehmann, 1976, fig. 72; Tanabe and Mapes, 1995, figs. 2-4, 4-2; *Cravenoceras*; Tanabe and Mapes, 1995, figs. 2-3, 4-1; *Girtyoceras*; Doguzhaeva *et al.*, 1997, figs. 5A, 6A) in the number of tooth elements in each row and the overall shape of each tooth, though there are some variations in the relative length of marginal and lateral teeth. Also, polygonal imprints of beccublasts observed in the upper jaw of our specimen have been found on the upper jaw lamella of *Girtyoceras* (Doguzhaeva *et al.*, 1997, figs. 5B) as well as on the inside surface of the lower jaws of *Gaudryceras* (Cretaceous Lytoceratina; Tanabe and Fukuda, 1983, figs. 2, 3) and an unidentified aspidoceratid (Upper Jurassic Ammonitina; Tanabe and Fukuda, 1999, fig. 19.5D).

To summarize the above comparison, the overall features and structure of the jaws and radula in the Tacket specimen show an affinity to those described from the Upper Paleozoic Goniatitina, although, there is a marked difference in the lower jaw shape of the Tacket specimen and other described goniatite mandibles. Because of this difference in lower jaw shape, we refer the Tacket cephalopod mouthpart to the Ammonoidea and to a superfamily other than the Gastrioceratoidea, Neoglyphioceratoidea, Gonioloboceratoidea, and Dimorphoceratoidea with reservation.

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Taxonomic and phylogenetic aspects of the shell ultrastructure of nine Cretaceous rhynchonellide brachiopod genera

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Abstract. The shell ultrastructure of nine Cretaceous rhynchonellide brachiopod genera was studied using SEM with the purpose of finding additional criteria for the taxonomy and phylogeny of Late Cretaceous rhynchonellides. The genus *Orbirhynchia* is characterized by a coarse fibrous basiliolidine type structure of the secondary shell. The genera *Cyclothyris, Cretirhynchia, Septatoechia, Belbekella, Lamellaerhynchia, Almerarhynchia*, *Burrirhynchia* and *Grasirhynchia* have a fine fibrous rhynchonellidine type structure. An outline of some diagnostic characteristics for each genus is presented. Some diagenetic alterations of the shell, such as silicification and recrystallization are also discussed.

Key words: Cretaceous, rhynchonellide brachiopods, shell ultrastructure, systematics

Introduction

Over the last four decades the shell ultrastructure of brachiopods has been extensively studied in order to throw light on the process of biomineralization. Since the contributions of Williams (1968a,b), MacKinnon (1974), and Smirnova (1984) shell ultrastructure has been used as an additional criterion for taxonomic and phylogenetic purposes. Shell ultrastructure of some Mesozoic rhynchonellides has been sporadically studied since the 1970's: Triassic - by Dagys (1974), Michalik (1993); Jurassic - by Baker (1971), Kamyshan (1977, 1986), Kamyshan and Adel (1979), Taddei Ruggiero and Ungaro (1983); Lower Cretaceous - by Smirnova (1984).

The shell ultrastructure of Late Cretaceous rhynchonellide brachiopod genera is poorly known. For the first time Nekvasilova (1974) briefly mentioned differences in the mosaic elements between the Late Cretaceous genera *Orbirhynchia* Pettitt and *Cretirhynchia* Pettitt. A short summary on some Late Cretaceous representatives from the Lesser Caucasus was published by Ali-zade *et al.* (1981), but without any illustrations. Gaspard (1990a, 1990b, 1996 etc.) published some illustrations of the microstructure of several species of the genus *Cyclothyris* McCoy, with emphasis on the growth patterns and effects of diagenesis. Motchurova-Dekova (1992) reported preliminary results on the shell ultrastructure of the genera *Cyclothyris* and *Orbirhynchia*. Recently the ultrastructure of some representatives of *Erymnaria* Cooper and the new genus *Costerymnaria* Motchurova-Dekova and Taddei Ruggiero was studied (Motchurova-Dekova and Taddei Ruggiero, 2000). The purpose of this paper is to describe the shell microstructure of additional Cretaceous rhynchonellide genera with emphasis on Late Cretaceous representatives. New characters are found, increasing the possibility of using shell microstructure as an additional criterion in taxonomy and phylogeny.

Material and methods

A comparative ultrastructural SEM analysis has been carried out on nine Cretaceous rhynchonellide genera. Depending on the available material, some genera were investigated extensively (*Orbirhynchia, Cyclothyris, Cretirhynchia, Septatoechia*), while others were examined briefly for comparative purposes (*Belbekella, Lamellaerhynchia, Almerarhynchia*, *Burrirhynchia, Grasirhynchia*). This preliminary study aims at discerning only certain general features. More detailed results will be published later.

Of importance in any ultrastructural comparison is the need for consistency in the location of longitudinal and transverse sections of adult shells. The sections should be the same for all specimens in order to be able to compare the ultrastructural details between different specimens.

For the present study SEM analyses were carried out on fifty transverse shell sections from thirty-four specimens belonging to twenty-nine species of nine Cretaceous rhynchonellide genera. In most specimens usually only two very close transverse sections of both valves were observed for each specimen. The sections were cut perpendicular to the plane of symmetry. Following the recommendation of Sass and Monroe (1967) the sections were made at the maximum width of the valves. In some specimens one of the sections was made more posteriorly and crossed the muscle field. Longitudinal sections in the plane of symmetry, made before this study, gave only general information about the thickness of the shell and the calcitic layers along the shell length and the length of the fibres.

The primary layer was normally affected by diagenetic processes and/or was not well preserved. Thus the characteristics of the secondary layer were mainly used as diagnostic features. The measurements of the cross-sections of fibres were taken in the central part of the transverse section. Because the long axes of fibres are usually inclined to the shell surface at about 10°, the real values of the width and thickness of the fibres presented here could be slightly overestimated. This usually holds true for all measurements taken, so principally it should not affect the way of comparison because similar values are compared.

The longer axis in the cross-sections of the fibres, usually parallel to the shell surface, is the **width (W)** of the fibre; the shorter axis, perpendicular to the longer axis, is the **thickness (T)** of the fibre. A **coefficient "C"** is introduced here representing the ratio between the width and the thickness of the fibre in the cross-section. "**C_1**" is the ratio W/T in the larger fibres, which usually make up the main part of the shell. "**C_2**" is the ratio W/T of the thinner fibres, usually building the outer or the innermost sublayer of fibres in the shell, or forming thin bands of finer fibres inside the section. The shape of the cross-sections of the fibres and the differentiation of the secondary layer were used as additional diagnostic criteria. The reported **W** and **T** values, measured at the central part of the maximum width section of each specimen, were compared. The range of their variation (lowest and highest values) was taken into consideration.

The following is a brief summary of the results. Detailed data about the occurrences of the mentioned species can be found in the cited references. When a species is first mentioned here, the name of the collection is given and open nomenclature is used in some cases. Abbreviations: NHM - Natural History Museum London; NMNHS - National Museum of Natural History-Sofia.

