

日本古生物学会
報告・紀事

Transactions and Proceedings
of the
Palaeontological Society of Japan



New Series No. 183

September 30, 1996

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Cover : A terminally resorbed maxillary tooth of iguanodontids (*Ornithischia* : *Ornithopoda*). The specimen is from the Kuwajima Formation, the Neocomian section of the Tetori Group, in Shiramine-mura, Ishikawa County, Ishikawa Prefecture, the west coast of Central Honshu, Japan (Shiramine-mura Board of Education, Coll. Cat. No. SBEI 001, 23 mm in dorsoventral length).

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Early loop ontogeny of some Recent laqueid brachiopods

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Received 14 July 1995; Revised manuscript accepted 10 April 1996

Abstract. The early loop ontogenies of nine Recent laqueid species from Japanese waters were examined using scanning electron microscopy. Although juvenile specimens representing certain early loop stages were not available for some species, all the examined species appear to share roughly the same early stages of loop development as described by Richardson (1975). However, some differences and characteristic features exist in the early stages of loop ontogeny, such as the disposition of the septal flanges and presence or absence of septal bifurcation, characters which appear to be invariable at the genus level. A prime example is the case of the affinity between *Laqueus* and *Frenulina*, which have occasionally been included in the same subfamily. Inspections of loop morphology of early growth stages, especially of the above characters, indicate that these two genera may not be as closely related as previously thought.

Comparison of relative timing of loop development as standardized by shell length reveals some variation within a species, but no major variation among species. Heterochrony is evident in one laqueid species, '*Frenulina*' sp., in which adult individuals have a loop of juvenile morphology in other species.

Key words : Brachiopods, Laqueidae, loop development, ontogeny, heterochrony

Introduction

In terebratulide brachiopods, the lophophore is supported by a calcareous brachidium, or loop. The form of the loop undergoes considerable change during ontogeny, and both the form of the loop and its mode of development have been of prime importance in terebratulide classification. For example, Richardson (1975) investigated relationships among long-looped Cenozoic terebratelloid genera belonging to the Dallinidae, Laqueidae, and Terebratellidae, and proposed that patterns of resorption of the ring (an element of the loop at an earlier developmental phase) can be used as a diagnostic character to separate these families.

MacKinnon (1993) has drawn attention to the potential for studies of early loop ontogeny to provide valuable clues for establishing phylogenetic relationships in terebratulide brachiopods. However, the early growth stages of many species have not yet been satisfactorily studied.

This paper describes the loop development of nine extant species belonging to the family Laqueidae based on material from Japanese waters. The loop development of laqueid brachiopods has been described by several authors such as Atkins (1959) for *Terebratalia transversa*, Hatai (1939) for *Coptothyris grayi*, Konjukova (1948, 1957) for *Laqueus californicus* and *Terebratalia coreanica*, and Richardson (1973a) for *Frenulina sanguinolenta*. However, none of these studies

utilized scanning electron microscopy (SEM) which allows detailed observations of microstructures even for very small specimens. Gunji (1987) studied the mechanisms of loop ontogeny after the late haploid (or diploform (MacKinnon, 1993)) phase for dallinid and laqueid species, and explained the inter-specific variations in terms of developmental constraint. But inter-specific variations before the haploid phase remained unquestioned. The present investigation, utilizing SEM, aims to describe and compare the morphology, particularly of early growth stages, growth patterns, and relative timing in the development of the loop of the laqueid species available to this study.

Material and Methods

Samples of a total of nine laqueid species were available for this study (Table 1).

They include both living and dead specimens. With living specimens, care was taken in the removal of soft tissues using domestic grade bleach (sodium hypochlorite: approximately 5% (v/v)), as described by Mackay *et al.* (1994). After opening the conjoined valves of dead specimens using a scalpel blade, dorsal valves were placed briefly in the bleach solution. Each specimen was then washed, allowed to dry, and mounted on SEM stub. Specimens were coated with Pt-Pd alloy prior to observation by scanning electron micro-

Table 1. Samples used in this study. All localities are in Japan.

Species	Locality	Depth	Status
Terebratulida			
Laqueidae			
<i>Laqueus</i> sp.	off Hachinohe, Tohoku	125-193 m	D
<i>Laqueus rubellus</i> (Sowerby)	Sagami Bay	80-186 m	L
	off Hachinohe, Tohoku	82-144 m	D
<i>Picthothyris picta</i> (Dillwyn)	off Shimoda	52- 98 m	L
<i>Picthothyris</i> sp.	off Tsukumi, Bungo Channel	72- 76 m	D
<i>Terebratalia coreanica</i> (Adams and Reeve)	Otsuchi, Tohoku	50 m	D
	Wakkanai, Hokkaido	32- 35 m	D
<i>Coptothyris grayi</i> (Davidson)	Otsuchi, Tohoku	50- 75 m	D
	Wakkanai, Hokkaido	22- 75 m	D
<i>Frenulina sanguinolenta</i> (Gmelin)	Miyako Island, Okinawa	12- 40 m	D
	Ogasawara Islands	20- 30 m	L
' <i>Frenulina</i> ' sp.	off Shimoda	52- 98 m	D
<i>Jolonica nipponica</i> Yabe and Hatai	Izu Islands	104-106 m	L

Abbreviations in the 'Status' column : L=living specimens when collected ; D=dead specimens when collected.

scope (Hitachi S-2400S). All of the specimens utilized except one (specimen 28498 in the collection of Tohoku University) are housed in the University Museum of the University of Tokyo (UMUT).

Loop terminology

Loop development is a continuous process, but for ease of description, loop ontogeny has been treated as a series of transient phases. The terminology applied in this study follows that of Richardson (1975) and MacKinnon (1993) with minor amendment (Table 2).

Results

Loop development of the examined species

Laqueus rubellus (Sowerby)

None of the available specimens of *Laqueus rubellus* exhibited the earliest growth phases of the loop.

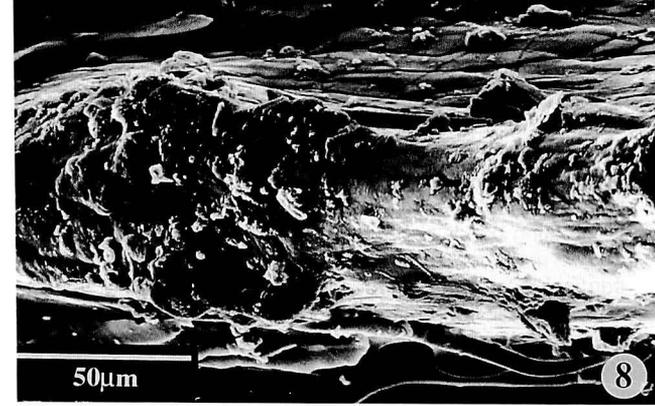
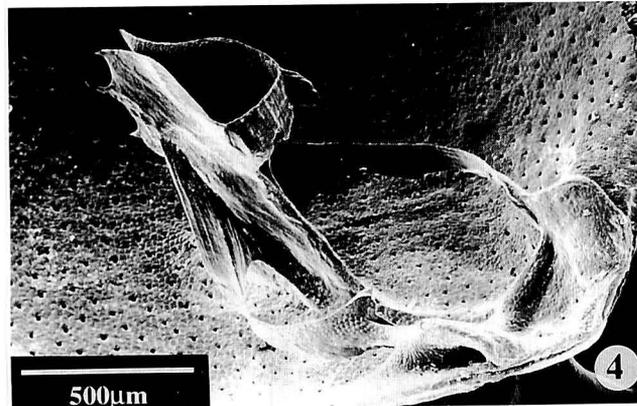
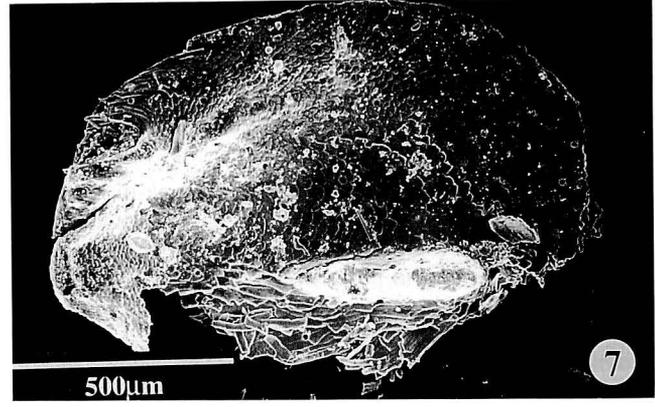
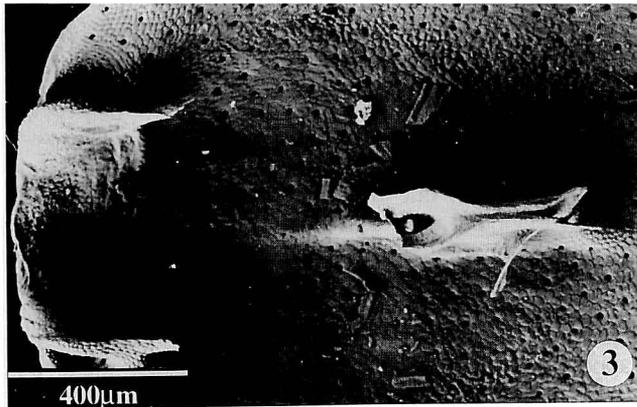
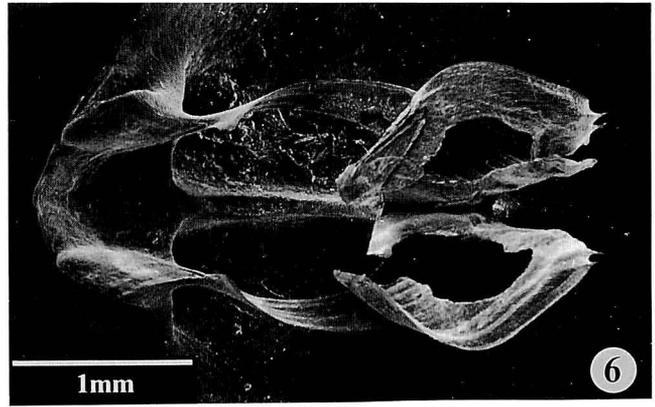
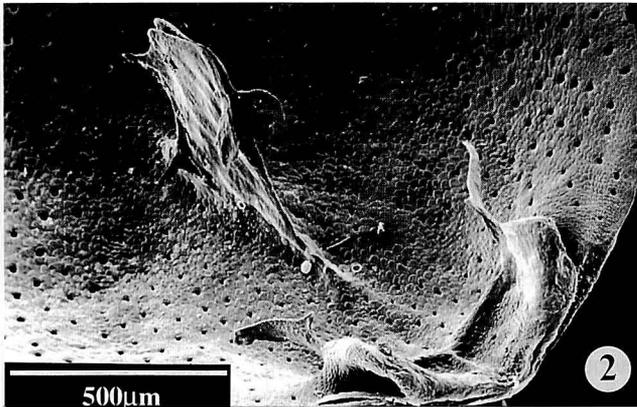
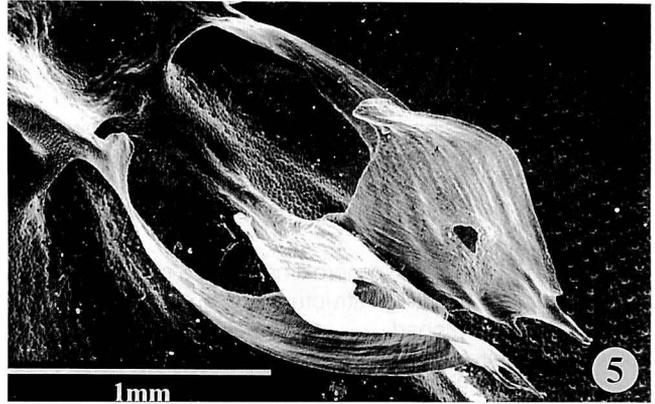
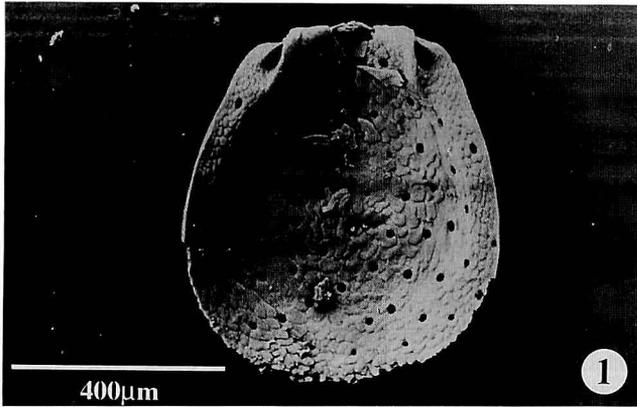
Annular phase

A specimen 3.8 mm long (the shell length described hereafter is that of the dorsal valve, and denoted as L) shows the loop pattern of phase 5 with a ring and complete descending branches.

Table 2. Definitions of the loop development phases used in this study.

Prebrachial phase : Dorsal valve without any brachial structures.
Axial phase (early) : Phase of loop development with a low medium septum.
Axial phase (late) : Phase of loop development with a septal pillar and flanges. This development of septal flanges is distinctive feature for laqueid brachiopods.
Cucullate phase : The formation of the septum and the hood.
Annular phase : The presence of a ring in place of the hood.
Haptoid phase : The anterior fusion of the attachments of the ring and the descending branches.
Bilacunar phase : The presence of two lacunae in dorsal segments of the band forming the ring.
Bilateral phase : The presence of two pairs of connecting bands, lateral and latero-vertical.
Latero-vertical phase : The presence of latero-vertical connecting bands only.
Trabecular phase : The presence of lateral connecting bands only.
Teloform phase : The absence of any connecting bands so that the loop is free of the septum.

Figure 1. 1-6. *Laqueus* sp. 1: Specimen UMUT RB19818 (L=0.6 mm : L is the length of the dorsal valve). 2: Posterior view (L=1.9 mm), specimen UMUT RB19819. 3: Dorsal view (L=2.0 mm), specimen UMUT RB19820. Part of the hood is broken. 4: Posterior view (L=2.7 mm), specimen UMUT RB19821. The descending branches from both septal pillar and crura have just united. 5: Oblique view (L=4.4 mm), specimen UMUT RB19822. The transverse band of the ring is broken. 6: Specimen UMUT RB19823 (L=4.2 mm), dorsal view. The transverse band of the ring is broken. **7-8.** *Picthothyris picta*. 7: Specimen UMUT RB19824, dorsal view (L=1.2 mm). The right hand part of the shell is broken. The septal pillar is the first brachial structure to appear and the cardinal process is also differentiated at this stage. 8: Details of the septal pillar in Figure 1-7 showing the small septal flanges on the posterior edge.



Bilacunar phase

A specimen (L=4.6 mm) exhibits the loop of the bilacunar phase.

Bilateral phase

Specimens larger than 5.9 mm in shell length show the adult loop pattern (bilateral phase).

Laqueus* sp.*Prebrachial phase**

The smallest specimen approximately 0.6 mm long displays no loop-supporting structures (Figure 1-1). Socket ridges are well developed.

Axial phase (late)

A specimen of 1.9 mm in length has an anteriorly bifurcate septal pillar (Figure 1-2). A pair of posterolaterally divergent septal flanges extend from the posterior edge of the septal pillar. Crura, bearing short crural processes, project from near the base of each inner socket ridge. Short segments of descending lamellae diverge anterolaterally from the distal ends of the crura.

Cucullate phase

In the next smallest specimen (L=2.0 mm, Figure 1-3) a hood forms on the posteroventral edge of the septal pillar which is bifurcate along both anterior and ventral edges. Two small septal flanges project from the posterior edge of the hood. Lower down on the septal pillar the rudiments of the descending lamellae appear as a pair of narrow triangular fins with smooth ends.

Annular phase

Shells of 2.7–4.6 mm in length show complete descending branches extending from the crura to the septal pillar and a ring having traces of flanges (Figure 1-4). As the shell length increases, the flanges become smaller due to resorption. The anterior edge of the septal pillar is strongly bifurcate and spinose.

Bilacunar phase

At the bilacunar phase (L=3.8–4.6 mm) a pair of lacunae are present in the dorsal segments of the bands that form the ring (Figure 1-5). At a shell length of 4.2 mm (Figure 1-6) the lacunae are enlarged and the growing (anterior) edge or the descending lamellae become progressively more divergent.

Pictothyris picta* (Dillwyn)*Axial phase (early)**

The first structure to appear, associated with the formation

of the loop, is the septal pillar which forms as a thickening of the midsection of the dorsal valve approximately 1.2 mm long (Figure 1-7). In this specimen, the socket ridges are low and the cardinal process is beginning to develop. The septal pillar is relatively wide and bears a pair of septal flanges on the posterior edge (Figure 1-8).

Annular phase

A specimen 3.2 mm long shows complete descending branches, and the ring (Figure 2-1). The anterior edge of the septal pillar is spinose but non-bifurcate.

Haptoid or bilacunar phase

A specimen 3.9 mm long has a loop in the haptoid or bilacunar phase, with two lacunae in the dorsal segment partly broken or the band forming the ring (Figure 2-2). The ascending and the descending branches are connected.

Bilateral phase

Specimens ranging 6.0–6.9 mm in length show the bilateral loop pattern (Figure 2-3) with two pairs of connecting bands, lateral and latero-ventral.

Latero-ventral phase

Specimens larger than 8 mm in length show the adult loop pattern (latero-ventral phase), with latero-ventral connecting bands only.

Pictothyris* sp.*Prebrachial phase**

The smallest specimen (L=0.6 mm) displays no loop-supporting structures (Figure 2-4). Socket ridges are low and the cardinal process is not developed.