Observations and results

All studied fossil rhynchonellides are impunctate and composed of two calcitic layers - primary microgranular and secondary fibrous (Figure 1A). The previously described tertiary prismatic layer in the genus *Cyclothyris* (Motchurova-Dekova, 1992, 1994) was not observed. Extensive SEM observations showed instead that a row of large calcite prisms, perpendicular to the internal surface was developed in many specimens. Though they look like a prismatic layer, they are a result of diagenetic calcite formation (Figures 1B, 2A, D). Recrystallized diagenetic calcite prisms forming a pseudo-tertiary layer were also observed in lenses in the interior of the secondary layer (Figure 5B). Such extensive SEM observations of the diagenetic alterations of the shell and the observation of this type of pseudo "tertiary layer" which is a result of secondary diagenetic processes, call into question the report of a tertiary layer in some rhynchonellides.

The **periostracum** is rarely preserved in fossil material. Gaspard (1982) reported a remarkable preservation of the organic cover of the Cretaceous terebratulid *Sellithyris*. Casts of periostraca on the external shell surface of living and fossil brachiopods are more frequently found. In the course of the present study neither of the above states of preservation of the periostracum were observed. However, in a particular spot of a transverse section of *Cyclothyris difforms*, the primary microgranular layer is overlain by an extremely thin calcite layer, only 2-10 µm thick (Figure 1D-F). It could be possibly interpreted as a diagenetically formed calcitic pseudomorph on the organic periostracum.

The **primary layer** is composed of isometric or elongate microgranular calcitic prisms perpendicular or slightly inclined to the shell surface. In most specimens the primary layer is fully or partly recrystallized (Figure 3F). It is interesting to note that in shells affected by strong silicification the primary layer is usually not silicified (Figure 1C, D). This is because the primary layer is not porous and is more compact than the fibrous layer when the organic sheets in the secondary layer are dissolved during early diagenesis.

The **secondary layer** is built up of fibres with long axes subperpendicular to the growth lines of the shell. The fibres display variable shapes in cross-section. The shape may be rhomboidal or parallelogram with variously outlined sides and angles (Figure 2E); or may have an anvil-like outline, formed by two arcs - larger and smaller, connected laterally by two sides; or the small arc can be missing (Figures 3F, 5D). Those species characterized by more isometric rhombic cross-sections of the fibres have lower values of the coefficient C, whereas species with fibres that are anisometric (elongate) anvil-like or rhombic in sections have higher values of C. In some specimens the secondary layer is strongly silicified (Figures 1B, 5F). When the silicification is not complete, siliceous pseudomorphs of the organic sheets are observed, representing a high relief silica grid enveloping the fibres (Figure 1E, 2E). In this case it is considered that the fibres, although recrystallized, have preserved their original shape.

Orbirhynchia Pettitt, 1954

Seven species of *Orbirhynchia* were studied: *Orbirhynchia reedensis* (Etheridge), (Figure 2C), Upper Turonian, described in Nekvasilova (1974); *O. mantelliana* (J. de C. Sowerby), Middle Cenomanian (Coll. Eric Simon, Cran d'E cailles); *O.* aff. *mantelliana*, *O.* aff. *boussensis* Owen (Figure 2E), *O. parkinsoni* Owen, *O. wiesti* (Quenstedt), Cenomanian (Motchurova-Dekova, 1996), and *Orbirhynchia* sp.1, Bulgaria, Lower Maastrichtian (Coll. NMNHS). The shell is relatively thin - 300-400 µm. The primary layer is rarely preserved, 20-40 µm thick and usually recrystallized. The secondary layer is built up of fibres that are anisometric