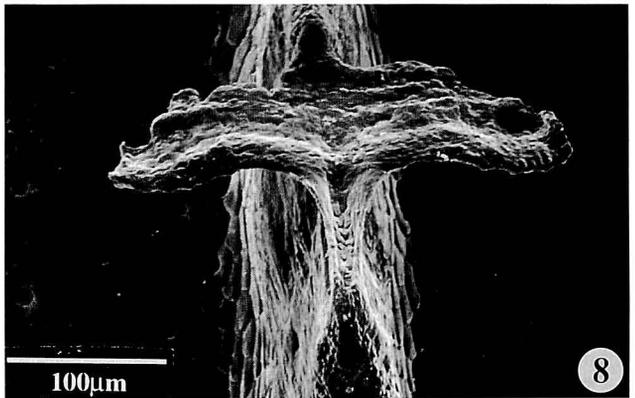
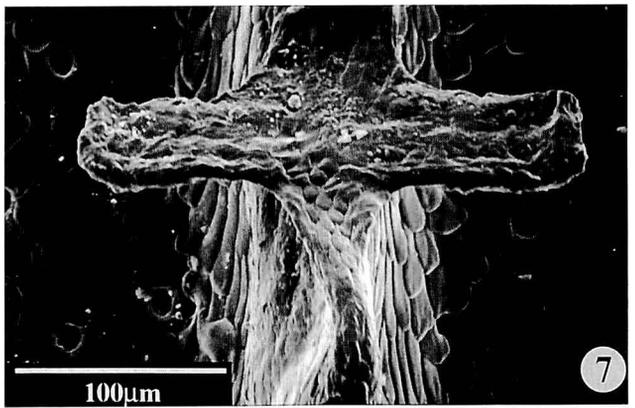
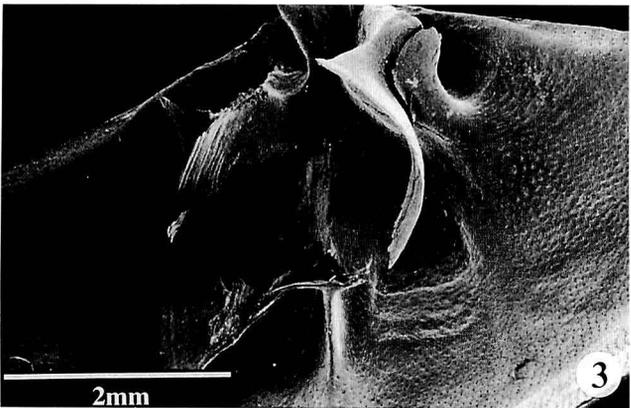
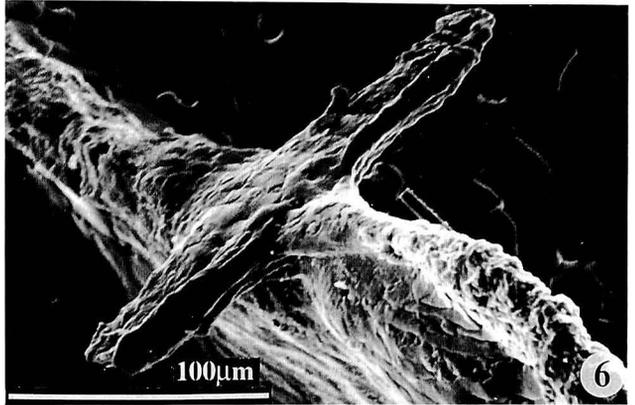
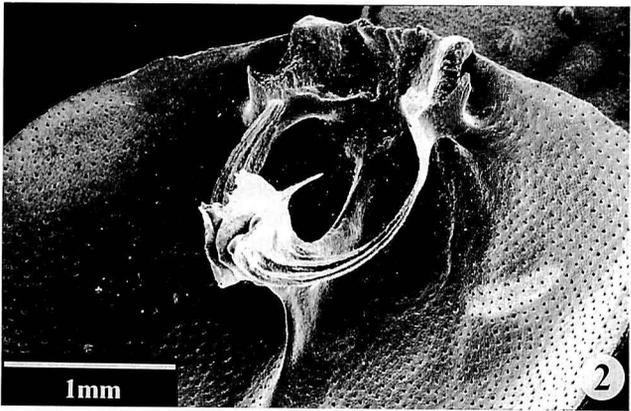
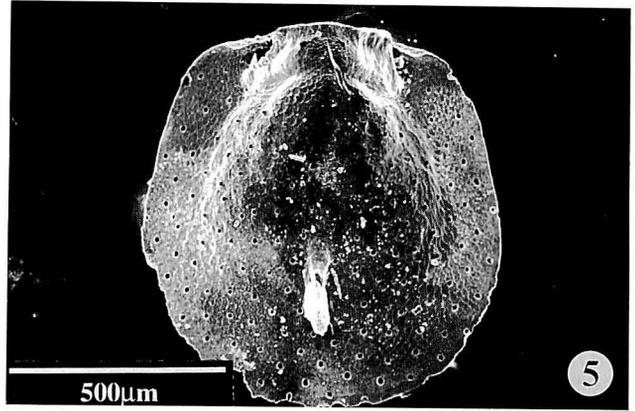
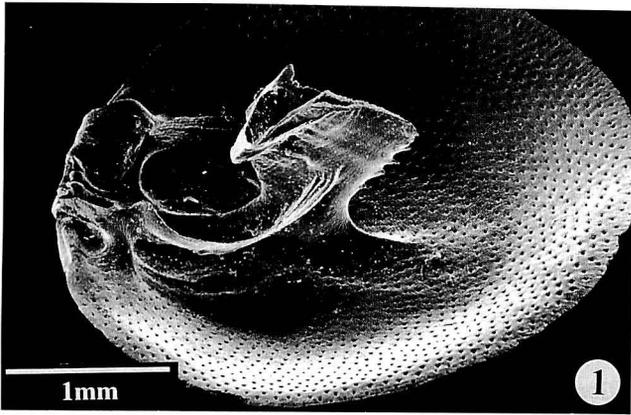
Axial phase (early)

The next smallest specimen (L=0.8 mm) has a low septal pillar, but cardinal process is not yet developed (Figure 2-5).

Axial phase (late)

A specimen 1.5 mm in length shows well-developed, laterally directed septal flanges and a high septal pillar. At this growth phase, the ventral (growing) edge of the septal pillar is non-bifurcate, but just anterior of the septal flanges a narrow triangular area develops. The edges of the flanges and the anterior triangular border attached to the flanges are smooth (Figure 2-6). In another specimen of length 1.5 mm, a slight depression begins to form on the ventral surface of the triangular area, and very small secondary layer fibers appear within its margins (Figure 2-7). This indicates the beginning of a groove to form a hood (Figure 2-8). The cardinal process begins to develop during this stage, and

Figure 2. 1-3. *Pictothyris picta*. 1: Lateral view (L=3.2 mm), specimen UMUT RB19825. 2: Anterior view of dorsal interior, specimen UMUT RB19826, (L=3.9 mm), showing the bilacunar phase. Most of the ring is broken. 3: Specimen UMUT RB19827 (L=6.9 mm), anterior view, showing the bilateral phase. Although most of the loop is broken, lateral connecting bands and right latero-ventral connecting band are seen. 4-8. *Pictothyris* sp. 4: Specimen UMUT RB19828 (L=0.6 mm), dorsal view. 5: Dorsal view (L=0.8 mm), specimen UMUT RB19829. The septal pillar has formed, but the cardinal process is not yet developed. 6: Detail of the septal flanges of specimen UMUT RB19830 (L=1.5 mm). 7: Detail of the septal flanges, dorsal view (L=1.5 mm), specimen UMUT RB19831. Secondary shell mosaic is developed in the triangular depression just in front of the septal flange. 8: Details of the flanges, dorsal view (L=1.7 mm), specimen UMUT RB19832. The ventral edge of the septal pillar bifurcates to form a groove which is overlapped in turn by the septal flanges thereby forming a hood.



rudiments of the descending branches appear on the septal pillar and as extensions of the crura (Figure 3-1).

Cucullate phase

A specimen 2.1 mm long presents a small hood (Figure 3-2). The hood becomes deeper, and the shape becomes more rounded with growth (Figure 3-3). The crura and the descending branches extend further toward one another and posterior resorption of the septum also occurs.

Annular phase

The specimen UMUT RB 19836 (L=2.3-2.5 mm, Figure 3-4) shows the ring with rudiments of the flanges and still unconnected descending branches. In specimens of shell length ranging from 2.8 to 3.1 mm, the descending branches are complete.

Haptoid phase

In specimens 3.4-3.8 mm in length, the leading edges of the ring and the descending branches unite and being to separate from the septal pillar (Figure 3-5). These specimens of *Pictothyris* sp. are similar to *P. picta* when 3.9 mm long.

Bilacunar phase

At a shell length of 4.9-5.2 mm (Figure 3-6) the fused ascending and descending loop elements extend well forward of the septal pillar and lacunae perforate the anterior and dorsal segments of the ring.

Bilateral phase

A specimen approximately 7 mm long has the loop in the bilateral phase, with lacunae perforating the anterior and dorsal segments and lateral connecting bands extending from the septal pillar to the inner edges of the descending branches.

Latero-vertical phase

Through resorption of the lateral connecting bands (Figure 3-7), the descending branches become completely free from the median septum (latero-vertical phase). Specimens larger than 8 mm in length exhibit this adult loop pattern.

Terebratalia coreanica (Adams and Reeve)

Two small specimens of *Terebratalia coreanica* collected at Otsuchi Bay provide some knowledge concerning the loop development of *Terebratalia coreanica*.

Annular phase

The smaller specimen (L=3.3 mm) shows the ring which retains the rudiments of the flanges (Figure 3-8). The anterior part of the median septum is bifurcate and the cardinal process is well developed. This growth phase of

the loop is similar to that seen in *Laqueus* sp. at shell lengths of 2.7-4.6 mm (Figure 1-4).

Bilacunar phase

In the larger specimen (L=4.7 mm), although both the descending branches and almost the entire ring are broken, the posterior part of the septum and lacunae in the lower part of the ring can be identified (Figure 4-1, 4-2). The loop pattern at this growth phase is similar to that described for *T. transversa* at a shell length of 6.4 mm (Atkins, 1959).

Trabecular phase

Specimens with a shell length of more than 8.1 mm show the adult loop pattern (trabecular phase).

Coptothyris grayi (Davidson)

Axial phase (late)

The youngest specimen of *Coptothyris grayi* (L=1.3 mm) displays a low median septum (Figure 4-3). The anterior edge of the septum is bifurcate, and on the posterior border of the septum, a pair of small, ventrolaterally directed septal flanges are developed (Figure 4-4). The leading edge of the flanges and the middle part of the septum are smooth. Both socket ridges and a low, transversely oval cardinal process are developed; a pair of rudimentary crura is also present. In a specimen 1.8 mm in length (Figure 4-5), the ventral (growing) edge of the septal pillar is prominently bifurcate. The bifurcation widens slightly posteriorly until it terminates against, and appears to be overstepped by the median section of the septal flanges. Within the zone of septal bifurcation, small secondary layer fibers appear.

Cucullate phase

At a shell length of 2.4 mm, the septal flanges form the posterior border of the hood. Crura extend from areas at the base of the inner socket ridges (Figure 4-6).

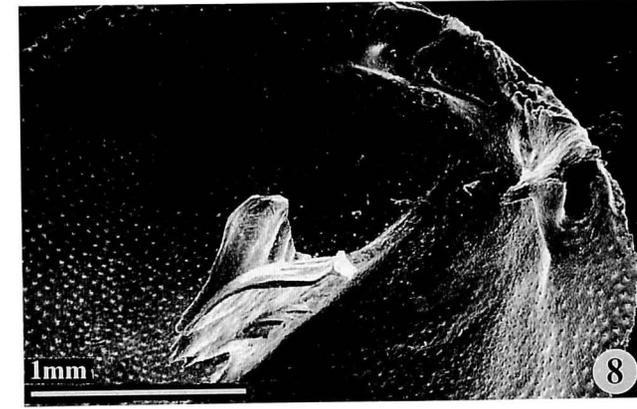
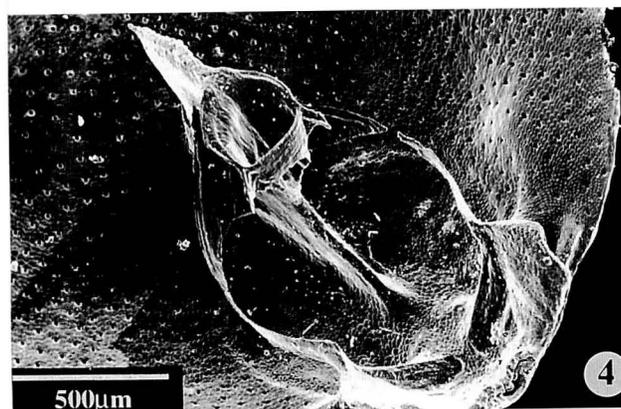
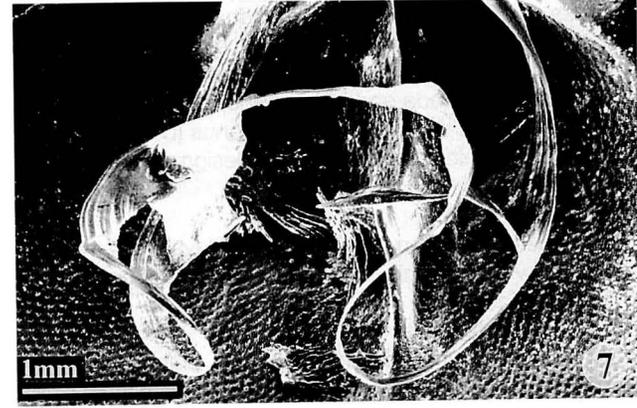
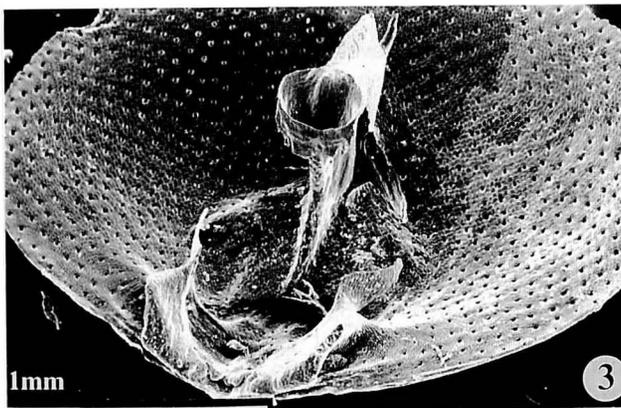
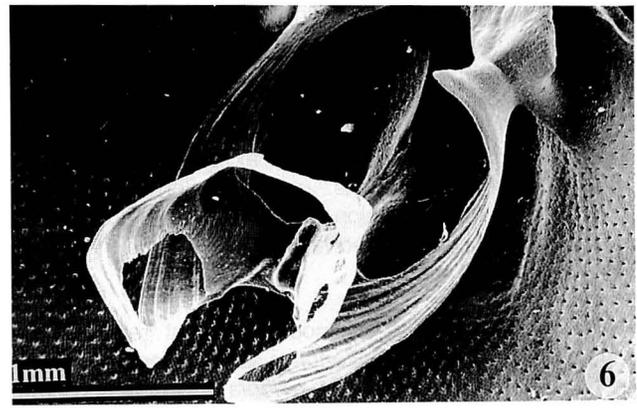
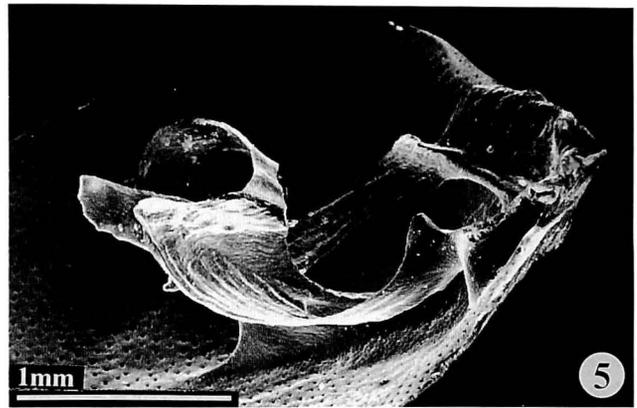
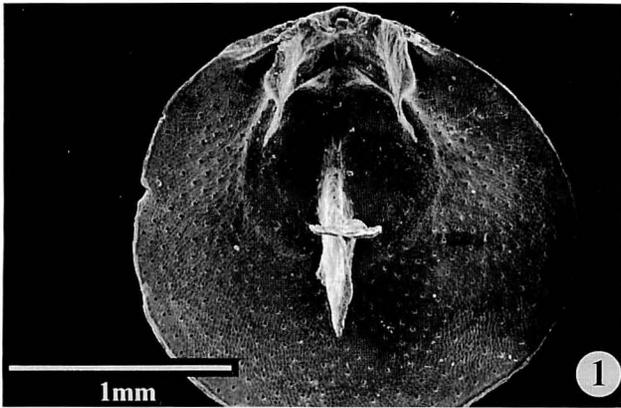
Annular phase

Although most parts of the loop are broken, the loop pattern of a specimen 3.2 mm long (Figure 4-7) displays a bifurcate medium septum and part of the ring. The loop pattern of this specimen indicates some similarity to that of *Laqueus* sp. at 2.7-4.6 mm, *L. californicus* at 5.2-5.5 mm (Konjukova, 1957), and *T. transversa* at a shell length of 5.4 mm (Atkins, 1959).

Bilacunar phase

In a specimen 4.7 mm long, lacunae perforate the ring, and the anterior part of the septum is strongly bifurcate, but anterior fusion of the growing edges of the ring and the

Figure 3. 1-7. *Pictothyris* sp. 1: Specimen UMUT RB19833 (L=1.8 mm), dorsal view, showing a small hood, septal flanges, extending crura, and small plates (future descending branches) on the septal pillar. 2: Specimen UMUT RB19834 (L=2.1 mm), posterior view. The anterior end of the hood is beginning to expand. 3: Posterior view, specimen UMUT RB19835 (L=2.3 mm). 4: Posterodorsal view, specimen UMUT RB19836 (L=2.5 mm), showing the ring with rudiments of the flanges, descending branches are not united. 5: Lateral view, specimen UMUT RB19837 (L=3.8 mm). 6: Specimen UMUT RB19838 (L=4.9 mm), details of the loop. 7: Detail of junction between the left descending branch (right-hand side in the figure) and the septum, specimen UMUT RB19839 (L=7.8 mm). As a result of resorption of the lateral connecting band, the right descending branch has become completely free from the median septum. 8. *Terebratalia coreanica*. Oblique view. Specimen UMUT RB19840 (L=3.3 mm). The descending branches and the top part of the ring are broken.



descending branches has not yet occurred (Figure 4-8).

Teloform phase

Specimens larger than 7.8 mm in length show the adult loop pattern (teloform phase).

Frenulina sanguinolenta (Gmelin)

Prebrachial phase

In a specimen 0.7 mm long, no loop-supporting structure is present (Figure 5-1). At this growth phase, low socket ridges are seen and a rudiment of the cardinal process and the anterior borders of the developing hinge plates are developed as thickenings on the valve floor.

Axial phase (early)

At a dorsal valve length of 1.0 mm, the area of the cardinal process is defined, higher socket ridges are developed, and the septal pillar begins to form on the valve floor (Figure 5-2).