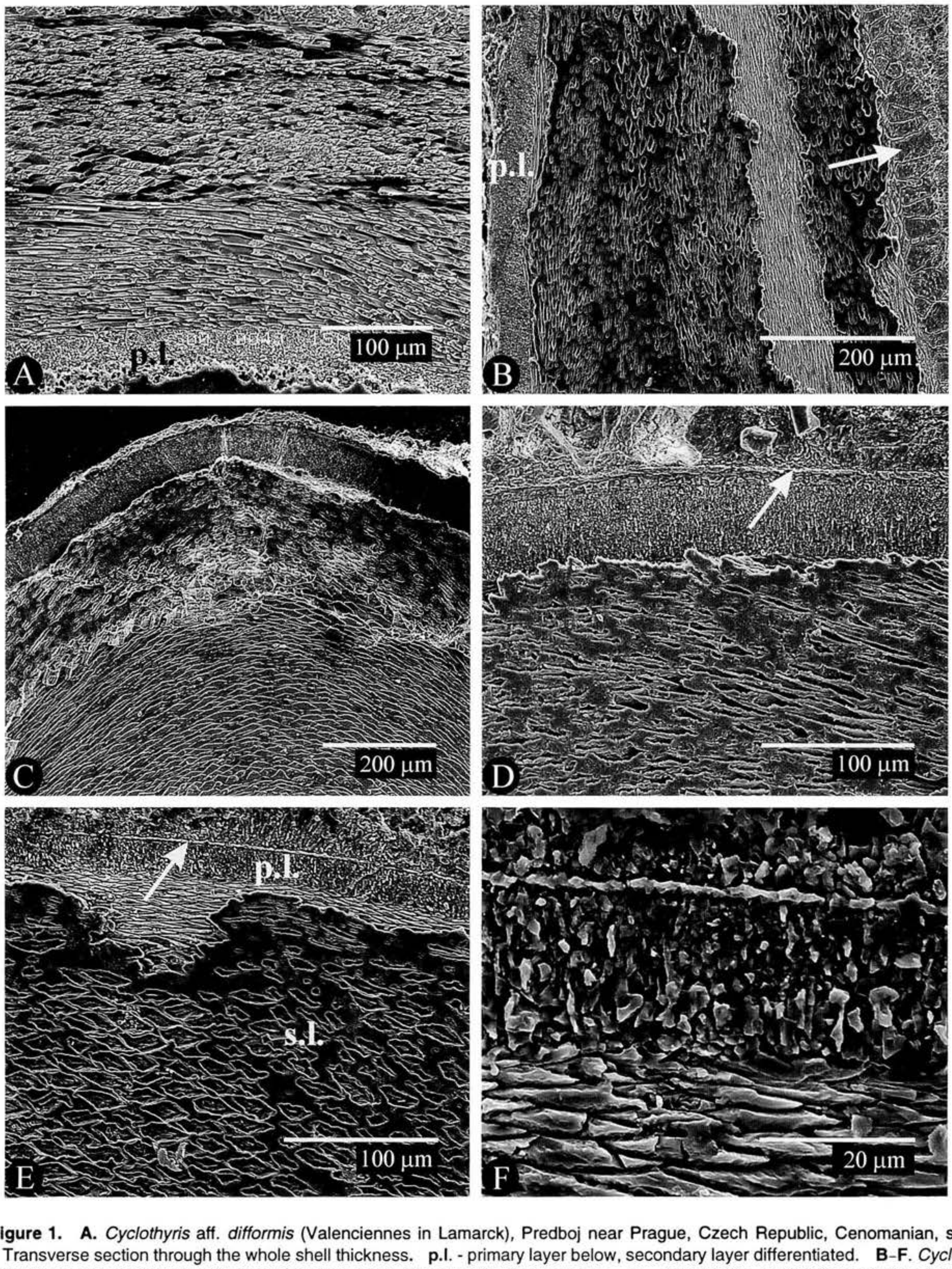

Figure 1. **A.** *Cyclothyris* aff. *difformis* (Valenciennes in Lamarck), Predboj near Prague, Czech Republic, Cenomanian, sample 18a. Transverse section through the whole shell thickness. **p.l.** - primary layer below, secondary layer differentiated. **B-F.** *Cyclothyris difformis* (Valenciennes in Lamarck) from Dobreva chuka, NE Bulgaria, Cenomanian. **B** - sample 43a, section through the whole shell thickness; **p.l.** - primary layer on the left, not silicified, secondary layer partly silicified; arrow on the right-diagenetic calcite underlying the secondary layer. **C** - sample 42b, rib; primary layer above, recrystallized, but not silicified, secondary layer-partly silicified close to the primary layer. **D** - sample 42b, strongly silicified secondary layer-below and recrystallized, but non silicified primary layer above. The primary layer is overlain by a thin cover layer, supposed to be the calcitic pseudomorph of the periostracum - arrow. **E** - sample 43a, partly silicified secondary layer (**s.l.**) and non silicified primary layer (**p.l.**), covered by thin calcitic layer, probably a pseudomorph of the periostracum - arrow. **F** - close up of the area arrowed in **E**.

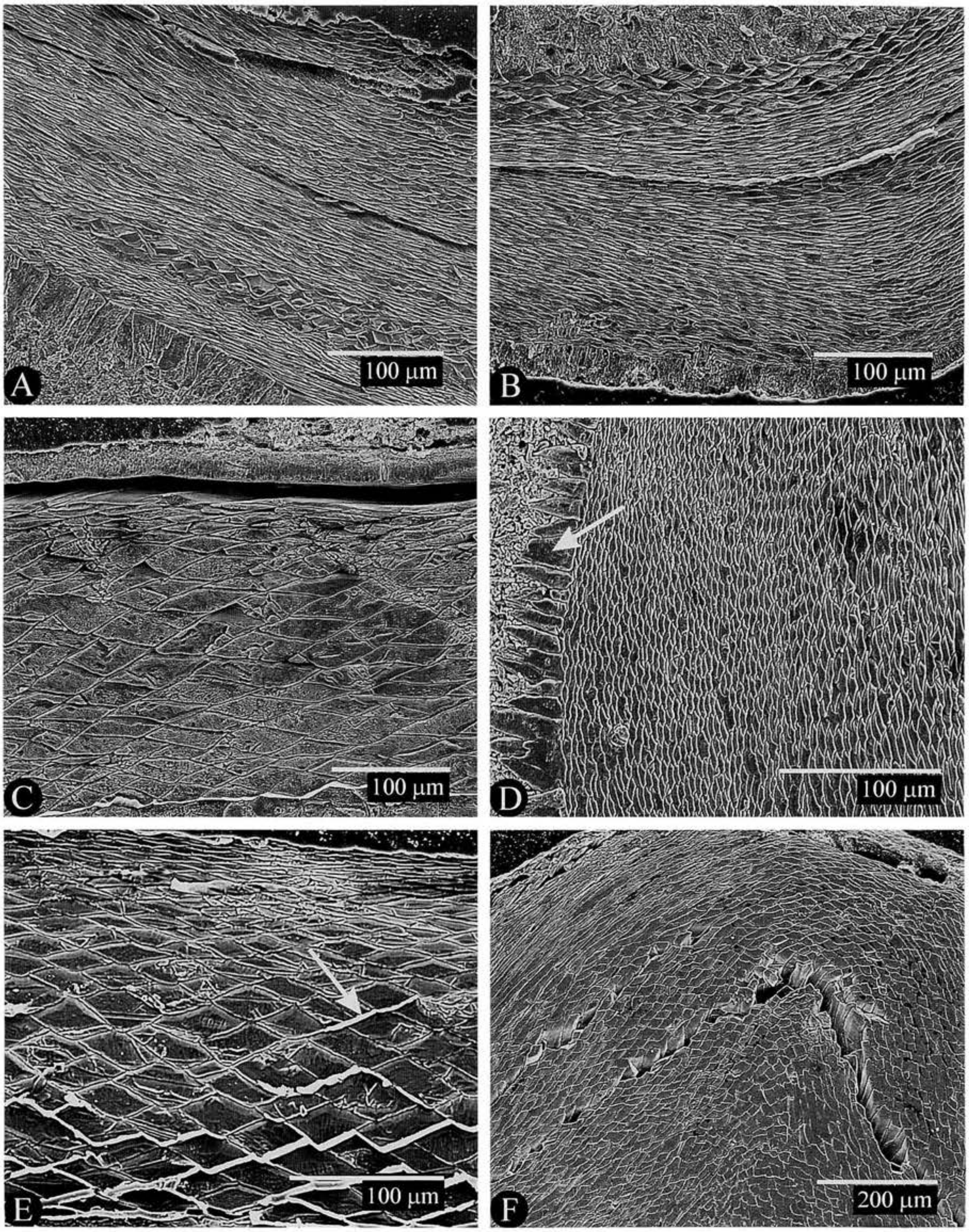

Figure 2. **A, B.** *Cyclothyris antidichotoma* (Buvignier), Shenley Hill, Leighton Buzzard, Bedfordshire, England, Lower Albian, *L. regularis* Subzone. **A** - sample 13a, section through the whole shell thickness, primary layer missing. Internal shell surface in the lower left corner encrusted with diagenetic calcitic prisms. **B** - sample 13, Section through the whole shell thickness. Primary layer below, recrystallized. **C.** *Orbirhynchia reedensis* (Etheridge), Bohemia, Czech Republic, Upper Turonian, sample 21a. Whole shell thickness, primary layer above. **D.** *Burrirhynchia leightonensis* (Walker), Leighton Buzzard, Bedfordshire, England, Lower Albian, *L. regularis* subzone, sample 4a. Secondary fibres. Internal shell surface, vertical, on the left, overgrown by diagenetic calcite crystals (arrow), perpendicular to the surface. **E.** *Orbirhynchia* aff. *boussensis* Owen, Kaspichan, NE Bulgaria, Cenomanian, sample 37. Secondary layer, rhomboidal or parallelogramic fibres; siliceous pseudomorphs on the organic sheets in the lower half of the picture (arrow). **F.** *Cretirhynchia plicatilis sensu* Aliev and Titova, 1988, Lesser Caucasus, Russia, Coniacian-Santonian, sample 34b. Section through a rib, secondary layer.

in cross-section, representing well-shaped rhombi or parallelograms, with straight sides and well defined angles. Rarely the cross-sections of the fibres are anvil-like. The fibres are very large (W = 35-120 µm, T = 10-50 µm; C_1 = 1.1-4, usually 2-3). The stacking of the fibres is uniform. In some species thinner fibres are developed close to the external surface, passing gradually into larger fibres towards the internal part of the shell.

Cyclothyris McCoy, 1844

Cyclothyris antidichotoma (Buvignier), (Figure 2A, B), Lower Albian (Owen, 1962); *C.* aff. *difformis*, (Figure 1A), Cenomanian (Nekvasilova, 1973), *C. difformis* (Valenciennes in Lmk), (Figure 1B-F), Cenomanian (Motchurova-Dekova, 1996), *C. zahalkai* Nekvasilova, Lower Turonian, (Nekvasilova, 1973) and *C. vespertilio* (d'Orbighy), France, Santonian (Coll. NHM) were examined. The shell thickness is 300-350 µm in *C. zahalkai* and *C. antidichotoma,* and reaches 700-1000 µm in *C. difformis* and *C. vespertilio.* The primary layer is relatively thick in *C.* aff. *difformis* and *C. difformis,* reaching up to 20% (50-80 µm) of the total shell thickness. It is interesting to note that both species with thick primary layers inhabited a very shallow transgressive sea floor, namely the sublittoral zone near its boundary with the littoral zone (Nekvasilova, 1973). All species are characterized by the predominance of anisometric anvil-shaped (to rarely rhomboidal) fibres in the secondary layer, 15-30 µm thick and 2-10 µm wide. C_1 is usually between 4 and 5, but can reach a maximum value of 8. The secondary layer is usually composed of several packages of fibres with different orientation, so that the distribution of the fibres is not uniform in any particular cross-section (Figure 1A). In *Cyclothyris antidichotoma* a band of distinctly more isometric fibres is noted near the interior of the shell (Figure 2B), which looks like fibres close to the anterior margin of muscle scar tissue.

Cretirhynchia Pettitt, 1950

The summary given below concerns only some species attributed to *Cretirhynchia* by different authors. The type species *Cretirhynchia plicatilis* (J. Sowerby) was not studied due to lack of material. The revision of this genus was still in progress during the preparation of this paper. In the recently published first step in the revision (Simon and Owen, 2001), the genus was split in four subgenera and one new genus was proposed. This probably could explain the variability in the shell ultrastructure of the studied species.

The thick-shelled species of *Cretirhynchia* constitute a group that is easily distinguished from the other representatives of *Cretirhynchia* (Motchurova-Dekova, 1993). In the current study these are *Cretirhynchia plicatilis sensu* Aliev and Titova, 1988 (Figure 2F) from Lesser Caucasus, Coniacian-Santonian (Aliev and Titova, 1988), *Cretirhynchia* sp. 1, Upper Campanian, and *Cretirhynchia* sp. 2 (Figure 3A), Lower Maastrichtian from Bulgaria (Coll. NMNHS). They seem to be close to the type species *Cretirhynchia plicatilis* (J. Sowerby). The three species studied here are characterized by thickening of the umbonal parts with callus, which blurs the outline of the internal morphology. The serial sections show strongly convergent dental plates, short ventrally deflected hinge plates, simple subquadrate crural bases, and radulifer crura keeping close together anteriorly. However, their serial sections are more similar to the sections of *C. norvicensis* Pettitt, published by Owen (1962), than to the sections of *Cretirhynchia plicatilis* published by Pettitt (1950). The shell of the three studied species (*Cretirhynchia plicatilis sensu* Aliev and Titova, 1988; *Cretirhynchia* sp. 1 and *Cretirhynchia* sp. 2) is very thick: 1000-1800 µm. Where preserved, the primary layer was strongly recrystallized, built up of acicular crystals perpendicular to the shell surface. The secondary layer is characterized by the prevalence of comparatively isometric fibres (Figures 2F, 3A), which have rhombic or rarely anvil-like outlines (W = 20-40 µm; T = 15-25 µm; C_1 having lower values - 1.2 to 2.5, rarely reaching 3.5). In these species the anisometric fibres are usually confined to the outermost part of the shell, reaching higher coefficients C_2 - up to 8-10 (Figure 3A).

According to Simon and Owen (2001), the group of species with the above mentioned internal details constitute the subgenus *Cretirhynchia* (*Cretirhynchia).* SEM investigations on the type species *Cretirhynchia plicatilis* (J. Sowerby) are also necessary to confirm the above remarks about the shell ultrastructure of the "true" *Cretirhynchia.*

The remaining species attributed to the genus *Cretirhynchia* display a different fabric of shell ultrastructure.

The shell of *Cretirhynchia exsculpta* Pettitt, Lower Campanian (Pettitt, 1950) is 350-600 µm thick. The primary layer is 30-40 µm thick and composed of fine acicular calcite crystals, almost perpendicular to the shell surface. The pattern of the secondary layer is different in two sections at a distance of 2 mm. In the section posteriorly to the mid-line, two kinds of fibres are developed (Figure 3B): (1) more isometric (W = 25-50 µm; T = 10-20 µm; C_1 = 1.8-3) and (2) more anisometric, (W = 40-65 µm; T = 4-15 µm; C_2 = 3-6). The prevailing part of the fibres is rhombic to parallelogram, but some are anvil-like. The thinner fibres seem to be distributed in thin subparallel bands within the section, but recrystallization blurs the original pattern. The second section situated more anteriorly, shows monotonously arranged fibres with no obvious signs of recrystallization, although the bands of thinner (or differently oriented) fibres could also be noticed (Figure 3C).

Cretirhynchia aff. *cuneiformis,* Upper Turonian (Nekvasilova, 1974). Most probably this Bohemian species is quite distinct from *Cretirhynchia cuneiformis* Pettitt (1950), which has just been assigned as the type species of the new genus *Woodwardirhynchia* by Simon and Owen (2001). The maximum shell thickness in *Cretirhynchia* aff. *cuneiformis* is 370 µm, the primary layer being 30µm thick and built up of acicular crystallites (Figure 3D). The secondary fibres have rhombic to anvil-like outlines. Relatively isomeric fibres are sporadically distributed in bands or lenses (W = 25-38 µm; T = 7-17 µm; C_1 = 2-3.5). The anisometric fibres prevail (W = 20-50 µm; T = 3-14 µm; C_2 = 3.5-6.5). These peculiarities are reminiscent of *Cyclothyris,* but the fibres in *Cyclothyris* have a maximum of 40 µm width.