Axial phase (late) to bilateral phase

Further development of *F. sanguinolenta* (Figures 5-3-8) follows that of Australian populations in the patterns described by Richardson (1973a). The axial phase (late) of *F. sanguinolenta* (Figure 5-3) is unique among examined species because the direction of the flanges is downward. This feature will be discussed later.

'*Frenulina*' sp.

'*Frenulina*' sp. from off Shimoda was first reported by Harada and Mano (1960), as *Frenulina sanguinolenta* (Gmelin). They noted that *Frenulina sanguinolenta* is a common brachiopod and distributed in the waters of Hawaii, Australia, the Philippines, Okinawa Islands, etc., and that their finding was the first from Honshu, the main island of Japan. But, as discussed later, the population that was thought of as *F. sanguinolenta* by Harada and Mano (1960) is now considered to belong to a new species of a new genus (D. MacKinnon, personal communication), so it is designated here as '*Frenulina*' sp.

Axial phase (early)

The smallest specimen (L=0.7 mm) displays a low median septal pillar which, at this stage, is essentially smooth and non-fibrous (Figure 6-1).

Axial phase (late)

A specimen 0.9 mm long shows a high, plate-like septal pillar with small, laterally directed septal flanges (Figure 6-2).

Cucullate phase

At shell lengths of 1.5-1.8 mm, the ventral edge of the septal pillar becomes bifurcate and is overlapped posteriorly by the septal flanges thereby forming a depression (Figure 6-3), giving rise to the hood (Figure 6-4).

Annular phase

In shells between 2.3 and 2.8 mm in length, the hood becomes a ring still bearing rudiments of the flanges (Figures 6-5, 6). At this stage the descending branches are not yet complete. The cardinalia is similar to that of young specimens of *Laqueus* sp. and *Pictothyris* sp. in some features such as the morphology of the inner hinge plates and absence of the cardinal process. An individual 4.2 mm long shows more extensive descending branches and the ring (Figure 6-7).

Specimens larger than 4.7 mm in length (the largest specimen ever collected is 5.8 mm in length) show the annular loop pattern with a ring and complete descending branches (Figure 6-8). In most adult specimens a ventral segment of the ring is resorbed, so the ring is commonly incomplete, but occasionally the ventral parts of the ascending lamellae may unite secondarily to once again form a complete ring.

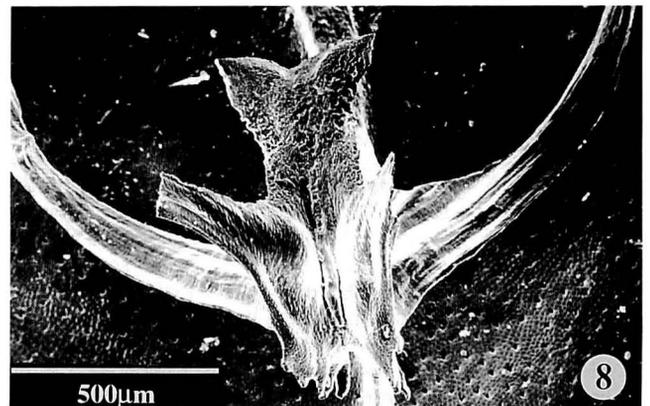
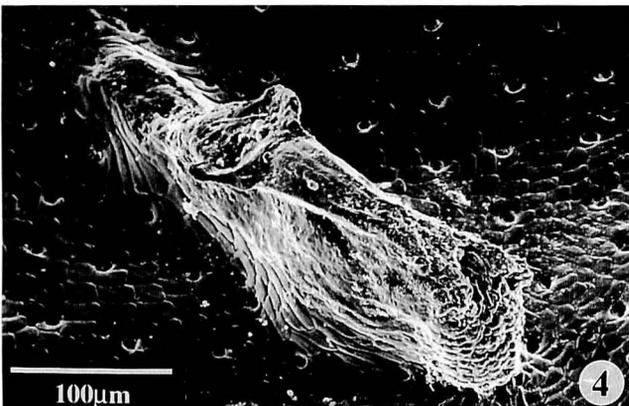
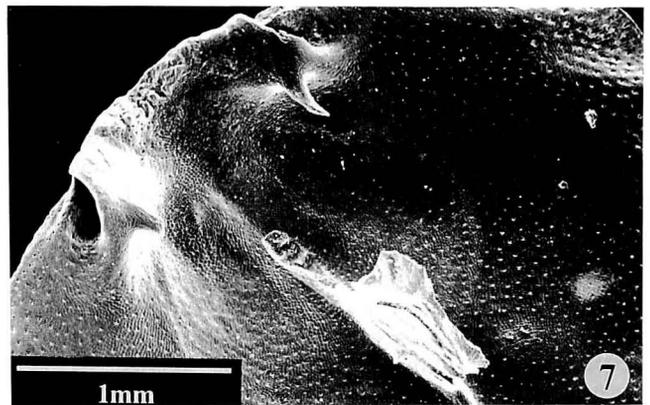
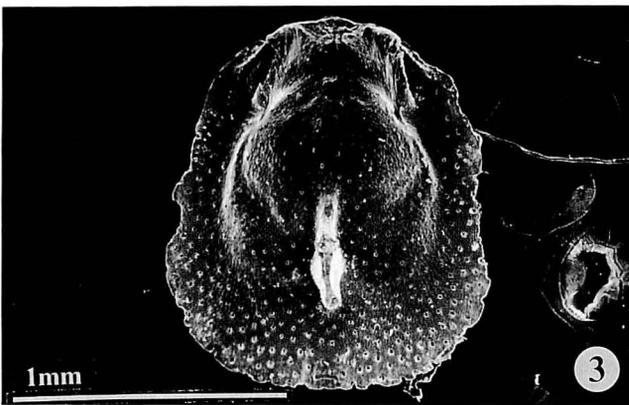
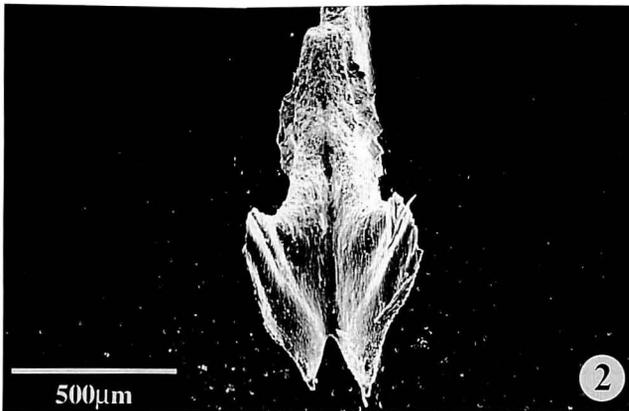
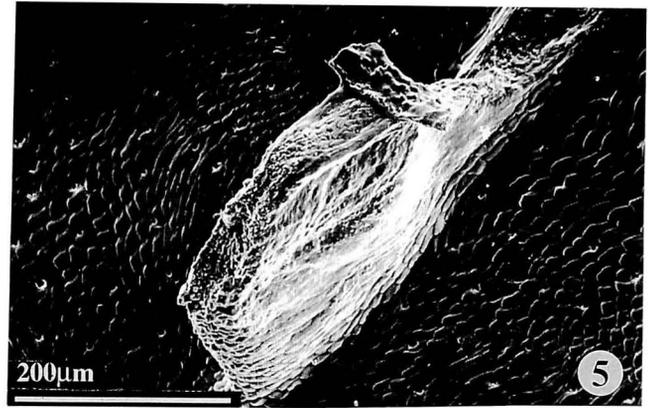
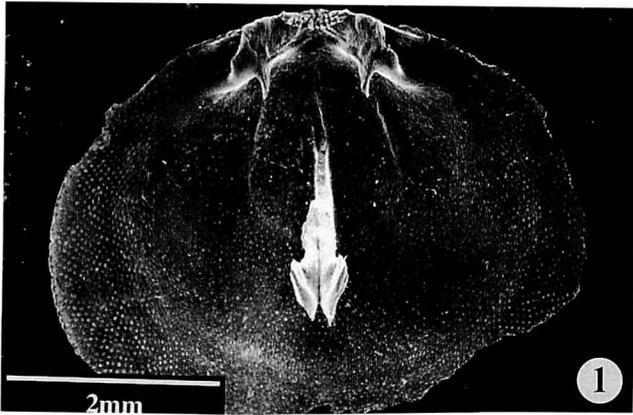
Jolonica nipponica Yabe and Hatai

At present, juvenile specimens of *Jolonica nipponica* are not available. Some adult specimens of *Jolonica nipponica* collected from the Izu Islands have been examined. These specimens (the smallest one being 6.3 mm in shell length) show a loop in the bilacunar phase as described by Richardson (1975).

Comparison of loop developmental patterns

The size range of shell length for each phase of loop development has been plotted for each species examined in order to compare loop development amongst the various laqueid species (Figure 7). However specimens at certain phases are presently unavailable for some species (e.g. juvenile phases of *J. nipponica*). From the available data (Figure 7) it appears that all examined species share essentially the same early stages of loop development as described by Richardson (1975), but there were some differences within species with respect to the shell sizes at which particular phases of loop development were attained. For example, in *Frenulina sanguinolenta*, ontogenetic variation in the rate of loop development can be seen. The second

Figure 4. 1-2. *Terebratalia coreanica*. 1: Specimen UMUT RB19841 (L=4.7 mm), ventral view. The lacunae are seen although the top part of the ring is broken. 2: Details of the loop in Figure 4-1. 3-8. *Coptothyris grayi*. 3: Ventral view of specimen 28498 (L=1.3 mm), in the collection of Tohoku University. 4: Detail of the flanges in Figure 4-3, oblique view. 5: Details of the flanges in specimen UMUT RB19843 (L=1.8 mm). Secondary layer fibers appear on the middle part of the edge of the septum. 6: Specimen UMUT RB19844 (L=2.4 mm), oblique view. 7: Oblique view (L=3.2 mm), specimen UMUT RB19845. Although most parts of the loop are broken, the anterior division and resorption of the posterior part of the medium septum are seen. 8: Specimen UMUT RB19846 (L=4.7 mm), details of the lacunae. Even though anterior fusion of the attachments of the ring and the descending branches has not occurred, the lacunae are perforating the bands of the ring and bifurcation of the septum progresses.



point is that no major discrepancy among species exist in the relative timing of loop development. The developmental patterns of '*Frenulina*' sp. is unusual because, as discussed later, the adult individuals possess an annular loop, which is typical of juvenile individuals in other species.

Discussion

It is important to note that there is some ontogenetic variation in the loop development within species. In *Frenulina sanguinolenta*, for example, several specimens of approximately 4 mm length indicate four different loop phases (i.e. annular phase, haptoid phase, bilacunar phase, and bilateral phase). These similar-sized specimens differ not only in their shape, thickness and size but also in the timing of the modification of the ring and/or septum as described by Richardson (1973a). One explanation for this variation may be that the growth speed vastly varies among individuals in this species. Gunji (1987) found three types of loop structure within a single species *Nipponithyris afra*, and attributed this variation to the very wide deviation of growth speed in *N. afra*. However, as the mode of absolute growth has not been known for *Frenulina sanguinolenta* or for other brachiopod species, this hypothesis is yet to be tested.

Although the earliest loop phases are not presently known in some species, it seems likely that all nine laqueid species examined trace virtually the same early phases of loop development, which are comparable to the loop development pattern for laqueids described by Richardson (1975). However when looked at more closely, some differences between taxa are apparent.

For example, anterior bifurcation of the septal pillar is observed in some species but is not observed in other species. Richardson (1975) suggested that in *Dallinella obsoleta*, *Fallax dalliniformis*, *Dallina septigera*, and *Laqueus californianus*, it is doubtful whether the septum bifurcates anteriorly, because in these species the appearance of splitting could be confused with the anterior fusion of attachments of the ring and the descending branches (i.e. haptoid phase). However, in the species observed in this study, it is evident that the anterior split in the septum occurs before the growing (anterior) edges of the ring and the descending branches fuse to form a haptoid loop. In *Laqueus* sp., specimens of the axial phase exhibit the anterior bifurcation of the median septum. The early anterior division of the

median septum also occurs in *C. grayi* and *T. coreanica*, but is not observed in the other species. In *Pictothyris picta*, *Pictothyris* sp., and *F. sanguinolenta*, by contrast, their haptoid and bilacunar loop phases show a non-bifurcate median septum projecting anteriorly between the divergent ascending and descending lamellae (Figures 2-2, 3-5, 5-6). This indicates that in these three species the anterior fusion of attachments of the ring and the descending branches occurred without any anterior bifurcation of the septum, and the loops of these species developed in a way different to that of *Laqueus* sp., *C. grayi*, and *T. coreanica*.

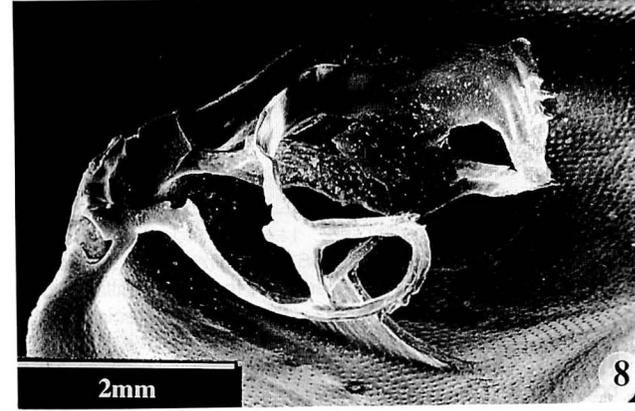
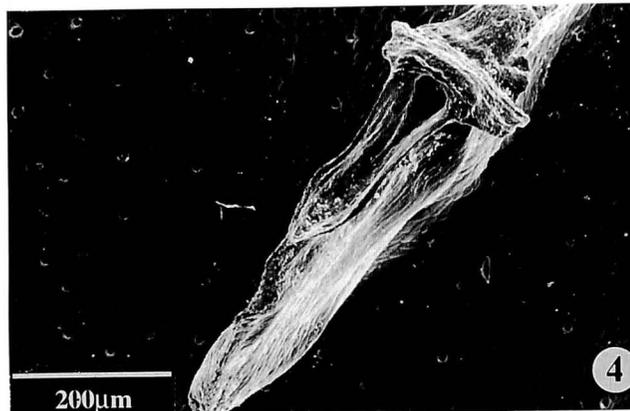
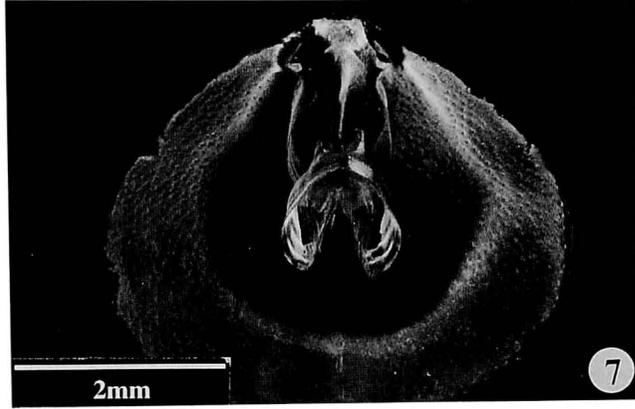
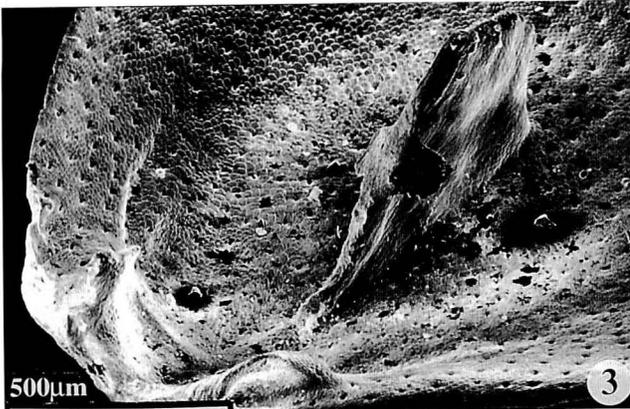
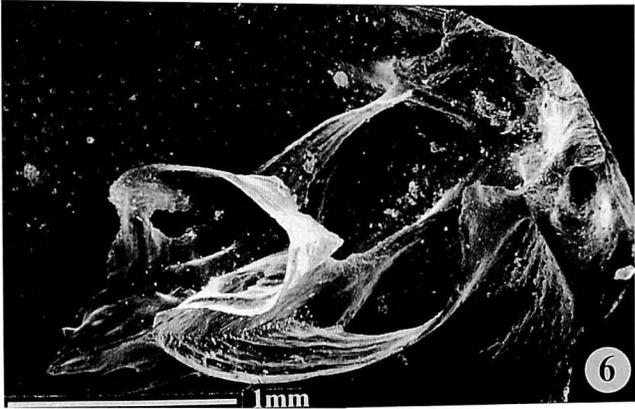
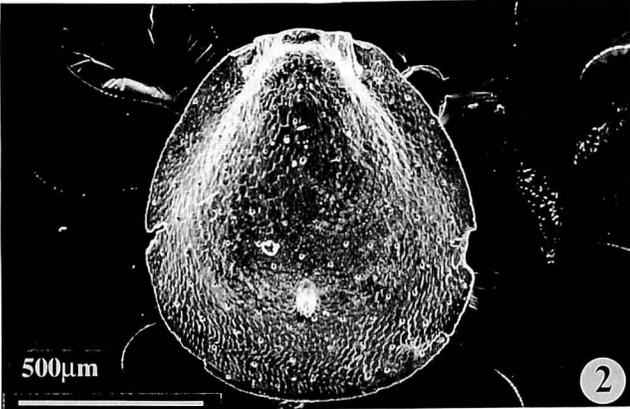
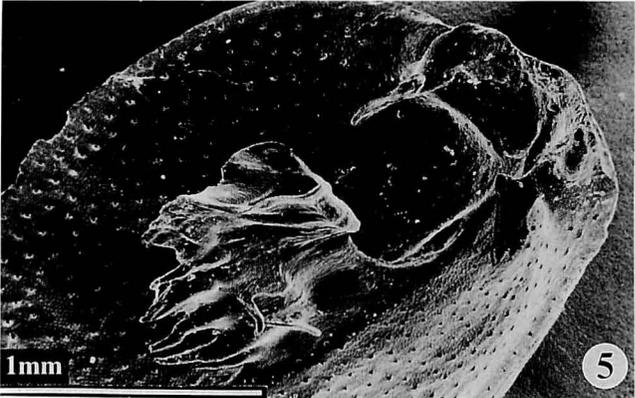
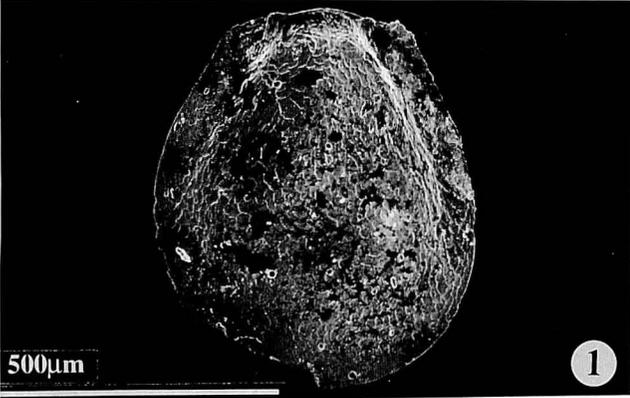
Another feature of interest is the disposition of the flanges in the axial and cucullate phases. The direction of the septal flanges is downward forward of the dorsal valve floor in *F. sanguinolenta*, but lateral in the other species examined. It may be worth pointing out that *Laqueus* and *Frenulina* were included in the same subfamily Kingeninae by Richardson (1975) mainly based on the loop pattern of the adult phases. However as mentioned before, *Laqueus* sp. and *F. sanguinolenta* differ in the early phases in such characters as the presence or absence of bifurcation of the septal pillar and the disposition of the septal flanges. The flanges in *Laqueus* sp. are laterally directed but in *F. sanguinolenta* the direction of the flanges is downward. These differences in the early loop phase indicate the possibility that these genera are more distantly related than previously believed.