Cretirhynchia minor Petitt, Upper Turonian (Nekvasilova, 1974) was recently removed from the genus *Cretirhynchia* (Simon and Owen, 2001). The shell of this minute

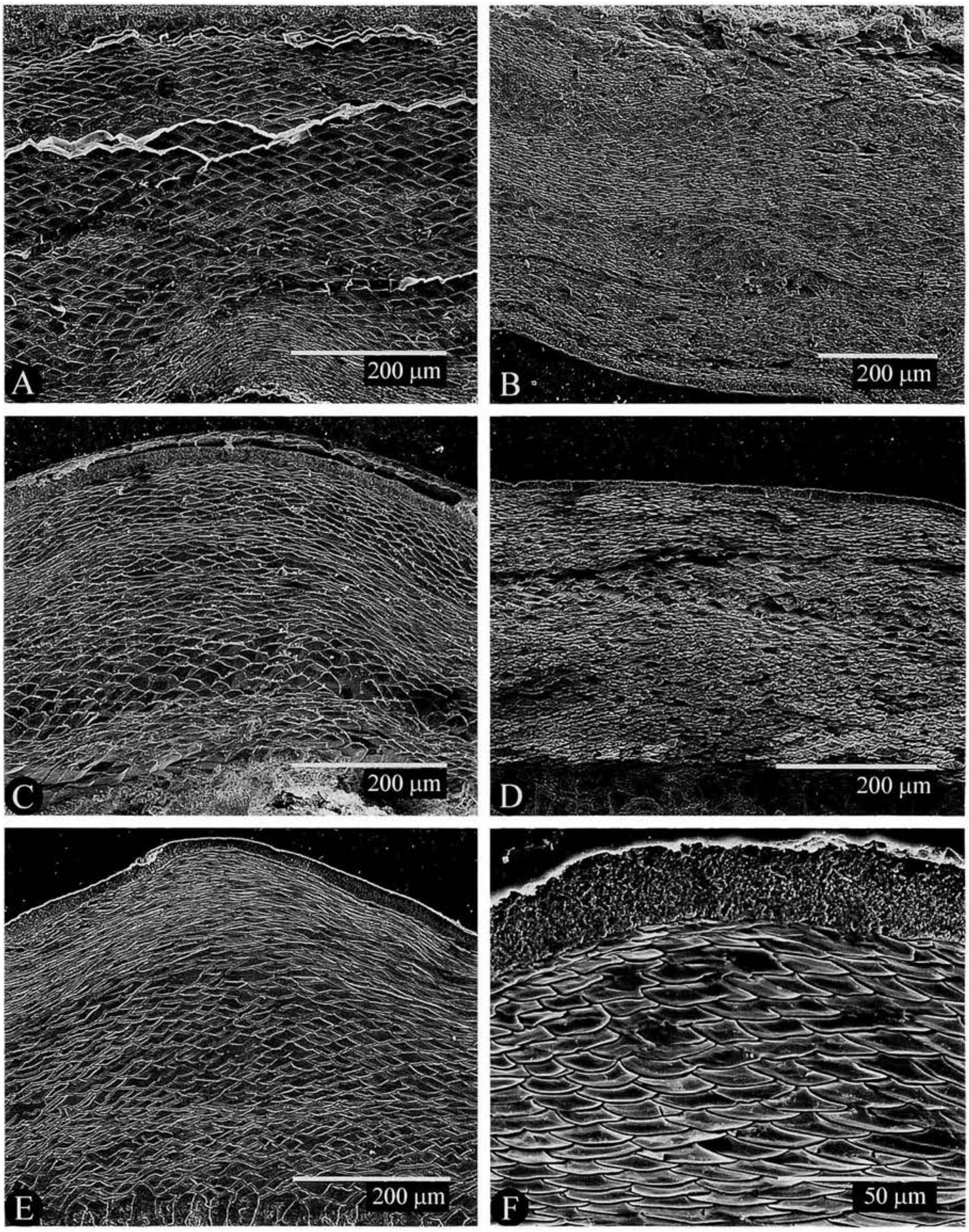

Figure 3. **A.** *Cretirhynchia* sp. 2, Nikopol, Lower Maastrichtian, Bulgaria, sample 45-10. Sulcus - section through the whole shell thickness, external surface below. Primary layer missing. Sublayer of finer anisometric fibres in the outermost part of the shell. **B.** *Cretirhynchia exsculpta* Pettitt, Brighton, E. Sussex, England, Lower Campanian, *Marsupites* Zone, sample 7a. Whole shell thickness. Primary layer below. **C.** *Cretirhynchia exsculpta* Pettitt, Brighton, E. Sussex, England, Lower Campanian, *Marsupites* Zone, sample 7b. Section through the rib. Primary layer above. **D.** *Cretirhynchia* aff. *cuneiformis* Pettitt, Čížkovice near Lovosice, Czech Republic, Upper Turonian, sample 19. Whole shell thickness, primary layer above. **E, F.** *Cretirhynchia minor* Pettitt, Čížkovice near Lovosice, Czech Republic, Upper Turonian, sample 22b. **E** - Section through a rib. **F** - Boundary between the primary and the secondary layers, anvil-like fibres.

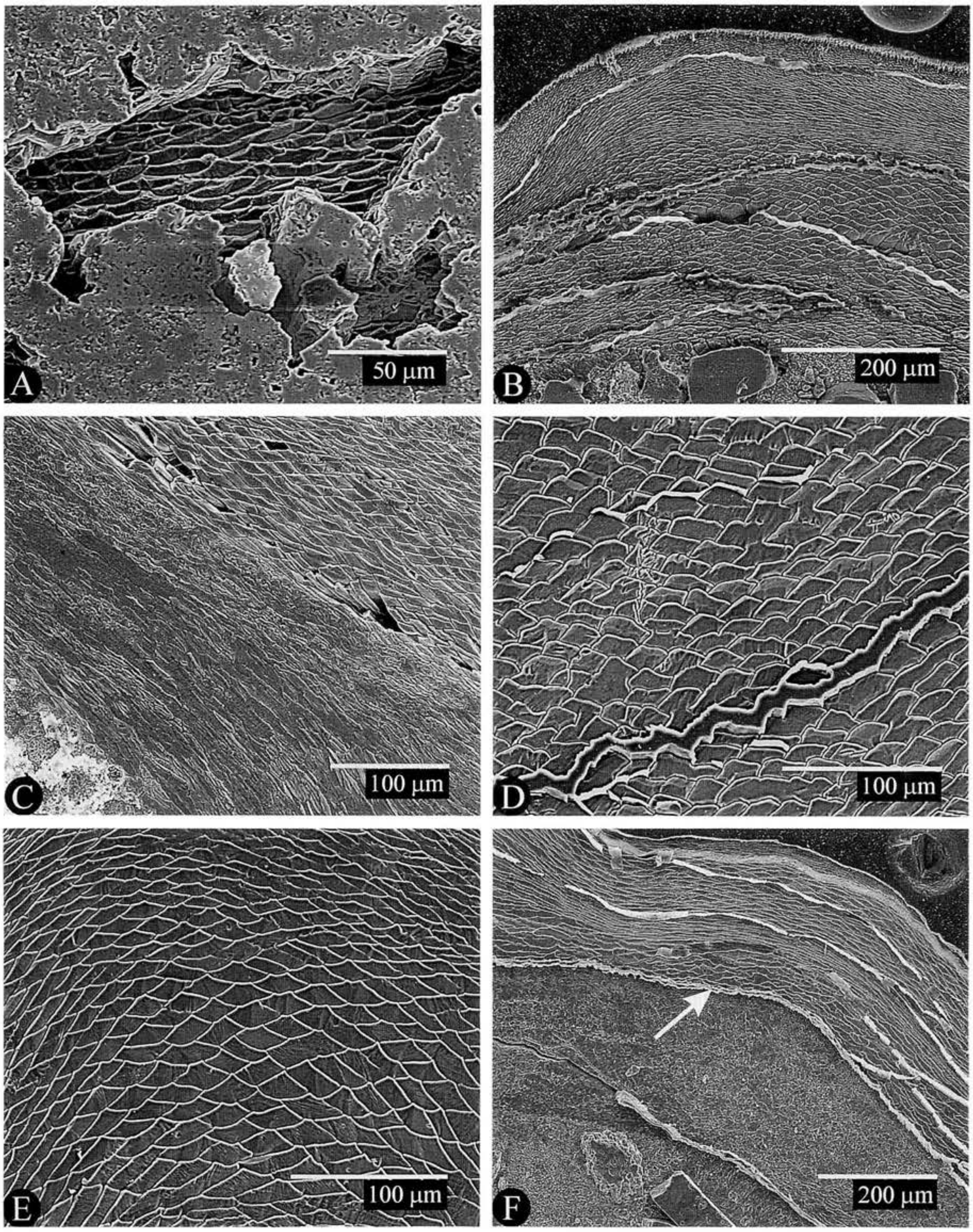

Figure 4. **A.** *Cretirhynchia bohemica* (Schloenbach), Malnice near Louny, Czech Republic, Lower Turonian, sample 20b. Small fragment of non silicified fibres (low relief), strong silicification (high relief). **B.** *Septatoechia inflata* Titova, Tuarkir, Turkmenistan, Upper Maastrichtian, sample 26b. Section through a rib, primary layer missing, secondary differentiated. High relief silicified organic sheets subparallel to the shell surface separate the bundles of fibres with different orientation. **C.** *Septatoechia inflata* Titova, Novachene, Bulgaria, Upper Maastrichtian, sample 52a. Boundary between the secondary fibres (upper right corner) and a very thick myotest (lower left half) in the ventral valve. **D.** *Septatoechia amudariensis* (Katz), Nardyvaldivaly, Badhyz region, East Turkmenistan, Upper Maastrichtian, sample 27a. Secondary fibres crossed by two subparallel bands of high relief silicified organic sheets. **E.** *Septatoechia* aff. *Rhynchonella baugasii* d'Orbigny, Komunari, Bulgaria, Upper Campanian, sample 51b. Orthodoxly stacked fibres in a rib. **F.** *Belbekella mutabilis* Lobatscheva, Kuibyshevo, SW Crimea, Russia, Berriassian, sample 32b. Section through the whole shell. Myotest occupying the interior half of the shell thickness separated by a silicified organic sheet (arrow).

rhynchonellide is 450 µm thick. The primary layer is microgranular, partly recrystallized (Figure 3F) and 20-25 µm thick. Close to the exterior, at about one third of the shell thickness, finer anisometric fibres are developed; W=30-45 µm; T = 6-10 µm; C_2 = 3.5-6.5. The remaining part of the shell is built up of uniformly arranged more isometric fibres, (W = 25-40 µm; T = 10-17 µm; C_1 = 2.2-3.5); (Figure 3E).

Cretirhynchia bohemica (Schloenbach), Lower Turonian (Nekvasilova, 1974) was strongly silicified and only some isolated fragments of the original structure were preserved. The shell is relatively thick - 480 µm and the primary layer is recrystallized, 30-40 µm thick. Judging from the narrow spots of non-altered secondary shell (Figure 4A), the fibres are anisometric, very fine and anvil-like (W = 16-40 µm; T = 4-8 µm; C = 3.2-7). These are amongst the most anisometric fibres of all the studied species, referable to *Cretirhynchia,* and are very similar to the fibres in *Cyclothyris.* As Nekvasilova (1974) suggested, the generic assignment of this species is uncertain and new data are necessary to elucidate in detail its affinities.

Septatoechia Lobatscheva and Titova, 1977

The type species *Septatoechia inflata* Titova was investigated using representatives from the type locality in Turkmenistan, Lower Maastrichtian (Figure 4B) (Lobatscheva and Titova, 1977) and from Bulgaria, Upper Maastrichtian (Figure 4C) (Motchurova-Dekova, 1996). In addition, two other species were studied: *Septatoechia amudariensis* (Katz) from the Upper Maastrichtian in Turkmenistan (Figure 4D) (Lobatscheva and Titova, 1977) and from Bulgaria, and *Septatoechia* aff. *Rhynchonella baugasii* d'Orbigny, Upper Campanian from Bulgaria (Figure 4E) (Motchurova-Dekova, 1996). This genus is characterized internally by a very high median septum and subparallel to convergent dental plates. The shell is very thick, reaching 1000-2000 µm. The primary layer is relatively thin: 30-50 µm. The secondary layer is composed of many packages of differently orientated relatively isometric fibres. They are 15-40 µm wide and 8-30 µm thick. C_1 starts from very low values (C_1 = 0.8-3). Externally and internally thinner anisometric fibres are developed. Centrally, the shell is built up of relatively isometric thicker fibres. The main part of the fibres is rhombic, or less commonly anvil-like, especially the thinner fibres. Before erecting the genus *Septatoechia* (Lobatscheva and Titova, 1977), its representatives were assigned to the genera *Cyclothyris* or *Cretirhynchia* because of internal and external similarities. In fact *Septatoechia* represents an interesting mixture of morphologic characteristics, typical of *Cyclothyris* and *Crtirhynchia.* Judging from ultrastructural evidence, *Septatoechia* is much closer to *Cretirhynchia sensu stricto,* displaying a very thick shell, and relatively isometric and similarly sized rhombic fibres in the secondary shell. As in *Cretirhynchia,* the rhombic cross-sections of the fibres in *Septatoechia* have rounded edges. In both genera the myotest is typically very thick (Figure 4C). The fibres in *Septatoechia,* however, are more isometric and the secondary layer seems to be differentiated (Figure 4B).

Single representatives of five other Cretaceous rhynchonellide genera were studied for comparison.

Belbekella Moisseev, 1939

The shell thickness in the type species *Belbekella airgulensis* Moisseev, Berriassian (Lobatscheva, 1993) is 600 µm. The primary layer, built up of acicular calcite, is 40-100 µm thick. The fibres are uniformly arranged and anvil-like (W = 15-40 µm; T = 2-6 µm; C_1 = 4-7). A more posterior cross-section, cutting the muscle field of the pedicle valve of *Belbekella mutabilis* Lobatscheva, Berriassian (Lobatscheva, 1993) was studied. A very thick myotest (up to 300 µm) was observed (Figure 4F).