A comparison of the loop ontogeny of '*Frenulina*' sp. from off Shimoda with the ontogenies of the other species reveals that '*Frenulina*' sp. resembles *F. sanguinolenta* externally, but differs significantly in adult loop pattern and mode of loop development.

In young shells of '*Frenulina*' sp., the valves are equally convex, and the lateral profile of the shell is rather flat, however the shells become more convex with growth. Specimens of '*Frenulina*' sp. with a ventral valve larger than 5 mm in length exhibit the thickened convex form, and their growth lines become crowded at the shell margins. Harada and Mano (1960) investigated the metamorphosis of '*Frenulina*' sp. by breeding, and observed matured gonads in the specimens with ventral valve length from 5 mm up to 7 mm. For the reasons given above, it is thus possible to state that '*Frenulina*' sp. attains the adult stage by the time a ventral valve length of 5 mm has been reached.

Turning now to the loop patterns of '*Frenulina*' sp., this species seems to be already at an adult stage when it has

Figure 5. *Frenulina sanguinolenta*. 1: Specimen UMUT RB19847 (L=0.7 mm), ventral view. 2: Ventral view (L=1.0 mm), specimen UMUT RB19848. Small septal pillar begins to emerge and the future cardinal process and the anterior borders of the developing hinge plates are indicated by thickenings on the valve floor. 3: Specimen UMUT RB19849 (L=1.3 mm), posterior view. Low socket ridges are seen. The direction of the flanges is downward. 4: Oblique view (L=2.2 mm), specimen UMUT RB19850. The hood with septal flanges. 5: Specimen UMUT RB19851 (L=3.3 mm), showing anteriorly spinous septal pillar and the ring. The crura and the descending branches extend. 6: Lateral view, specimen UMUT RB19852 (L=4.3 mm). Lacunae are perforating the bands of the ring. Scale Bar=1 mm. 7: Specimen UMUT RB19853 (L=4.4 mm) showing the anterior separation of the fused attachments and lacunae perforating the anterior and dorsal segments of the ring. 8: Lateral view, specimen UMUT RB19854 (L=6.6 mm). The adult loop.



the loop at a stage which is seen only in juveniles in other laqueid species. The fact that there is no fossil record for '*Frenulina*' sp., while all the other genera examined except for *Frenulina* are known from Neogene-Pleistocene deposits (Muir-Wood *et al.*, 1965) suggests that '*Frenulina*' sp. is probably a recently established species derived from an ancestor with a 'normal' loop like that observed in other Recent species. As figure 7 indicates, there is no major variation in the size ranges of early loop developmental phases amongst the examined species, but in '*Frenulina*' sp., loop development prematurely stops at the annular phase as a result of precocious sexual maturation. Viewed in this light, '*Frenulina*' sp. can be regarded as a pedomorphic species that evolved by a process of progenesis (Alberch *et al.*, 1979; McKinney and McNamara, 1991).

The pattern of early loop development in '*Frenulina*' sp. has some similarities with that of *Pictothyris picta*, *Pictothyris* sp., and *Frenulina sanguinolenta* in such features as the non-bifurcate septal pillar. Especially, the form of the median septum of '*Frenulina*' sp. is similar to that of *Pictothyris* sp., but the cardinalia resembles that of young phases of *Laqueus* sp. in some features such as morphology of the hinge plates and absence of cardinal process. Although close affinity among '*Frenulina*' sp., *Pictothyris* sp. and *Laqueus* sp. is strongly suggested, the relationships among these three species is an unsettled question.

It is interesting to consider the interspecific variations of the loop in terms of developmental constraint as described by Gunji (1987). He showed that in haptoid phase and phases later than bilacunar (i.e. bilateral, latero-vertical, trabecular, and teliform), loop transformation depends on the location of the 'loop center' and that interspecific variations of the loop ontogeny may be explained by shifting of the 'loop center'. It is, however, difficult to directly apply the concept of developmental constraint to the early stages prior to the haptoid phase, because the loop elements discussed by Gunji (1987) are only seen in the late haptoid phase of later. Although the factors responsible for the variations in

the early loop development are unknown, they should be important in understanding loop ontogeny.

Differences and similarities in the early loop developmental phases described herein demonstrate that they can be used to assess general relationships at the generic level, but a much more comprehensive study on both Recent and fossil forms and on a number of congeneric species is required in order to infer detailed relationships amongst laqueid brachiopods as a whole.

Summary

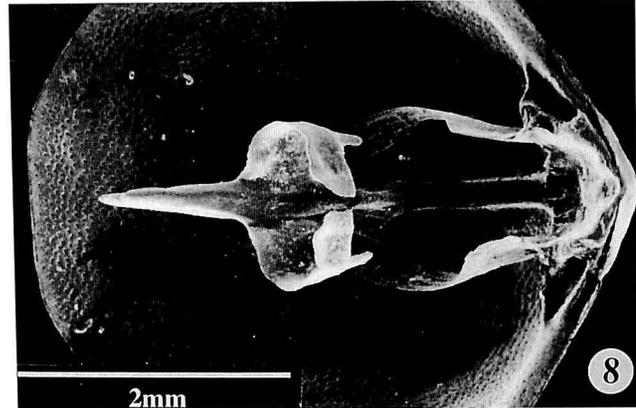
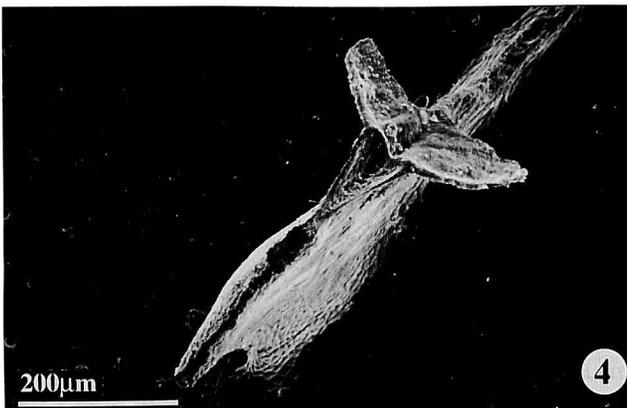
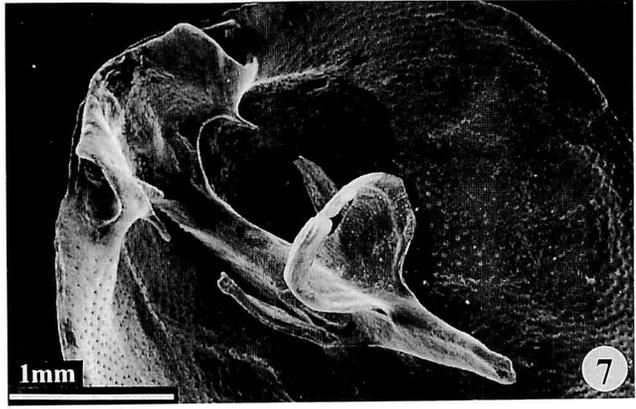
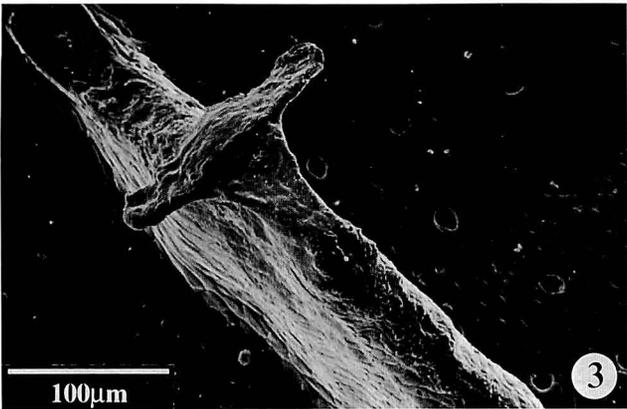
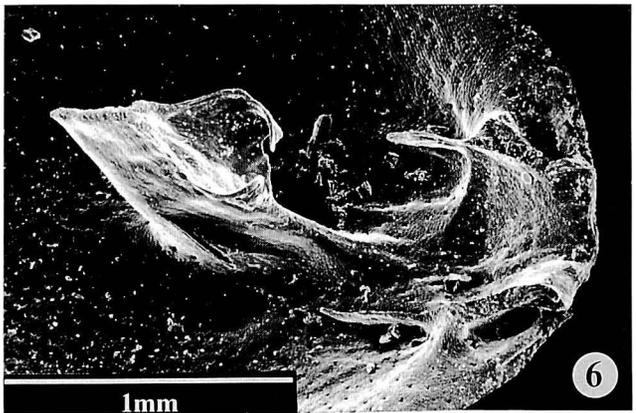
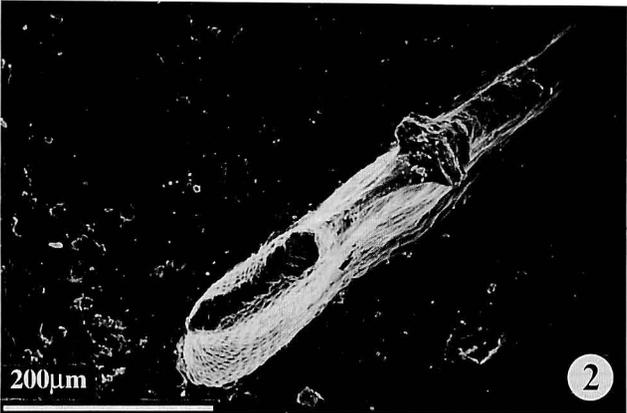
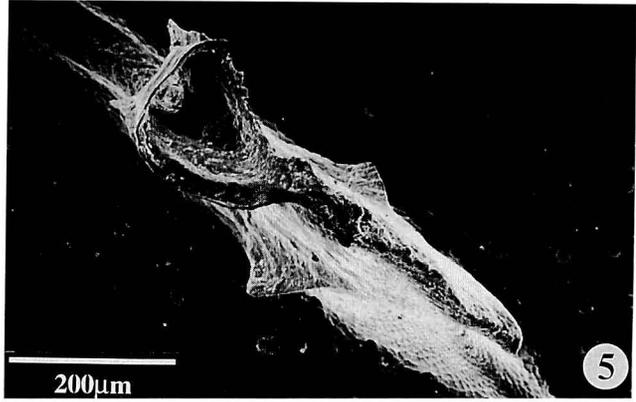
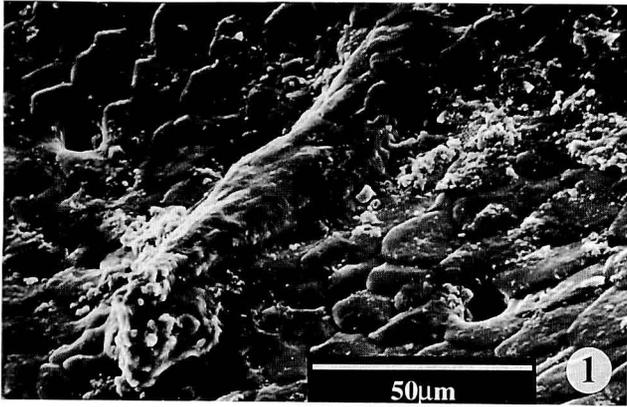
1. All the laqueid species examined appear to exhibit roughly the same phases of loop development as those described by Richardson (1975). However some morphological differences are seen in the early phases of the loop development. Although *Laqueus* and *Frenulina* are sometimes included in the same subfamily mainly based on the adult loop pattern, the early loop patterns of these two species are rather different. This fact suggests that these genera may not be as closely related as previously considered by Richardson (1975).

2. The following early loop characters are considered important in considering phylogenetic relationships of laqueid brachiopods: disposition of the septal flanges, presence or absence of bifurcation of the median septum, and the timing of separation of fused ascending and descending loop branches from the septal pillar.

3. Some intraspecific variations are observed in the relative timing of loop development for example, in *F. sanguinolenta*.

4. There is no major variation between the examined species in the relative timing of loop development. However, the loop developmental pattern of '*Frenulina*' sp. is unusual, suggesting a heterochronic relationship with other species. It seems likely that '*Frenulina*' sp. has been derived from a process of progenesis.

Figure 6. '*Frenulina*' sp. 1: A low non-fibrous septal pillar in specimen UMUT RB19855 (L=0.7 mm). 2: Oblique view, specimen UMUT RB19856 (L=0.9 mm) with septal pillar and small septal flanges. 3: Specimen UMUT RB19857 (L=1.5 mm), showing the ventral edge of the septal pillar and the extension of the flanges beginning to form a depression. 4: Specimen UMUT RB19858 (L=1.9 mm). 5: Specimen UMUT RB19859 (L=2.4 mm), showing a ring with rudiments of the flanges. 6: Lateral view, specimen UMUT RB19860 (L=2.8 mm). 7: Specimen UMUT RB19861 (L=4.2 mm), oblique view. The descending branches are not fused. 8: The adult stage loop with an incomplete ring and complete descending branches (L=4.7 mm). Specimen UMUT RB19862.



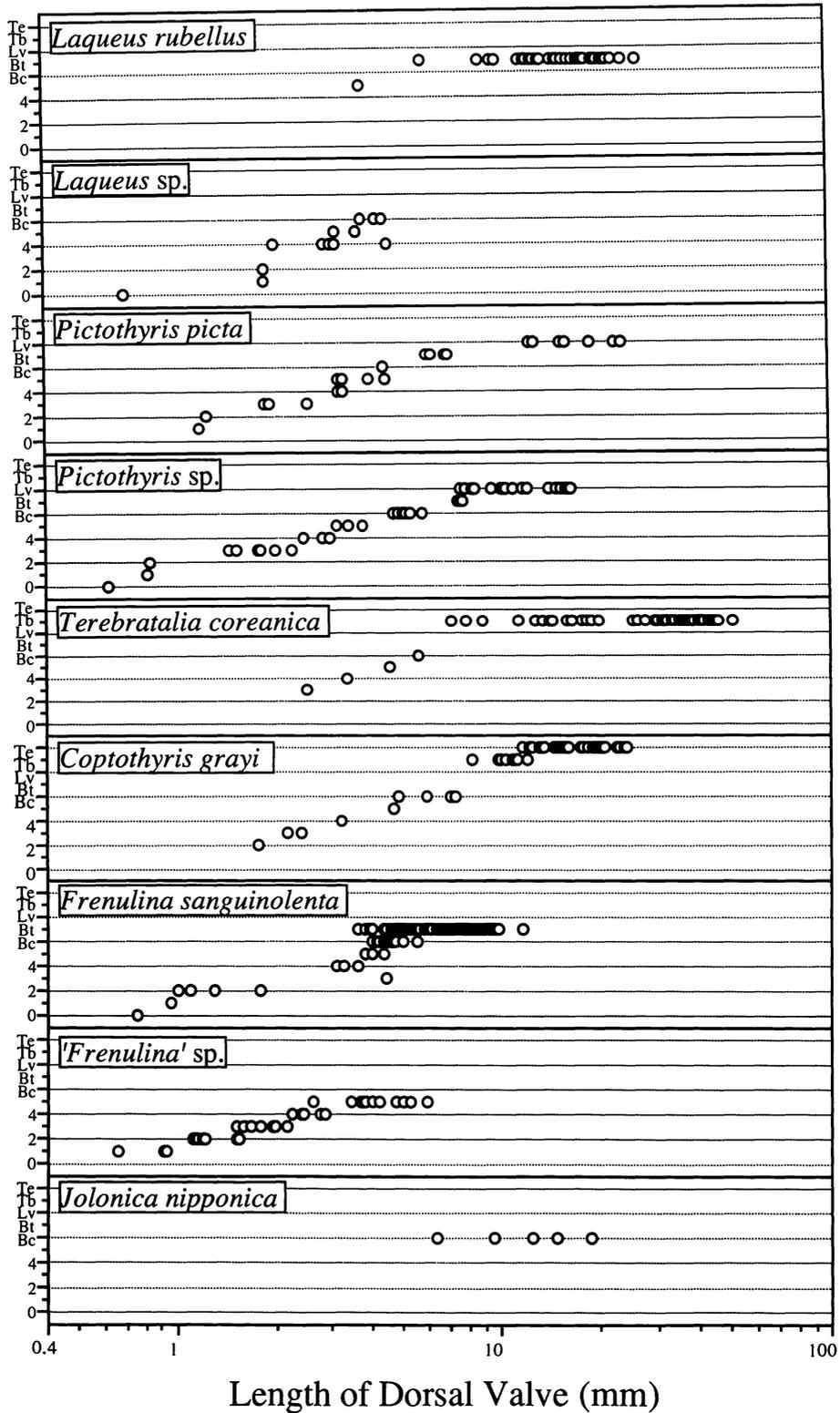


Figure 7. Size of each loop developmental phase plotted for the examined laqueid species. Each point indicates an individual specimen with the phase of loop development indicated. The right end of the plot for each species corresponds to the specimen of the maximum shell length so far collected for each species. Abbreviations in the vertical axis: Pb=Prebrachidial phase, Axe=Axial phase (early), Axl=Axial phase (late), Cu=Cucullate phase, An=Annular phase, Hp=Haptoid phase, Bc=Bilacunar phase, Bt=Bilateral phase, Lv=Latero-vertical phase, Tb=Trabecular phase, Te=Teloform phase.