Lamellaerhynchia Burri, 1953

Lamellaerhynchia geokderensis Moisseev, Upper Barremian, Turkmenistan (Coll. Lobatscheva) shows shell thickness of 700-1000 µm. The primary layer is microgranular and 20-25 µm thick. The secondary layer is built up of fibres, more anisometric and finer ones close to the exterior shell surface (W = 10-20 µm; T = 3-5 µm; C_2 = 3-5) and more isometric and larger ones toward the interior margin of the shell (W = 25-30 µm; T = 8-15 µm; C_1 = 2-3). The majority of the fibres have anvil-like cross-sections, but some of the larger and thicker fibres tend to have rhombic sections (Figure 5A).

Burrirhynchia Owen, 1962

The type species *Burrirhynchia leightonensis* Walker, Lower Albian (Owen, 1956) has a shell thickness of 500-600 µm. The primary layer is 20 to 50 µm thick. The secondary layer is composed of uniformly arranged anisometric anvil-like fibers (Figure 5D); W = 20-50 µm; T = 5-10 µm; C_1 = 3.5-6, with average values of C_1 around 5. Thinner fibres are developed close to the outer surface (Figure 5D), but there is no noticeable differentiation of the secondary layer (Figures 2D, 5C).

Almerarhynchia Calzada, 1974

Almerarhynchia pocoviana Calzada and Pocovi (1980), Upper Campanian has a relatively thin shell - 290 µm. The primary layer is 20 µm thick and strongly recrystallized. The secondary layer is built up of monotonously stacked rhombic and parallelogram, to rarely anvil-like fibres, with predominance of anisometric rhombic fibres. Although the majority of fibres (W = 25-35 µm; T = 4-10 µm; C_1 = 3-7) are anvil-like in cross sections (Figure 5E), they are not convex as in other species but tend to be rhombic. Close to the primary layer finer fibres are developed (W = 15-20 µm; T = 3-6 µm; C_2 = 3-6). Similar finer fibres, but not well differentiated, are developed close to the internal part of the shell. The finer fibres do not constitute a distinct sublayer. The overall appearance of the cross section of the secondary layer is uniform.

Grasirhynchia Owen, 1968

The shell thickness of the type species *Grasirhynchia grasiana* (d'Orbigny), Cenomanian, (Owen, 1968) is 300 µm. The primary layer is 15-20 µm thick. The shape of the fibers in the secondary layer is blurred by the strong silicification of the interfibre spaces, vacated after the early

Table 1. Comparative ultrastructiral characteristics of four Cretaceous rhynchonellide brachiopod genera.

Genus	Fibre dimensions			Peculiarities of the shell ultrastructure
	W (μm)	T (μm)	C=W/T	
Orbirhynchia	35-120	10-50	1-4	rhombic or parallelogramic, relatively more isometric fibres, uniformly arranged.
Cyclothyris	15-30	2-10	4-8	anvil-like anisometric fibres; often differentiated secondary layer.
Cretirhynchia (*C. plicatilis sensu* Aliev and Titova, 1988)	20-40	15-25	1.2-2.5	thick shell, rhombic, rarely anvil-like, relatively isometric fibres.
Septatoechia	15-40	8-30	0.8-3	very thick shell; rhombic, rarely anvil-like, relatively isometric fibres; often differentiated secondary layer.

diagenetic decay of the organic sheaths (Figure 5F). The silicification is stronger in the umbonal part of the shell. In this case it is probable that the shape and dimensions of the fibres were altered by the diagenesis. The secondary layer is built up of two kinds of uniformly distributed fibres: (1) finer close to the exterior (W = 15-25 μm; T = 2-5 μm; C_2 = 4.5-9) and (2) larger in the central and internal part of the shell (W = 35-55 μm; T = 8-12 μm; C_1 = 3-4.5). The transition from the finer to the larger fibres is continuous. The majority of the fibres are rhomboidal. Some of them, especially close to the primary layer, show anvil-like sections.

Conclusions

This study generally confirms the validity of the classification of Kamyshan (1977) who distinguished two types of fibrous structures of the secondary layer among Mesozoic rhynchonellides: **coarse-fibrous basiliolidine type** and **fine fibrous rhynchonellidine type**. The studied Cretaceous genera have been accommodated in this scheme, although large variation in fibre size is noticed. Data about fibre shape and size of genera, for which sufficient material was available, are given in Table 1.

Along with the previously studied genera *Erymnaria* and *Costerymnaria* (Motchurova-Dekova and Taddei Ruggiero, 2000), the genus *Orbirhynchia* is characterized by a coarse fibrous basiliolidine type microstructure of the secondary layer. *Orbirhynchia* has large fibres with well-defined rhombic cross-sections. It seems that during the Cretaceous the representatives of the pugnacoid stock (Manceñido and Owen, 1996, 2000) developed a coarse fibrous secondary layer.

All the remaining genera can be accommodated within the group of species with **a fine fibrous rhynchonellidine type** of ultrastructure, although they display a larger fibre size than those reported for the Jurassic and Lower Cretaceous representatives (Smirnova, 1984). When compared to the Upper Cretaceous *Orbirhynchia*, however, all the other studied genera are characterized by a smaller fibre size (Table 1).

Cyclothyris is characterized by a typical rhynchonellidine type ultrastructure *sensu* Kamyshan (1977).

Cretirhynchia and *Septatoechia* are also classified within the rhynchonellidine group. Both genera, however, have somewhat larger fibres than *Cyclothyris*, and with a peculiar relatively isometric shape in cross-section. It is suggested that *Cretirhynchia* and *Septatoechia* are more closely related to each other than to any of the other studied genera. Additional investigations on other representatives of *Cretirhynchia* are necessary to confirm this relationship.

Belbekella, *Lamellaerhynchia*, *Almerarhynchia*, *Burrirhynchia* and *Grasirhynchia* have anisometric fibres, similar to those of *Cyclothyris*. Their larger fibre size and undifferentiated secondary layers distinguish them from *Cyclothyris*.

Burrirynchia has uniformly arranged anisometric fibres quite distinct from the pattern of *Cretirhynchia plicatilis sensu* Aliev and Titova, 1988. *Burrirynchia* seems closer to *Cyclothyris* judging by similarities in the fibre shape. The fibre size in *Burrirynchia* shells, however, is larger. Before drawing conclusion about the relationship between *Burrirynchia* and *Cretirhynchia* suggested by Owen (1962), the shell ultrastructure of the type species *Cretirhynchia plicatilis* should also be studied.

In summary it appears that the genera belonging to the Cretaceous representatives of the hemithiridoid and rhynchonelloid stocks (Manceñido and Owen, 1996, 2000) display a fine fibrous rhynchonellidine type microstucture of the secondary layer.