Acknowledgments

The author wishes to thank Dr. K. Endo (University of Tokyo) for critical reading of the first draft, and Prof. K. Tanabe, Dr. T. Oji (University of Tokyo) for their helpful advice. I wish to thank Dr. M. Arita (Geological Survey of Japan), Mr. H. Fukuda (Tokyo Metropolitan University), Mr. T. Miyauchi (Wakkanai City), Prof. S. Ohta and Mr. E. Tsuchida (Ocean Research Institute, University of Tokyo) for their help in collecting samples, and Dr. D.I. MacKinnon of University of Canterbury, New Zealand for advice on techniques of sample preparation and providing me with important suggestions. This study was supported by a grant from the Fujiwara Natural History Foundation.

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Miocene decapod crustacea from the Chichibu Basin, Central Japan

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Received 17 July 1995; Revised manuscript accepted 14 May 1996

Abstract. Seventeen fossil decapods are described from the Miocene of the Chichibu Basin, Saitama Prefecture, Central Japan. The decapods occur in the Ushikubitoge Formation, Nagura Formation and Yokoze Formation. The following five are new: *Trachycarcinus inflatus*, *Cancer sakamotoi*, *Itoigawaia chichibuensis*, *Maja morii*, *Miosesarma nagurensis*. Six decapod assemblages are recognized in the basin. The fauna is characterized by the predominance of muddy bottom inhabitants of the lower sublittoral zone, represented by the *Miosesarma nagurensis* sp. nov. assemblage from the Nagura Formation. The occurrence of *Maja morii* sp. nov. is the first fossil record of the genus from the northern Pacific region.

Key words: Miocene, Crustacea, Decapoda, new species, Chichibu Basin, decapod assemblage.

Introduction

Tertiary strata of the Chichibu Basin have been studied in detail for over 60 years (Hayakawa, 1930; Watanabe *et al.*, 1950; Ijiri *et al.*, 1950; Arai, 1960; Kanno, 1960; Hyodo, 1986; Latt, 1990; Takahashi, 1992, *etc.*). It is well known that they yield numerous crabs. These fossil decapods, however, have never been described and studied up to the present, although many other fossil groups have been studied in detail.

Recently, 120 species of decapod crustacean fossils were described from the Cenozoic of Southwest Japan and their faunal changes in relation to climatic change were discussed (Karasawa, 1993). Nevertheless, knowledge of the decapod fauna from the Cenozoic of Northeast Japan is still fragmentary, with several records by Nagao (1932, 1941, *etc.*), Imaizumi (1951, 1958a, 1958b, 1961, 1962, *etc.*), Takeda and Fujiyama (1984) and Takeda *et al.* (1984).

The present study presents one of the faunal aspects of the Miocene fossil decapod assemblages from Northeast Japan.

General outline of geology in the study area

Tertiary deposits in the Chichibu Basin are distributed in an area about 15 km from east to west and 12 km from north to south (Figures 1, 3). The three major stratigraphic units of the Tertiary established by Arai (1960) and Kanno (1960) are the Ushikubitoge Formation, Oganomachi Group and the Chichibumachi Group, in ascending order (Figure 2). All of them are marine deposits.

The Ushikubitoge Formation unconformably overlies base-

ment rocks. It consists of a basal conglomerate and sandstone with inliers of the Tomita Siltstone Member and the Nenokami Sandstone Member. Decapod fossils were found in the loose sandy siltstone immediately above the basal conglomerate of the Ushikubitoge Formation distributed in

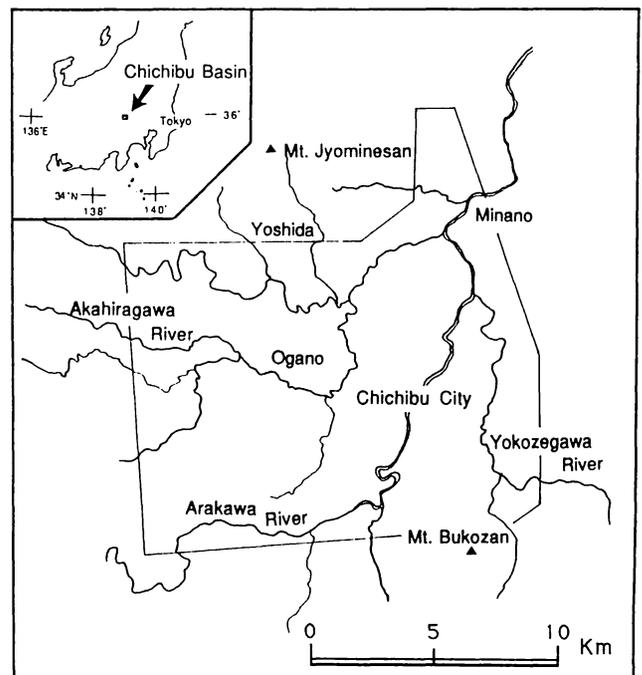
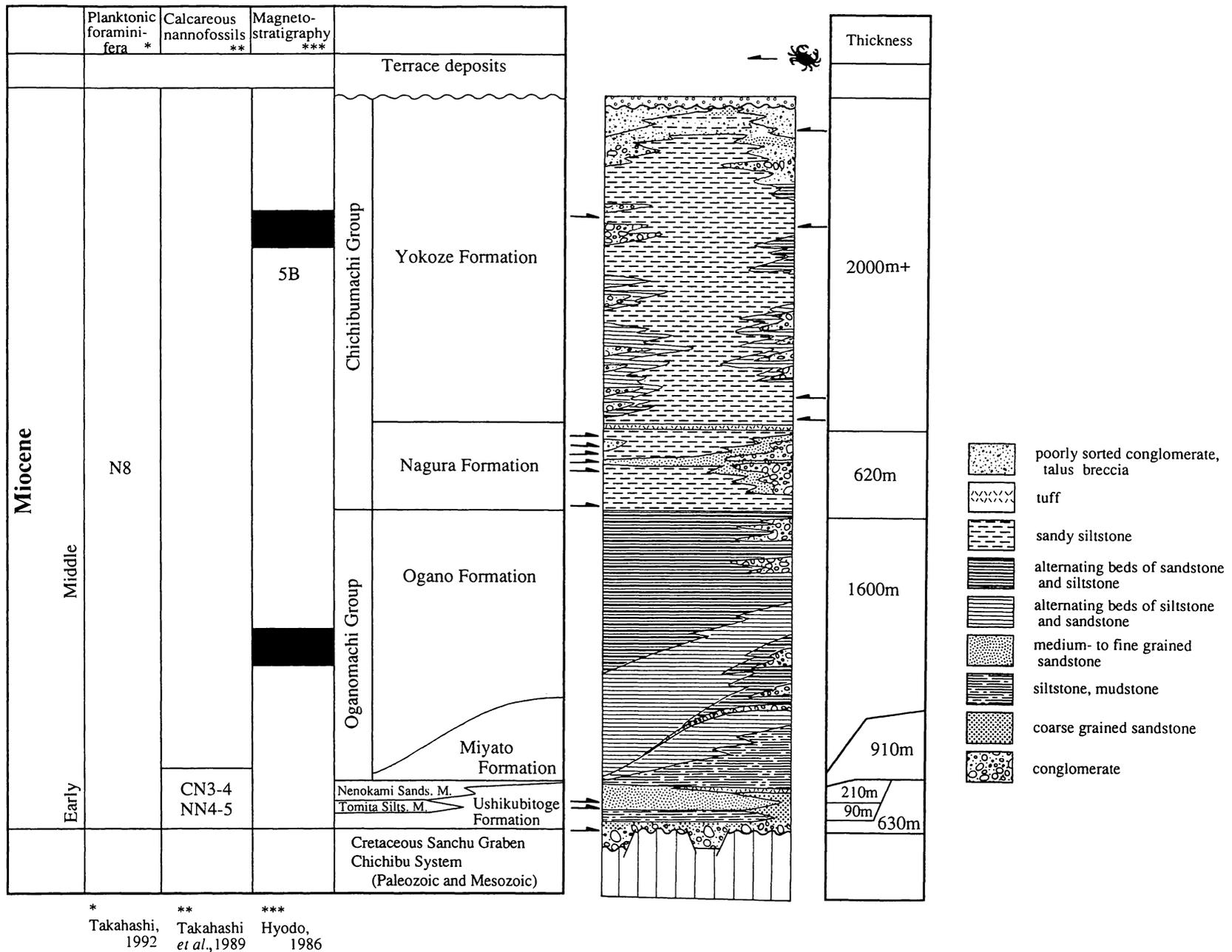


Figure 1. Map showing location of the study area.



* Takahashi, 1992
 ** Takahashi et al., 1989
 *** Hyodo, 1986

Figure 2. Synthetic stratigraphy and columnar section of Miocene formations of the Chichibu Basin. Arrows indicate decapod fossil bearing horizons.

the northwestern part of the basin and in the Nenokami Sandstone Member extending into the northeastern part of the basin. The Tomita Siltstone Member yields many molluscan fossils, but no decapod fossils. According to

Kanno (1960), the main part of the Ushikubitoge Formation was deposited in a shallow marine environment. The Nenokami Sandstone Member was deposited in shallow, warm to temperate water. Kanno described the molluscan

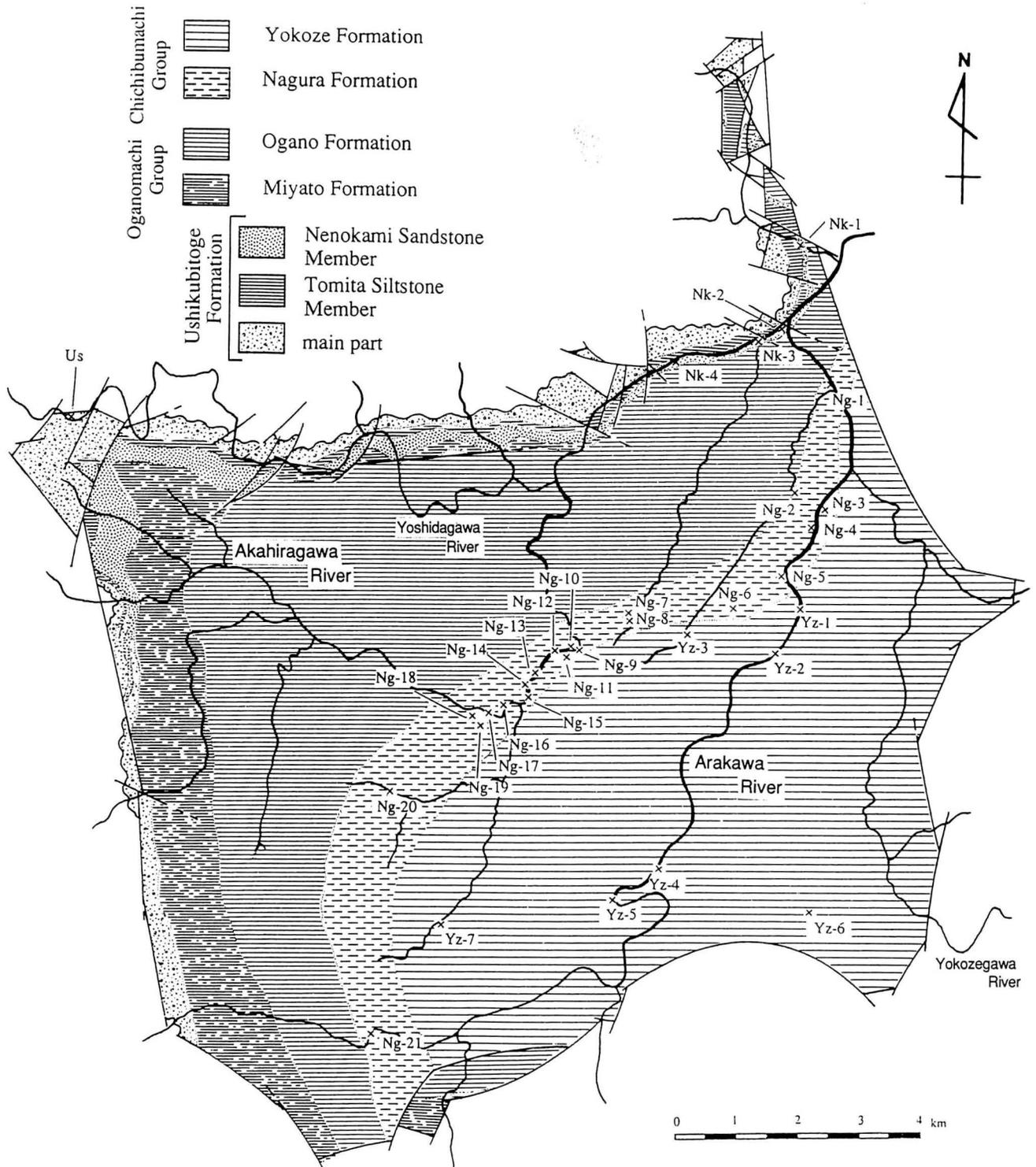


Figure 3. Map showing decapod fossil localities on the geological map of the study area.

assemblage of the Tomita Siltstone Member and inferred depths greater than 200 m. The microfossil evidence, however, suggests an inner neritic environment (Ujiie and Iijima, 1959; Takahashi, 1992).

The Oganomachi Group conformably overlies the Ushikubitoge Formation. It is characterized by thick turbidite sediments, consisting mainly of alternating beds of siltstone and sandstone that were deposited in bathyal environments (Takahashi, 1992). Megafossils are very scarce in this group, and decapod fossils were not obtained.

The Chichibumachi Group comprises the Nagura and Yokoze Formations. The Nagura Formation is dominated by fossiliferous, gray to light gray, massive to weakly bedded sandy siltstone which was deposited in a shallow-water environment (Kanno, 1960; Latt, 1990; Takahashi, 1992). Molluscan fossils are common in this formation and abundant decapod fossils occurred in the middle to upper part (Figure 2). The uppermost part of this formation is bounded by whitish tuff beds ('Tadenuma Tuff Beds' in Hyodo, 1986). The overlying Yokoze Formation is composed of massive sandy siltstone and coarse-grained marginal deposits of the sedimentary basin, such as poorly sorted conglomerate and talus breccia. This formation locally contains abundant molluscs and occasional decapod fossils. Although it is widely accepted that the molluscs from the coarse-grained sediments indicate a rocky or sandy bottom of warm, shallow water, the depositional environment of the uniform sandy siltstone distributed in the central part of the basin is still controversial. A deeper environment (Kanno, 1960), a semipelagic basin plain (Latt, 1990), and a shallow, inner sublittoral environment (Takahashi, 1992) have all been suggested.

In general, the sediments of the Oganomachi Group become coarser towards the southern border, intercalating a number of conglomerate layers. In contrast, those of the Chichibumachi Group become coarser either towards the southern and eastern border, intercalating numerous thick conglomerate layers.

The geologic age of these strata is given in Figure 2. Takahashi (1992) showed that the planktonic foraminifera obtained from throughout the Tertiary of the basin indicate zone N. 8 of Blow (1969). According to Takahashi *et al.* (1989), the calcareous nannofossils from the Ushikubitoge and Miyato Formations indicate zones CN 3-4 of Okada and Bukry (1980) or NN 4-5 of Martini (1971). Hyodo (1986) and Hyodo and Niitsuma (1986) suggested that the normal polarity observed in the upper part of the Oganomachi and Chichibumachi Groups is correlated with the ocean magnetic anomaly 5B.

The total thickness of the Tertiary sequences in this region attains a maximum of more than 5,000 meters. The thickness of each formation is given in Figure 2.

Decapod fossil preservation

The occurrence of decapod fossils in the Chichibu Basin may be placed into three categories. 1) Decapods that are preserved in nodules thought to represent burrows. Many *Upogebia* sp. specimens were preserved in this condition.

2) Decapods sporadically buried in sandy siltstone free of calcareous nodules or concretions. Many crabs are articulated, indeed, most crabs from the basin are preserved in this condition. They are more or less depressed, and some crabs are preserved in the open molt position (Schäfer, 1951; Bishop, 1986a). Since even these fragile exuviae are more or less articulated, these crabs may be autochthonous. 3) Crabs as disarticulated or fragmentary remains. This mode of occurrence was frequently observed in coarse-grained sediment (weakly consolidated sandy siltstone and conglomerate) of the Yokoze Formation.

Decapod assemblages

About 800 fossil decapods were collected from 33 localities which are listed in Table 1. Six decapod assemblages can be recognized on the basis of dominant species. This faunal analysis based on the characteristic species reveals the presence of two different decapod assemblages even in the sandy siltstone of the Nagura Formation; they are similar in appearance.

1. *Upogebia* sp. assemblage

This assemblage is defined by the predominance of *Upogebia* sp. which often shows *in situ* preservation. *Upogebia* sp. was commonly found in cemented burrows. Some carapaces were found retaining those abdominal parts which are very fragile and easily detached after death. Most of the Japanese living and fossil species of *Upogebia* are known from intertidal to sublittoral environments (Sakai, 1982; Karasawa, 1993). This assemblage was observed only in the basal part of the Ushikubitoge Formation, and confirms the conditions of the lower part of this formation described by Kanno (1960) from the molluscan evidence as those of 'the Shirasu Sandstone Member'.

Co-occurring molluscan fossils: *Nucula* sp., *Lucinoma* sp., *Acila* sp., *Macoma* sp., *Mya* sp., *Orectospira* ? sp., and *Thracia* sp.

Locality and horizon: Us (basal part of the Ushikubitoge Formation).

2. *Carcinoplax antiqua* assemblage

The *Carcinoplax antiqua* assemblage is defined by the abundance of *C. antiqua*. This assemblage is recognized in the Nenokami Sandstone Member and Nagura Formation. However, the modes of occurrences are slightly different between the two horizons. In the Nenokami Sandstone Member this assemblage includes *Munida* sp. which is considered to be a relatively deeper water taxon, and is associated with relatively diversified molluscs. On the contrary, in the Nagura Formation this assemblage yields less diversified molluscan and co-occurring decapod taxa. The *Carcinoplax antiqua* assemblage is here considered a sandy bottom assemblage of the lower sublittoral zone on the basis of the molluscan evidence by Kanno (1960; 1980) and the present study.

Co-occurring molluscan fossils: *Acila* sp., *Saccella* sp., *Modiolus* ? sp., *Felaniella* sp., *Chlamys* sp., *Mizuhopecten chichibuensis*, *Venericardia* (*Cyclocardia*) *pacifera*, *Macoma*

sp., *Cultellus izumoensis*, *Turritella* sp. *Tectonatica* sp., *Galeodea* sp. and *Dentalium* sp.

Locality and horizon: Nk-1, 2 (Nenokami Sandstone Member of the Ushikubitoge Formation); Ng-5, 19 (Nagura Formation).

3. *Miosesarma nagurensis* sp. nov. assemblage

This assemblage is defined by the predominance of *Miosesarma nagurensis* sp. nov. and contains *Carcinoplax antiqua* and *Mursia takahashii*. At several localities the Nagura Formation yields abundant *M. nagurensis* having wide ranges of carapace width (e.g. 6 mm–27 mm at Ng-13). These facts and the mode of preservation indicate that the assemblage may be autochthonous or nearly so. Considering the evidence of microfossils by Takahashi (1992) and molluscan fossils in this study, the environment of this assemblage is supposed to be a muddy bottom setting in the inner sublittoral zone. This interpretation corresponds to the fact that the *Miosesarma japonicum*-*C. antiqua* assemblage in the late Early Miocene of southwestern Japan is considered to be comprised of sandy or muddy inhabitants of the lower sublittoral zone (Karasawa, 1993).

Co-occurring molluscan fossils: *Acila* sp., *Portlandia* sp., *Yoldia rhombica* and *Cultellus izumoensis*.

Locality and horizon: Ng-13, 6, 10, 14.

4. *Trachycarcinus inflatus* sp. nov. assemblage

This assemblage is composed mainly of *Trachycarcinus inflatus* sp. nov., *Cancer sakamotoi* sp. nov., *M. takahashii*, *Itoigawaia chichibuensis* sp. nov. and *Callianopsis* sp. 1, and contains *Munida* sp. and *Eucalliax* sp. It is characterized by the absence of *Miosesarma nagurensis* sp. nov. and *C. antiqua*, and shows apparently high species diversity in comparison with the other assemblages in the basin. At locality Ng-4, this assemblage is accompanied by abundant molluscan fossils, including conjoined valves of the large pectinid *Mizuhopecten kimurai*. Therefore, this assemblage indicates a sublittoral environment. The microfossils of Takahashi (1992) and the molluscan fossils of the present study, however, suggest a slightly deeper environment than the former two assemblages. Despite the absence of *T. inflatus*, Ng-18 has a similar species composition.

Co-occurring molluscan fossils: *Acila* sp., *Portlandia watasei*, *Lucinoma* sp., *Mizuhopecten kimurai*, *Cultellus izumoensis*, *Periploma* sp. and *Apollon yabei*.

Locality and horizon: Ng-4 (Nagura Formation).

5. Xanthidae assemblage

Xanthid crabs, comparable with *Medaeus*, occurred in loose silty sandstone of the upper part of the Yokoze Formation (Yz-6). This formation, exposed near the southern and eastern borders of the basin, intercalates a number of conglomerate beds and talus breccia that occasionally contain abundant rocky shore molluscs and hermatypic corals. These conglomerates rarely contain poorly preserved dactyli and fixed fingers of xanthid crabs. At Yz-6, a few meters above and below the decapod horizon are intercalated cobble to granule conglomerate beds which contain abundant rocky shore gastropods such as *Turbo* sp. and

Conus sp. This assemblage is characterized by the epibionts on the rocky shore or sandy bottom in the marginal area of the basin.

Co-occurring molluscan fossils (Yz-6): *Concochele disjuncta*, *Lucinoma* sp., and *Cuspidaria* sp.

Locality and horizon: Yz-5, 6 (Yokoze Formation).

6. *Callianopsis* spp. assemblage

In contrast with marginal coarse sediments, the thick and monotonous sandy siltstone of the Yokoze Formation exposed in the central part of the basin yields frequent *Callianopsis* spp. in association with fossil burrows. Therefore this assemblage consists of autochthonous endobionts of muddy bottoms in the central part of the basin.

Co-occurring molluscan fossils: *Solemya* sp., *Portlandia* sp., *Lucinoma* sp., and *Periploma* sp.

Locality and horizon: Yz-4 (Yokoze Formation).

Discussion

The decapod fauna in the Chichibu Basin is represented by the predominance of muddy bottom inhabitants in shallow water environments as a whole. Recognition of six decapod assemblages signifies relatively high diversity of the fauna, considering that most of the decapods occurred in limited lithofacies (mainly sandy siltstone). While many of the decapod genera also occur in the Lower to Middle Miocene of Southwest Japan (11 out of 15 genera in Karasawa, 1993), the fauna shows less similarity on the species level (only 2 out of the 17 species). Tropical species reported from the early Middle Miocene of Southwest Japan, e.g. *Ozius collinsi* (Karasawa, 1992), *Thalassina anomala* (Karasawa and Nishikawa, 1991), *Euryozius* spp. (Karasawa, 1993) and *Daira perlata* (Karasawa, 1993), were not found in the basin studied, nor was *Scylla ozawai* Glaessner, 1933, which was a subtropical-tropical species described from the Kadonosawa Formation in Iwate Prefecture and several localities in Southwest Japan.

The most characteristic feature of the decapod assemblages from the Chichibu Basin is that almost all the specimens occurred in limited lithologic facies of limited stratigraphic horizons (Nenokami Sandstone Member and Nagura Formation; Table 2). At some localities (Ng-10, 13) the Nagura Formation yielded very abundant *Miosesarma nagurensis*, occasionally exceeding in number the associated molluscs. Bishop (1986b) discussed such decapod-dominated assemblages, and classified the mode of occurrences of decapods into 1) uncommon remains in molluscan fossil assemblages, 2) common remains in molluscan-dominated fossil assemblages and 3) dominant elements in decapod assemblages (e.g. the Upper Cretaceous *Dakoticancer* Assemblage by Bishop, 1986a; 1986b, etc., which is considered to have been caused by optimal conditions for the crab).

The predominance of *Miosesarma* in the Chichibu Basin may represent a similar mode of occurrence to the *Dakoticancer* Assemblage with respect to the numerical dominance of crabs over molluscs. Since the *Dakoticancer* Assemblage is found in quite limited stratigraphic horizons

Table 2. Stratigraphic distributions and dominant decapod species of each formation.

Formation	No. of species and material	Dominant species	No. of materials	%	Life Mode	Bottom character
Yokoze F.	8(19)	<i>Miosesarma nagureense</i> n. sp.	6	32	epibenthos	silty sand
		<i>Callianopsis</i> sp. 2	4	21	endobenthos	silty sand
Nagura F.	13(650)	<i>Miosesarma nagureense</i> n. sp.	368	57	epibenthos	silty sand
		<i>Carcinoplax antiqua</i>	81	12	epibenthos	silty sand-medium sand
		<i>Trachycarcinus inflatus</i> n. sp.	44	6.4	epibenthos	silty sand
		<i>Mursia takahashii</i>	35	5.8	epibenthos	silty sand
Ogano F.						
Miyato F.						
Nenokami Ss. M.	5(45)	<i>Carcinoplax antiqua</i>	30	56	epibenthos	silty sand-fine sand
Tomita Silts. M		<i>Munida</i> sp.	11	22	epibenthos	silty sand-medium sand
		<i>Miosesarma nagureense</i> n. sp.	9	20	epibenthos	silty sand-fine sand
Ushikubitoge F.	2(13)	<i>Upogebia</i> sp.	13	92	endobenthos	sandy silt

(3 m to 7 m thick) over widespread areas (15 km² to 1,500 km²) and occurs repeatedly, it is probable that this pattern represents periodic blossoming of the opportunistic decapod species in consequence of the change of the environmental conditions, as noted by Bishop (1986b). On the other hand, the stratigraphic horizons of the *Miosesarma nagureense* sp. nov. assemblage are not so limited and the lateral extension of the distribution of the assemblage is not clear.

The density of decapod crabs in the Chichibu Basin is not great as compared to recent submarine decapod communities (e.g. Thorson, 1957). Therefore, the abundance of the decapod fossils in the basin may have been due to sedimentary conditions which by chance favored their preservation. Some other decapod-dominant assemblages in Japan that are mainly composed of endobiont Thalassinidea 'shrimps' remain to be studied.

Acknowledgments

I wish to express my sincere gratitude to Professor Kei Mori of the Institute of Geoenvironmental Science, Graduate School of Science, Tohoku University, for helpful suggestions, continuous encouragement throughout this study, and critical reading of the manuscript. Deep gratitude is also expressed to Professor Rodney M. Feldmann and Ms. Carrie Schweitzer-Hopkins of Kent State University, Ohio and Dr. Joe S.H. Collins of London for their critical reading of the manuscript and many useful comments. I wish to express my hearty thanks to Professors Tsunemasa Saito and Kunihiko Ishizaki of Tohoku University for their useful suggestions and encouragement. I wish to thank Mr. Osamu Sakamoto of the Saitama Museum of Natural History for supporting the field survey and providing valuable comments. Thanks are also due to Dr. Hiroaki Karasawa of the Mizunami Fossil Museum, Dr. Masatsune Takeda of the

National Science Museum, and Drs. Akira Asakura and Tomoyuki Komai of Natural History Museum and Institute, Chiba for valuable suggestions regarding the systematic placements of several decapod taxa. Sincere thanks are also due to Drs. Masanori Shimamoto and Yoshikazu Noda of Tohoku University, and Dr. Masaki Takahashi of the Geological Survey of Japan. The author is much indebted to Mr. Yuji Takakuwa of the Gunma Museum of Natural History, Mr. Kiyohiko Ogai, Kazo City and Mr. Yoshiaki Mizuno, Nagoya City, for assistance in collecting and loan of specimens.

Systematic descriptions

The described and figured specimens are deposited in the collection of the Institute of Geology and Paleontology, Faculty of Science, Tohoku University, Sendai, 980-77 Japan (IGPS coll. cat. no. 102438-102442, 102713-103102).

Order Decapoda
 Infraorder Thalassinidea Latreille, 1831
 Superfamily Callianassoidea Dana, 1852
 Family Upogebiidae Borradaile, 1903
 Genus *Upogebia* Leach, 1814

Type species.—By monotypy *Cancer stellatus* Montagu, 1808 (ICZN Opinion 434).

Geologic range.—Cretaceous? to Recent.

Upogebia sp.

Figures 4-1a—3b

Material.—IGPS coll. cat. no. 102438-102443.

Occurrence.—Ushikubitoge Formation.

Description.—Carapace with trilobed front. Rostrum tri-

angular with an obtuse apex; two or three series of granules and a narrow median furrow. Lateral longitudinal ridge tuberculated and broadened in anterior part; gradually becoming narrower in posterior part. Lateral longitudinal groove deep in anterior part; slightly divergent backward. Cervical groove distinct. Posterior thoracic region with a row of granules along cervical groove in lateral part of dorsal surface and lateral surface.

First and 2nd abdominal somites longer than 3rd-6th somites.

First legs subchelate, equal in size and shape. Inner and outer surfaces of manus moderately swollen, rectangular in outline. Proximal and upper margins of inner surface fringed by row of granules. Outer surface of manus irregularly granulated; granules dense in lower half, clustered to form wrinkles. Fixed finger small, acutely triangular in lateral view, but dentition unknown. Carpus rectangular in upper view, outer surface with two shallow longitudinal grooves.

Remarks.—The present species is similar to the Recent *Upogebia major* (De Haan, 1839) from Japan in the features of the rostrum and propodus of the first leg, but detailed comparison between the two is difficult, because of the absence of the dactylus of the first leg.

Family Callianassidae Dana, 1852
Subfamily Eucalliinae Manning and Felder, 1991
Genus *Eucalliix* Manning and Felder, 1991

Type species.—By original designation *Callianassa quadracuta* Biffar, 1970.

Geologic Range.—Eocene to Recent.

Eucalliix sp.

Figures 4-4a, b

Material.—IGPS coll. cat. no. 102713-102717.

Occurrence.—Nagura Formation.

Description.—Slightly smaller right chela with acute, long fixed finger. Manus of right chela short; lower part of outer surface bearing clusters of tubercles; lower margin fringed by granules; lower proximal margin moderately arched outward. Fixed finger slightly shorter than manus, moderately curved upward; inner surface with broad, longitudinal depression and two or three granules on basal part.

Larger left chela stubby with short fixed finger. Distal part of outer surface of manus divided into upper thickened angle, middle part and base of fixed finger. Fixed finger about half as long as manus. Dactylus strongly bent downward; a strong, longitudinal keel on outer surface and large tubercles above keel.

Remarks.—The chelae of the present species resemble the larger chelae of *Callianopsis* spp. However, it is distinguishable from *Callianopsis* spp. by the absence of a large, triangular tooth on the proximal part of the fixed finger, and having a remarkably small fixed finger on the left chela. The present species is easily distinguished from *Eucalliix miyazakiensis* Karasawa, 1993 from the Pliocene Miyazaki Group which have chelae that are nearly equal in shape with

very short fixed finger.

Family Ctenochelidae Manning and Felder, 1991
Subfamily Callianopsinae Manning and Felder, 1991
Genus *Callianopsis* De Saint Laurent, 1973

Type species.—By monotypy *Callianassa goniophthalma* Rathbun, 1902.

Geologic range.—Eocene to Recent.

Callianopsis sp. 1

Figures 4-5, 6

Material.—IGPS coll. cat. no. 102721-102729.

Occurrences.—Nagura Formation; Yokoze Formation

Description.—Manus of larger cheliped rectangular in lateral view, slightly longer than high; lower part of outer surface with dense mammillated tubercles near base of fixed finger; inner surface with longitudinal depression at base of fixed finger. Fixed finger gently curved upward; outer surface with a rim bearing two small socket-like projections directed distally, along prehensile margin. Prehensile edge slightly flattened with large triangular tooth on proximal, and subconical tooth near longitudinal midpoint. Dactylus stout, about two-thirds length of manus; slightly longer than fixed finger; upper margin bearing two or three tubercles near proximal articulation. Strong keel in middle part of outer surface extending longitudinally; several tubercles arranged on keel proximally. Two or three small socket-shaped tubercles above, and three or four similar ones below keel. Inner surface with a longitudinal keel; lower part bearing broad, longitudinal depression and several small tubercles clustered near proximal articulation. Carpus rectangular; about one-third as long as, and slightly narrower than manus; lower distal angle slightly indented inward. Merus one and a half times as long as carpus, outer surface flattened, with two medial, longitudinal ridges. Ischium slender with fringed lower margin.

Smaller cheliped slender, elongate; about half as long as larger one. Fixed finger broader than dactylus with shallow longitudinal depression on inner surface; sporadic pits arranged longitudinally on lower margin. Dactylus rounded in cross section, with deep longitudinal groove and several pits on inner surface.

Remarks.—The chelipeds of the present species are similar to that of *Callianopsis muratai* (Nagao, 1932) from the Upper Eocene Poronai Group, in general proportions and in having a triangular tooth near the base of the fixed finger of the larger cheliped. The present species is, however, clearly distinguished from *C. muratai* by exhibiting a more tuberculated outer surface on the manus and having a weakly developed dactylus which is shorter than the manus.

Callianopsis sp. 2

Figures 4-7, 8

Material.—IGPS coll. cat. no. 102730-102733.

Occurrence.—Yokoze Formation.

Description.—Manus nearly quadrate; slightly broader than long. Lower part of outer surface bearing conical tubercles of various sizes near base of fixed finger. Several tubercles also exist near base of dactylus, some of which cluster to form irregular pustules. Fixed finger about two-thirds length of manus; stout with a blunt apex and oval in cross section; lower margin strongly curved upward and slightly curved inward. Prehensile edge flattened; subconical, weakly vaulted tooth on it slightly proximal to midlength. Two or three pits on a longitudinal rim along prehensile margin and several small pits along lower margin. Dactylus slightly longer than fixed finger; strongly turned downward; a strong ridge, with three or four socket-like, flattened tubercles above, extending along midpart of outer surface. Conical tubercles developed on outer surface around articulation; fused into large pustules.

Remarks.—This species resembles *Callianopsis* sp. 1 in the tuberculation on the outer surface of the manus and in having a longitudinal ridge with socket-like tubercles on the outer surface of the dactylus. However, *Callianopsis* sp. 2 is easily distinguishable from *C.* sp. 1 in having irregularly developed large pustules and a thick, strongly curved fixed finger.

Infraorder Anomala Boas, 1880
Superfamily Galattheoidea Samouelle, 1819
Family Galatheidæ Samouelle, 1819
Subfamily Galatheinæ Samouelle, 1819
Genus *Munida* Leach, 1820

Type species.—By monotypy *Pagurus rugosus* Fabricius, 1775 (ICZN Opinion 712).

Geologic Range.—Paleocene to Recent.

Munida sp. cf. *M. nishioi* Karasawa, 1993

Figure 4-9

Material.—IGPS coll. cat. no. 102744-102756.

Occurrences.—Nenokami Sandstone Member; Nagura Formation.

Description.—Carapace, excluding rostrum, slightly longer than broad; narrowing both anteriorly and posteriorly. Orbitofrontal margin strongly arched forward. Dorsal surface of carapace rugose. Rostrum, spine missing, with narrow base. Supraorbital spine separated clearly from rostral spine at the base. Small median spine on frontal region. A pair of slightly larger spines directed forward on either side of medial one. Regions well defined. An acute

spine directed forward at anterolateral angle. Hepatic region with a broadly triangular lateral spine. Epibranchial region with three lateral spines. An acute spine at posterolateral corner of gastric region.

Chelipeds oblong, slender, tuberculated. Propodus densely covered with asymmetrical tubercles directed distally.

Remarks.—*Munida* sp. most closely resembles *M. nishioi* Karasawa, 1993 from the Middle Miocene Yatsuo Group in the general shape and dorsal striations of the carapace. However, the present species is slightly different from *M. nishioi* in having densely tuberculated chelipeds. The rostrum is not preserved in any specimens obtained up to now. Since the precise comparisons and exact determination require the rostrum and spines on the anterior part of the carapace, the definite identification may have to be reserved.

Infraorder Brachyura Latreille, 1803
Section Heterotremata Guinot, 1977
Superfamily Calappoidea De Haan, 1833
Family Calappidae De Haan, 1833
Subfamily Calappinae De Haan, 1833
Genus *Mursia* Desmarest, 1823

Type species.—By monotypy *Mursia cristiata* H. Milne Edwards, 1837.