Finally it should be pointed out that the benefits of using shell microstructural data for the purposes of distinguishing taxa should not be overestimated. Sometimes the dimensions of the fibres and the texture of the secondary layer were found to vary widely from one section to another, even in one specimen. A complete pattern of the shell ultrastructure can be obtained only if a set of sections, both transverse and longitudinal, is made and examined and if sufficient numbers of species from each genus are studied.

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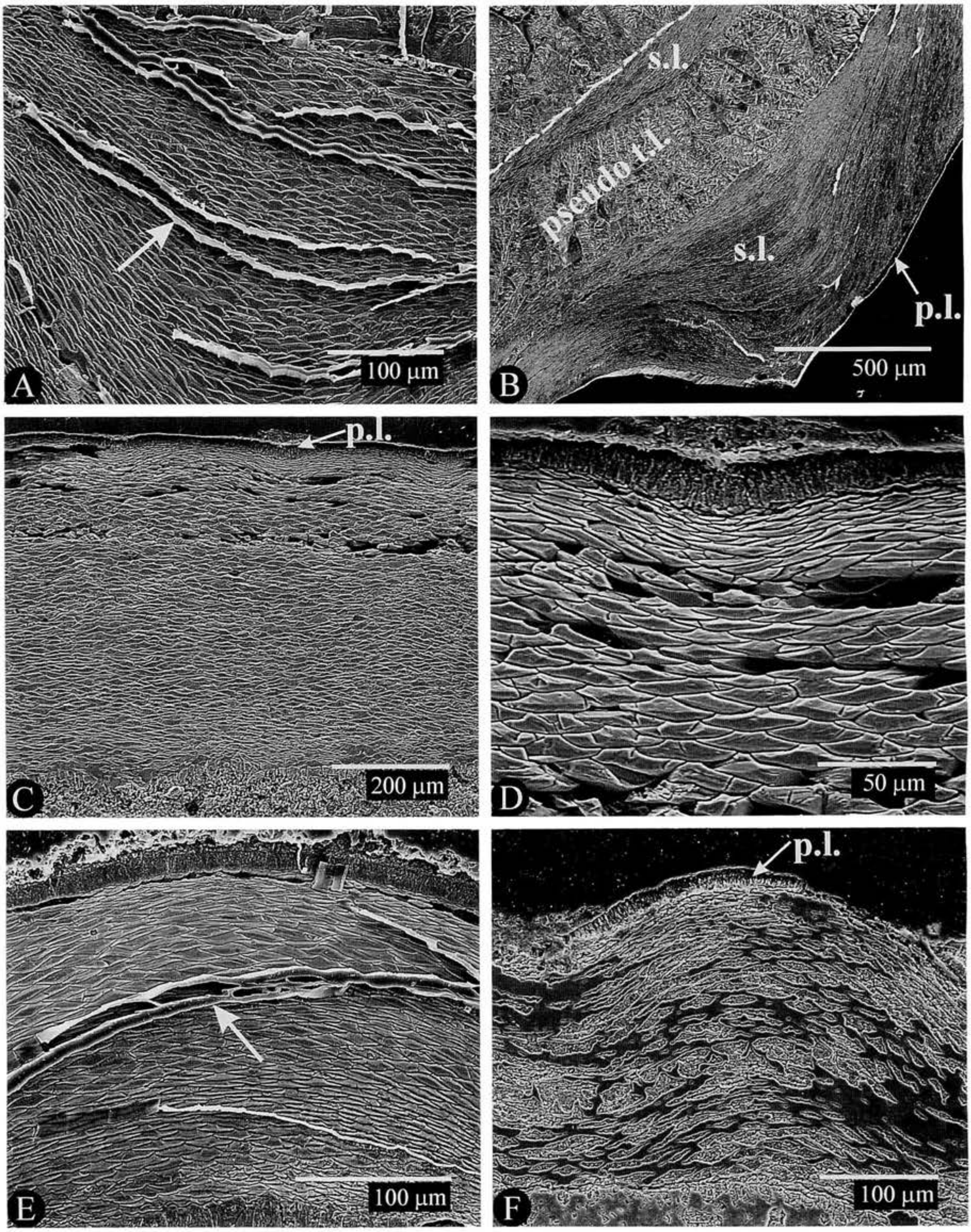

Figure 5. **A, B.** *Lamellaerhynchia geokderensis* (Moisseev in Weber) from Keldje, Tuarkyr, Turkmenistan, Upper Barremian. **A** - sample 30a, rib, internal shell surface on the top. Secondary shell, subparallel silicified organic sheets crossing the shell (arrow). **B** - sample 30b, rib. Primary layer (**p.l.**) partly preserved. A pseudo-tertiary (diagenetic) layer (**pseudo t.l.**) of calcite prisms is developed in the interior of the secondary layer (**s.l.**). The dashed white line indicates the internal surface of the shell overgrown by diagenetic calcite prisms in the upper left corner. **C, D.** *Burrirhynchia leightonensis* (Walker), Leighton Buzzard, Bedfordshire, England, Lower Albian, *L. regularis* subzone, **C** - sample 4b. The whole shell thickness, primary layer (**p.l.**) above. **D** - close up of the area arrowed in **C**. **E.** *Almerarhynchia pocoviana* Calzada and Pocovi, Sierra de Mont-Roig, Spain, Upper Campanian, sample 25a. The whole shell thickness, primary layer above, recrystallized. Silicified organic sheets crossing the section (arrow). **F.** *Grasirhynchia grasiana* (d'Orbigny) from Warminster, Wiltshire, England, Lower Chalk, Cenomanian, sample 9b. Section through a rib, strongly silicified and recrystallized secondary shell; partly preserved primary layer (**p.l.**) above.

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Ager, D. V., 1963: *Principles of Paleoecology*, 371p. McGraw-Hill Co., New York.

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行事予定

◎第151回例会は，2002年1月26日（土），1月27日（日）の両日にわたりに鹿児島大学理学部で開催されます．1月27日（日）午後に公開講演として「21世紀は自然史の時代　—古生物学・フィールド科学からの提言—：世話人，森　啓・矢島道子；平成13年度科研費研究成果公開発表（B)」を実施致します．また1月26日（土）には，昨年と今年度の学術賞受賞者の特別講演5件を予定しております．一般講演の申し込み締切は2001年11月30日（金）です．

◎2002年年会・総会は福井県立恐竜博物館（福井県勝山市）で開催します．開催日程は6月中～下旬で現在調整中です．なお講演の申し込み締切は2002年5月7日（火）です．

◎古生物学会では，小人数で実施されるワークショップやショートコースを主催しております．これには学会から補助金を得ることができます．企画をお持ちの方は行事係りまでお問い合せ下さい．

個人講演・シンポジウム案の申し込み方法

個人講演の申し込みは予稿原稿を下記まで直接お送り下さい．E-mail やファックスでの申し込み先は，原則として受け付けておりません．また行事全般に関するお問い合わせも行事係か行事幹事までお寄せください．

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