Geologic range.—Oligocene to Recent.

Mursia takahashii Imaizumi, 1952

Figures 4-10-13

Mursia takahashii Imaizumi, 1952, p. 88-95, figs. 1-4; 1958b, p. 309, figs. 1-3; 1959, p. 15-21, fig. 6; Sakumoto *et al.*, 1992, p. 449-50, pl. 61, figs. 4, 5; Karasawa, 1993, p. 46, pl. 8, fig. 4.

Material.—IGPS coll. cat. no. 102757-102780.

Occurrences.—Nagura Formation; Yokoze Formation.

Superfamily Cancroidea Latreille, 1803
Family Atelecyclidae Ortmann, 1893
Genus *Trachycarcinus* Faxon, 1893

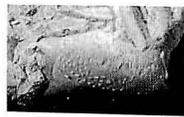
Type species.—By monotypy *Trachycarcinus corallinus* Faxon, 1893 (ICZN Opinion 73).

Geologic range.—Oligocene to Recent.

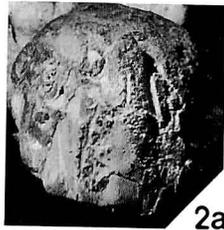
Figure 4. 1-3. *Upogebia* sp. 1: a and b. inner and outer views of manus of left chela. IGPS 102440, Us, $\times 1.5$. 2: a and b. dorsal and lateral views of carapace. IGPS 102439, Us, $\times 1.2$. 3: a and b. dorsal and lateral views of carapace and abdominal somites. IGPS 102438, Us, $\times 1.0$. 4. *Eucalliix* sp. a and b. outer and inner views of chelae (plaster cast). IGPS 102713, Ng-4, $\times 1.0$. 5-6. *Callianopsis* sp. 1. (plaster cast). 5: chelipeds. IGPS 102727, Ng-18, $\times 1.0$. 6: chelipeds. IGPS 102721, Ng-4, $\times 1.0$. 7-8. *Callianopsis* sp. 2. 7: outer view of left chela. IGPS 102730, Yz-4, $\times 1.2$. 8: outer view of left chela. IGPS 102731, Yz-4, $\times 1.2$. 9. *Munida* sp. cf. *M. nishioi* Karasawa. dorsal view of carapace. IGPS 102755, Ng-21, $\times 1.2$. 10-13. *Mursia takahashii* Imaizumi. 10: outer view of left chela. IGPS 102773, Ng-9, $\times 1.2$. 11: dorsal view of carapace. IGPS 102770, Ng-10, $\times 1.0$. 12: dorsal view of carapace. IGPS 102771, Ng-9, $\times 1.0$. 13: carapace with chelipeds. IGPS 102772, Ng-9, $\times 1.0$.



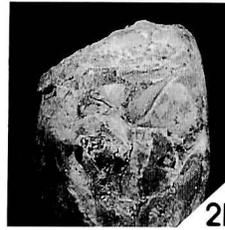
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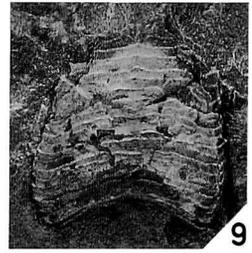
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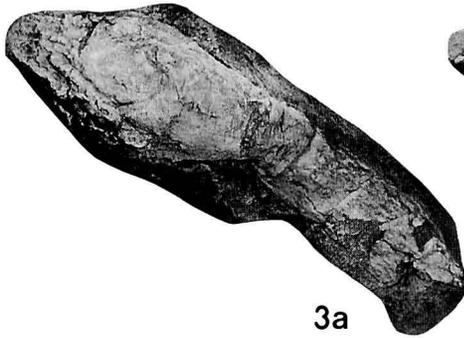
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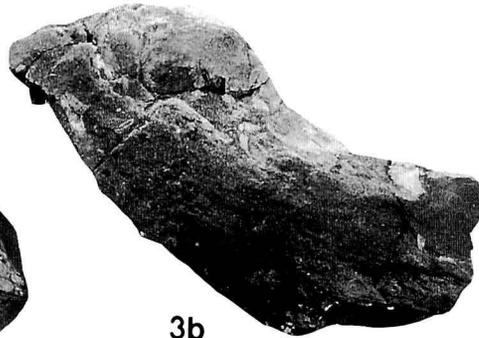
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9



3a



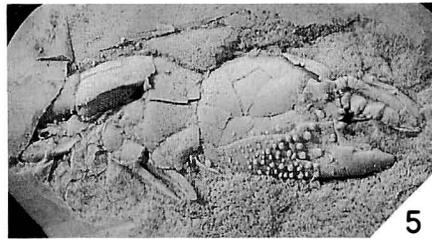
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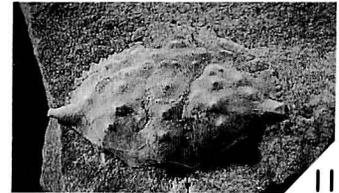
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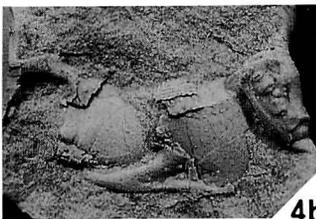
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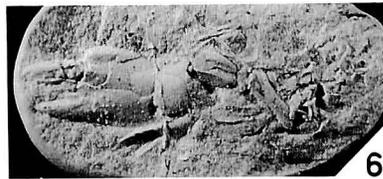
5



11



4b



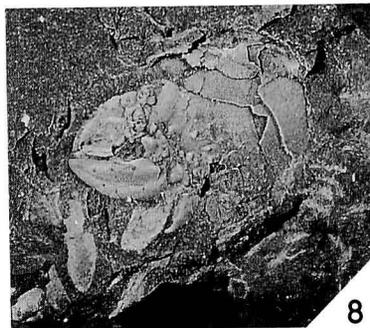
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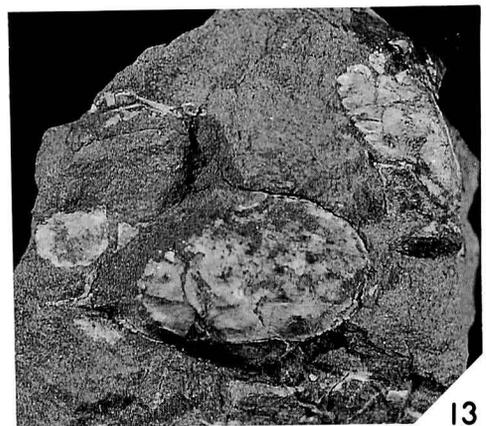
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Trachycarcinus inflatus sp. nov.

Figures 5-1a-4

Material.—IGPS coll. cat. no.102781-102806. Holotype: IGPS, coll. cat. no.102783 (carapace). Paratypes: IGPS, coll. cat. no.102784 (carapace, plaster cast); 102784 (right chela).

Occurrence.—Nagura Formation.

Etymology.—From the elevated dorsal regions.

Diagnosis.—*Trachycarcinus* with dense, flattened granules on elevated dorsal regions. Dorsal regions terrace-shaped, marked by deep furrows. Surface of manus of male larger cheliped smooth, without granules.

Description.—Carapace pentagonal in outline; slightly longer than wide. Dorsal surface strongly convex. Dorsal regions well marked by deep furrows, strongly elevated with dense, flattened granules. Protogastric region strongly convex. Mesogastric region triangular, separated from metagastric region by a shallow furrow. Hepatic region strongly granulated. Cardiac region consisting of two conical swellings arranged transversely. Intestinal region weakly elevated with sparse granules. Posterior margin broad. Carapace transversely constricted behind intestinal region. Rostrum with three spines directed forward, slightly upturned. Median rostral spine produced slightly more forward than laterals. Inner supraorbital spine triangular, without granules. Outer supraorbital and postorbital spines acute. Anterolateral margin with four spines including postorbital one. Postorbital spine directed forward. Second spine near posterior end of hepatic region, directed obliquely forward. Third and 4th spines on lateral margin of epi- and mesobranchial regions, directed laterally. Each spine ornamented by granules variable in size.

Manus of male larger cheliped oblong with smooth surface. Dactylus slender, distinctly longer than fixed finger. Both fingers without remarkable granules or grooves. Six to seven conical teeth observed on the cutting edge of dactylus.

Remarks.—The present new species closely resembles *Trachycarcinus huziokai* Imaizumi, 1951 from the Miocene Oguni Group of Yamagata Prefecture in the general shape and ornamentation of the carapace and in the shape of the male larger cheliped. Besides the type locality, Imaizumi (1958a) has documented eight localities of *T. huziokai* from the Early to Middle Miocene of Japan including the Chichibu Basin. Karasawa (1990) added an additional locality for this species from Southwest Japan.

Examinations of the plaster cast from the outer mould of

the carapaces, however, reveal that the present material is clearly distinguishable from *T. huziokai* by having terrace-shaped dorsal regions of the carapace with flattened granules that are marked by deep furrows, and male larger chela without remarkable granules on the inner and outer surfaces of the manus and fingers without grooves.

Among the living species, *T. crosnieri* Guinot, 1986 resembles the present new species in the general arrangement of the dorsal regions and shape of the anterolateral spines, but differs in the shape of the rostral spines. *Trachycarcinus alcocki* (Doflein, 1904) resembles *T. inflatus* in the general outline of the carapace, but possesses spiniform large tubercles on the lateral margin and dorsal surface of the carapace.

Family Cancridae Latreille, 1803
Genus *Cancer* Linnaeus, 1758

Type species.—By subsequent designation of Latreille, 1810; *Cancer pagurus* Linnaeus, 1758.

Geologic range.—Miocene to Recent.

Cancer sakamotoi sp. nov.

Figures 5-5-9b

Cancer sanbonsugii Imaizumi, 1962, p. 235, 237, pl. 40, figs. 2, 3, 7 (paratypes nos. 1, 2, 5 by original designation).
not. Imaizumi, 1962, p. 233, 234, pl. 40, figs. 1, 4, 5 (holotype, paratype no. 3).

Material.—IGPS coll. cat. no.102807-102833. Holotype: IGPS, coll. cat. no.102807 (inner cast and outer mould of carapace). Paratypes: IGPS, coll. cat. no.102808 (carapace with chelipeds); 102809 (carapace with cheliped).

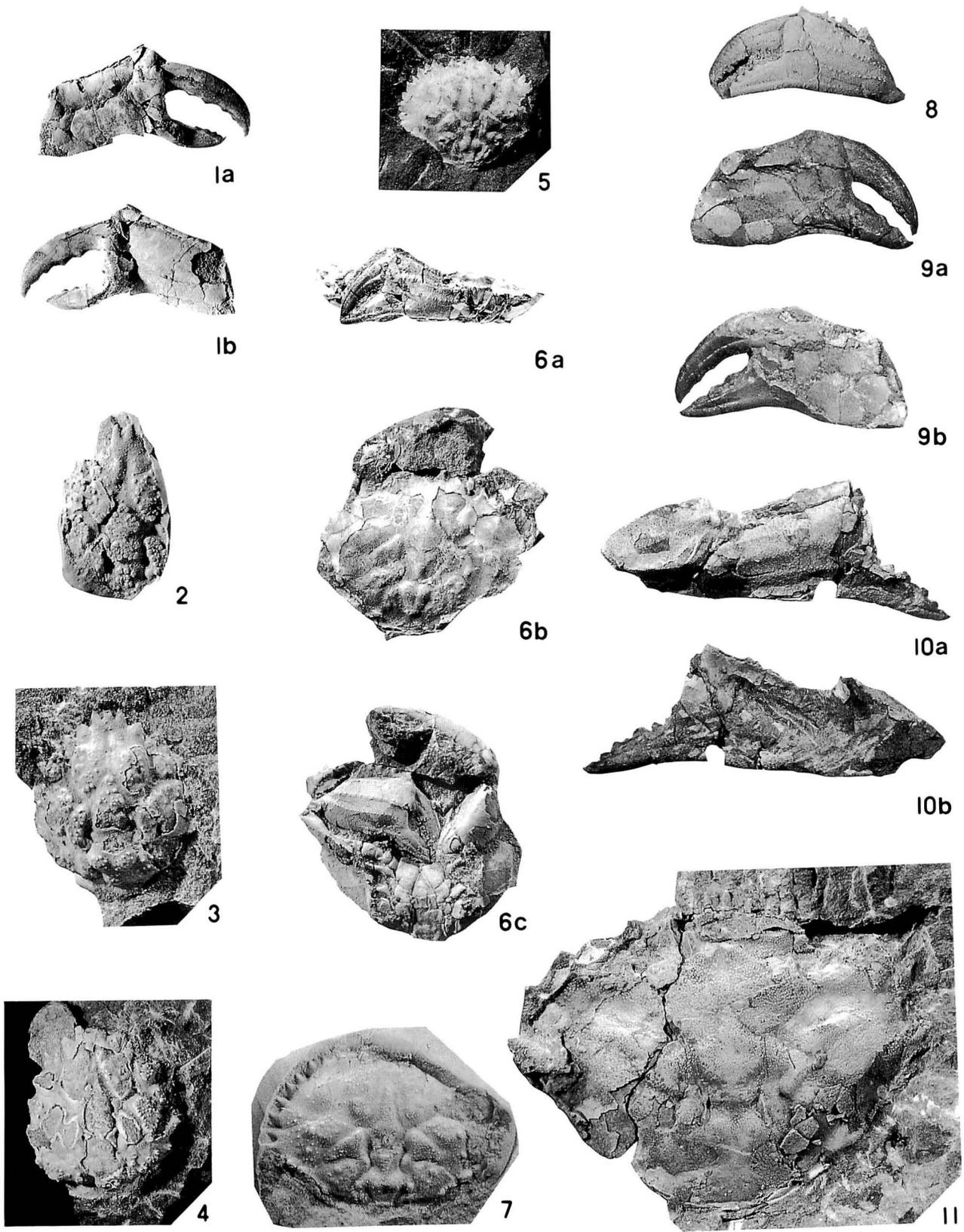
Occurrence.—Nagura Formation.

Etymology.—In honor of Mr. Osamu Sakamoto who has made large contributions to paleontology of the Chichibu Basin.

Diagnosis.—Moderate-sized *Cancer* with variable sized granules on restricted dorsal regions. Anterolateral teeth with pointed tips; separated from each other by closed fissures. Manus with a ridge armed with three subconical teeth on upper margin and four longitudinal granulated ridges on outer surface.

Description.—Carapace transversely oval in outline. Regions covered with scattered granules of variable size; well divided by deep, wide furrows. Proto- and mesogastric regions most convex. Hepatic region bearing a triangular node. Epibranchial region bearing two tubercles among

Figure 5. 1-4. *Trachycarcinus inflatus* sp. nov. 1: paratype, a and b. outer and inner views of right chela. IGPS 102781, Ng-4, $\times 1.0$. 2: paratype, dorsal view of carapace (plaster cast). IGPS 102784, Ng-4, $\times 1.0$. 3: holotype, dorsal view of carapace. IGPS 102782, Ng-4, $\times 1.2$. 4: dorsal view of carapace. IGPS 102783, Ng-4, $\times 1.2$. 5-9. *Cancer sakamotoi* sp. nov. 5: dorsal view of carapace. IGPS 102811, Ng-9, $\times 1.0$. 6: paratype, a, b and c. left cheliped, dorsal and ventral views of carapace with chelipeds. IGPS 102808, Ng-4, $\times 1.0$. 7: holotype, carapace (plaster cast), IGPS 102807, Ng-4, $\times 1.0$. 8: paratype, outer view of left chela, IGPS 102809, Ng-4, $\times 1.5$. 9: a and b. outer and inner views of right chela. IGPS 102812, Ng-4, $\times 1.0$. 10. *Cancer* sp. a and b. outer and inner views of right chela. IGPS 102834, Ng-4, $\times 1.0$. 11. *Itoigawaia chichibuensis* sp. nov. holotype, dorsal view of carapace, IGPS 102837, Ng-4, $\times 1.0$.



scattered granules. Mesobranchial region possessing two granulated tubercles. Metabranchial region with two or three swellings. Two conical nodes situated transversely on cardiac region. Frontal margin with five spines including small, but clearly acutely triangular inner supraorbital ones. Medial one smallest and depressed. Anterolateral margin bearing nine acutely pointed spines separated from each other by short closed fissures; fringed by granules. Second and 4th spines slightly smaller than neighboring spines. Posterolateral margin bearing three or four blunt, upturned spines diminishing in size posteriorly.

Chelipeds nearly equal in size and shape. Manus with five granulated carinae extending longitudinally on upper margin and outer surface; the uppermost, on upper margin possessing three subconical, granulated spines; second obscure with sparse granules; 3rd and 4th distinct, densely granulated. Fixed finger with five conical teeth, suboval in section; lower margin straight, thickened; tip slightly upturned. Inner and outer surfaces of fixed finger grooved along lower margin and lined with pits along opposing margin. Dactylus with blunt, conical teeth on cutting edge; coarsely granulated on upper margin near proximal articulation; three longitudinal grooves with rows of pits on outer surface and near lower margin on inner surface. Carpus possessing five granulated carinae. Merus triangular in cross section.

Remarks.—Critical examinations of the type series of *Cancer sanbonsugii* Imaizumi, 1962 from the Middle Miocene Matsukawa Formation ("Odaira Formation" in Imaizumi's description) of Fukushima Prefecture, together with material subsequently collected from the type locality and specimens from the Chichibu Basin, led to the conclusion that the type series included two distinct species. Of Imaizumi's specimens, his holotype and paratype no. 3 (p. 233, 234, pl. 40, figs. 1, 4, 5) are here considered to belong to *C. sanbonsugii*, and paratypes nos. 1, 2 and 5 (p. 235, 237, pl. 40, figs. 2, 3, 7) to the new species *C. sakamotoi*.

C. sakamotoi closely resembles *C. sanbonsugii* in the general shape of the carapace, but may be distinguished by having a densely granulated rather than smooth dorsal surface of the carapace, and in having granulated and carinated chelae. Among the species living in Japanese water, *C. amphioetus* Rathbun, 1898 resembles *C. sakamotoi* in having strongly elevated dorsal regions as already suggested by Imaizumi (1962). Moreover, *C. sakamotoi* resembles the Recent *C. gibbosulus* (De Haan, 1833) from Japan in the shape of frontal and anterolateral spines of the carapace.

Cancer sp.

Figures 5-10a, b

Material.—IGPS coll. cat. no. 102834.

Occurrence.—Nagura Formation.

Description.—Manus long with six longitudinal carinae on outer and upper surfaces. Uppermost one on upper margin bears nine triangular spines. Third, 6th and 9th spines, smaller than others. Each spine finely granulated. Second carina gently swollen. Third extending along boundary between upper and outer surfaces. Third to 6th carinae weakly developed. Fixed finger covered with densely mammillated tubercles on both surfaces, slightly inclined. A row of pits lie within a groove on outer surface. A broad, shallow groove with a row of pits on middle part and a row of slightly larger pits at base of cutting edge discernible on inner surface. Cutting edge armed with seven teeth of variable size.

Outer and inner surfaces of carpus covered with a microscopic mesh of pores, bounded by a strong carina. Outer angle of upper surface forming a large spine projecting distally.

Remarks.—This species resembles *Cancer (Cancer) tomowoi* Karasawa, 1990 from the Miocene Mizunami Group in the general proportion and ornamentation of the outer surface of the chela, but there are some differences between the two in the following: the cutting edge of the fixed finger of the present species is armed with seven teeth while *C. (C.) tomowoi* has five teeth; the upper margin of the manus has nine spines, whereas *C. (C.) tomowoi* possesses only three.

Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Polybiinae Ortmann, 1893
Genus *Itoigawaia* Karasawa, Sakumoto and Takayasu, 1992

Type species.—By monotypy *Portunites minoensis* Karasawa, 1990.

Geologic range.—Miocene.

Itoigawaia chichibuensis sp. nov.

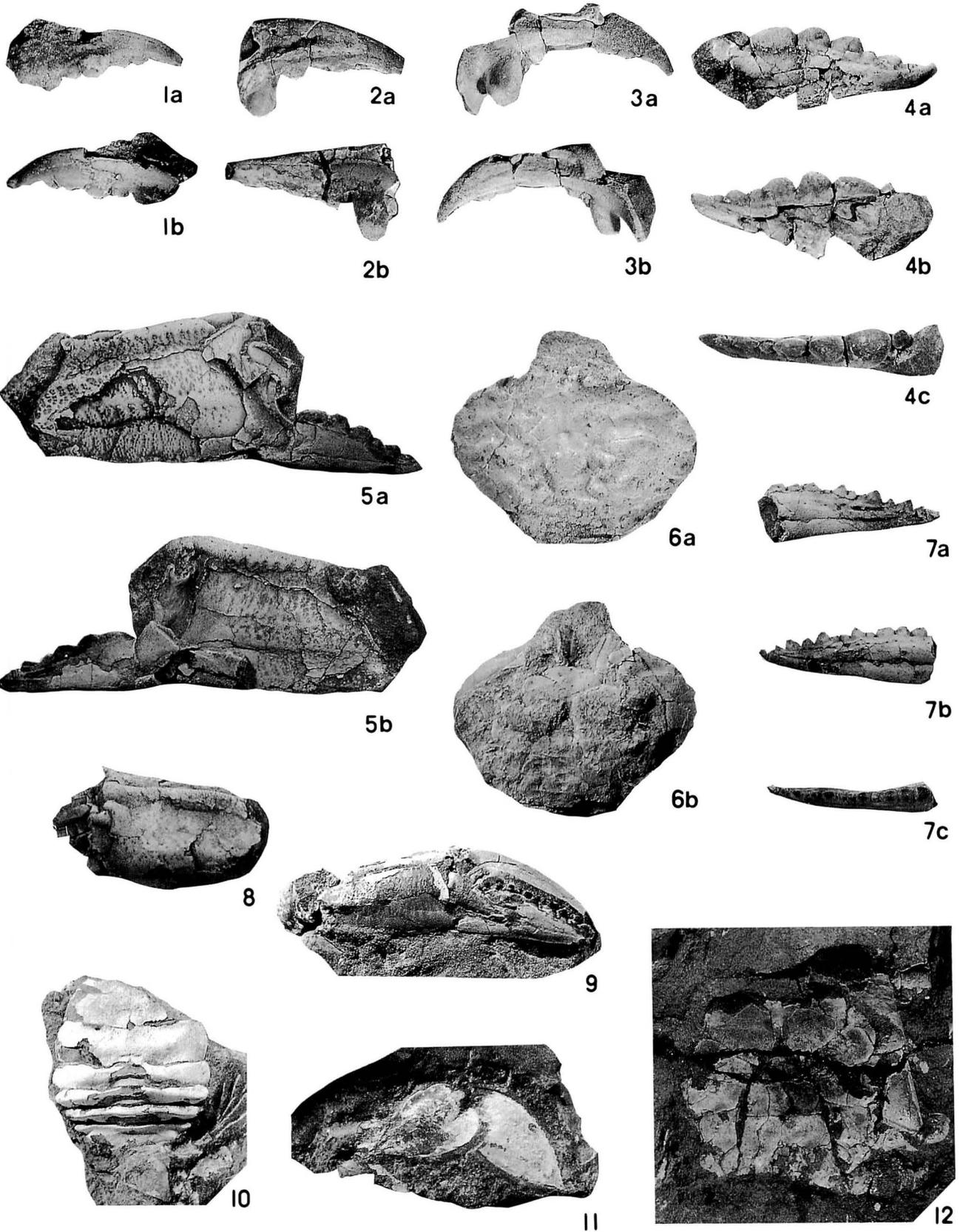
Figures 5-11; 6-7a-12

Material.—Holotype: IGPS coll. cat. no. 102837 (carapace); Paratypes: IGPS coll. cat. no. 102840 (chelipeds); 102843 (male abdomen and thoracic sternites).

Occurrence.—Nagura Formation.

Etymology.—From the Chichibu Basin.

Figure 6. All figures except 7 are natural size. 1-6. *Minohellenus*? sp. 1-3: a and b. outer and inner views of dactylus of right cheliped, 1: IGPS 102858, Ng-4. 2: IGPS 102859, Ng-4. 3: IGPS 102861, Ng-4. 4: a, b and c. inner, outer and upper views of left fixed finger, IGPS 102860, Ng-4. 5: a and b. outer and inner views of right manus, IGPS 102862, Ng-4. 6: a and b. dorsal and ventral views of carapace, IGPS 102863, Ng-4. 7-12. *Itoigawaia chichibuensis*, sp. nov. 7: a, b and c. inner, outer and upper views of left fixed finger. IGPS 102838, Ng-4, $\times 1.2$. 8: left manus, IGPS 102839, Ng-4. 9: right chela, IGPS 102840, Ng-4. 10: female abdomen, IGPS 102842, Ng-4. 11: fifth pereopod, IGPS 102841, Ng-4. 12: male abdomen and thoracic sternum, IGPS 102843, Ng-4.



Diagnosis.—*Itoigawaia* with broadly triangular inner supraorbital angle and acutely pointed outer supraorbital spine. Upper surface of manus bounded by two keels.

Description.—Carapace broader than long; covered all over with dense granules which coarsen in anterior portion of carapace. Regions well defined. Frontal and hepatic regions depressed in contrast to swellings of gastric and branchial regions. Protogastric region broad, strongly convex; steeply sloped anteriorly. Meta- and mesogastric regions well marked. Urogastric region depressed. Cervical groove between gastric and branchial regions broad, deep, granules less developed. Epibranchial region strongly convex, forming broad, arched ridge terminating near cervical furrow. Mesobranchial region strongly convex. Cardiac region gently convex. Frontal margin with four acute spines. Median pair projecting slightly beyond laterals. Outer supraorbital spine acutely triangular, projected forward. Suborbital spine acute with broad base, directed forward.

Anterolateral margin gently convex with five subequal spines. First (exorbital) sharp, directed forward. Second to 4th almost equal in shape and size. Fifth directed obliquely anteriorly. Posterior margin narrow, slightly convex.

Chelipeds subequal in size and shape. Manus relatively short, hexagonal in cross section. Upper surface marked by two keels with distal projections; inner projection developed into a conical spine. Fixed finger triangular in lateral view; cutting edge bears 10 teeth; lower margin almost straight, but tip slightly upturned; outer and inner surfaces with two rows lined with small pits. Dactylus weakly curved downward; cutting edge armed with 13 or more small teeth.

Merus of walking legs broad; dactylus longitudinally carinated. Dactylus of fifth leg flattened, typically ovate in outline; propodus also flattened; carpus without carina. Telson of male abdomen broader than long; proximal margin indented into much broader 6th somite. First-4th somite of female abdomen forming pleats. Third thoracic sternite rectangular, longer than broad in both left and right portion.

Remarks.—*Itoigawaia chichibuensis* is characterized by having a large carapace which is covered with coarse granules. This species is distinguished from the type *Itoigawaia minoensis* (Karasawa, 1990) from the Lower Miocene Mizunami Group in having a large, triangular inner supraorbital spine, an acutely projecting outer supraorbital spine and angular chelae with densely serrated fingers. In *I. chichibuensis* the dorsal surface of the carapace has well defined regions which are more elevated than in *I. minoensis*. *Itoigawaia umemotoi* Karasawa, 1993 from the Mizunami Group resembles the present new species in having acute frontal spines and a large, fan-like carapace; *I. chichibuensis* differs from *I. umemotoi* by having the large inner supraor-

bita spine and two keels and projections on the upper surface of the chelipeds.

Genus *Minohellenus* Karasawa, 1990

Type species.—By monotypy *Charybdis (Minohellenus) quinquedentata* Karasawa, 1990.

Geologic range.—Oligocene to Miocene.

Minohellenus ? sp.

Figures 6-1a—6b

Material.—IGPS coll. cat. no. 102858-102869.

Occurrence.—Nagura Formation.

Description.—Carapace suboval in outline. Front narrow, separated from supraorbital spine by a distinct notch. Upper orbital margin concave, rounded; interrupted laterally by two fissures. A distinct transverse ridge extending from mesogastric region to hepatic region. An arched ridge formed by epi- and mesobranchial regions extending from 5th anterolateral spine terminates at cervical furrow.

Manus relatively short; exhibiting, in part, a meshy surface. Fingers robust, stout, oval in cross section. Fixed finger triangular in lateral view; cutting edge armed with a row of strong teeth, of which proximal two or three have conical, flattened crushing surface. Dactylus strongly arcuate downward and slightly curved inward with five longitudinal rows of pits; cutting edge armed with seven conical teeth, proximalmost tooth largest.

Remarks.—This species is recognized by the features of the fronto-orbital margin, well developed transverse ridges on the carapace and stout fingers with conical crushing teeth on the cutting edges. The present species is quite different from the type *Minohellenus quinquedentatus* Karasawa, 1989 from the Miocene Mizunami Group and *M. macrocheilus* Kato and Karasawa, 1994 from the Oligocene Ashiya Group in having the large chelae with stout fingers mentioned above.

Superfamily Xanthoidea MacLeay, 1838

Family Xanthidae MacLeay, 1838

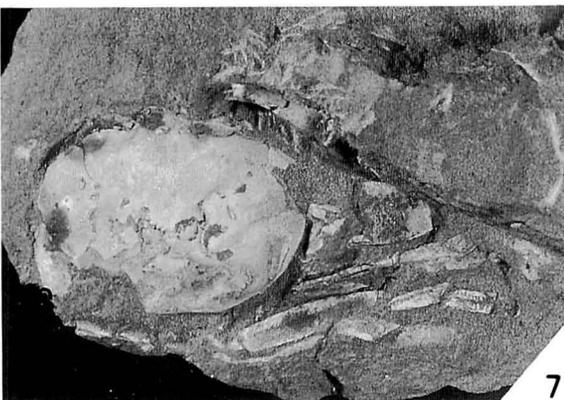
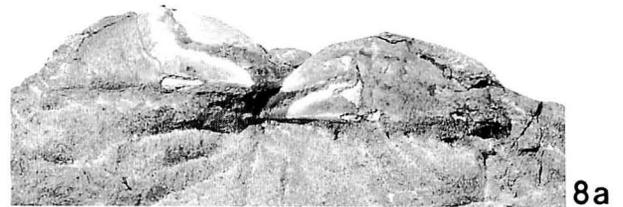
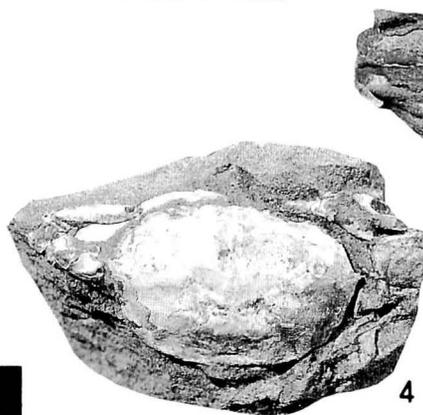
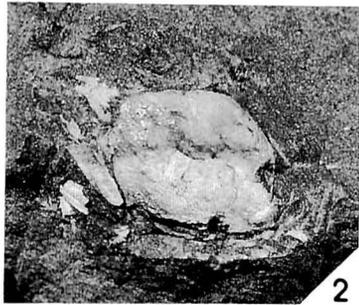
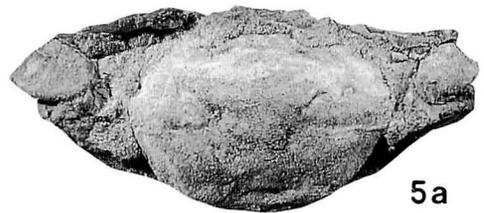
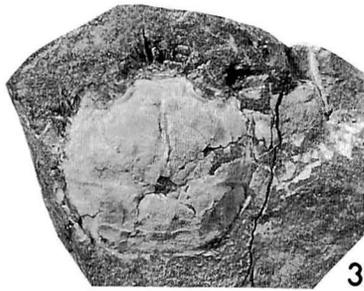
Subfamily Euxanthinae Alcock, 1898

Genus *Medaeus* Dana, 1851

Type species.—By monotypy *Medaeus ornatus* Dana, 1852 (ICZN Opinion 712).

Geologic range.—Miocene to Recent.

Figure 7. 1. *Medaeus* ? sp. dorsal view of carapace. IGPS 102895, Yz-6, $\times 1.0$. 2. *Typhrocarcinodes* ? sp. dorsal view of carapace, left chela and walking legs. IGPS 102973, Ng-18, $\times 2.0$. 3. *Carcinoplax* sp. carapace with right cheliped. IGPS 102972, Ng-6, $\times 1.5$. 4-8. *Carcinoplax antiqua* (Ristori). $\times 1.0$. 4: carapace with chelipeds. IGPS 102922, Ng-9. 5: a and b. dorsal and ventral views of carapace and chelipeds. IGPS 102923, Ng-9. 6: carapace with cheliped. IGPS 102924, Ng-9. 7: carapace with right cheliped and walking legs. IGPS 102925, Ng-9. 8: a and b. outer view of chelae and dorsal view of carapace. IGPS 102965, Ng-3.



***Medaeus* ? sp.**

Figure 7-1

Material.—IGPS coll. cat. no. 102895-102896.*Occurrence*.—Yokoze Formation.

Description.—Carapace transversely octagonal in outline. Front broadly projected forward; anterior margin slightly concave, but not divided into two lobes. Lateral angle of frontal lobe forming forwardly directed spine. Inner orbital spine distinct but hiatus indiscernible. Regions well defined by deep sculpture, but anterior portion of carapace almost eroded. Proto-, meso- and metagastric, cardiac, epi-, meso- and metabranchial regions tumid, covered with granules densely. Mesogastric region nearly regularly triangular. Metagastric fused with mesogastric region at median longitudinal. Epibranchial region clearly defined by deep furrow. Fused cardiac and intestinal region lozenge-shaped; widest in preserved regions. Posterior margin long.

Orbital margin badly preserved. Anterolateral margin bearing five spines. First (external orbital spine) and 2nd acutely triangular, nearly equal in size. Third and 4th apparently small. Fifth largest and acutely triangular, projecting laterally.

Remarks.—The present species resembles the Recent *Medaeus serratus* Sakai, 1965 from Japan in the general shape of the carapace, but differs from *M. serratus* in the absence of the V-shaped frontal notch and in having a frontal spine on the lateral frontal angle. This species is distinguished from other *Medaeus* species in the absence of the frontal notch and in having the posterior margin unusually wider than that of the living species. Additional specimens of this species are necessary in order to make an exact generic assignment.

Family Goneplacidae MacLeay, 1838
Subfamily Carcinoplacinae H. Milne Edwards, 1852
Genus ***Carcinoplax*** H. Milne Edwards, 1852

Type species.—By subsequent designation by Glaessner, 1929; *Cancer (Curtonotus) longimanus* De Haan, 1833.

Geologic range.—Eocene to Recent.

***Carcinoplax antiqua* (Ristori, 1889)**

Figures 7-4—8

Curtonotus antiquus Ristori, 1889, p. 4.

Carcinoplax antiqua Glaessner, 1933, p. 17; Imaizumi, 1961, p. 164, text-fig. 4, pl. 12, pl. 13, figs. 1-11, pls. 14-5, pl. 16, figs. 4-5, pl. 17, figs. 2-11; 1969, pl. N-8, fig. 1; Fujiyama, 1982, p. 370, figs. 1834-5; Karasawa, 1990, p. 23-25, pl. 7; Sa-

kumoto *et al.*, 1992, p. 451, pl. 62, fig. 3, pl. 63, fig. 1.
Carcinoplax senecta Imaizumi, 1961, p. 172, pl. 18, figs. 1-3.

Material.—IGPS coll. cat. no. 102897-102971.

Occurrences.—Nenokami Sandstone Member; Nagura Formation; lower part of the Yokoze Formation.

Remarks.—There are remarkable size differences between specimens from the Nenokami Sandstone Member and from the Nagura Formation. The carapace width of those from the Nenokami Sandstone Member ranges between 12-25 mm, while those from the Nagura Formation measure 14-44 mm (typically 23-38 mm). Similar size differences between materials from two horizons are also observed in *Munida* sp.

***Carcinoplax* sp.**

Figure 7-3

Material.—IGPS coll. cat. no. 102972.

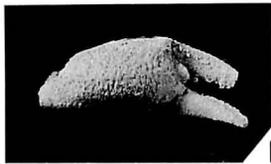
Occurrence.—Nagura Formation.

Description.—Carapace rounded hexagonal in outline; weakly convex dorsally. Hepatic region discernible. Protogastric region broad, weakly swollen. A pair of short ridges situated transversely at boundary between frontal and protogastric regions. Furrow between proto- and mesogastric regions discernible. Anterior part of mesogastric region tapering into median furrow. Metagastric region narrow, indistinguishable. Cervical groove distinct. Cardiac region slightly swollen. Frontal region separated into two lobes by a furrow, however, frontal margin nearly straight without distinct notch. Orbital margin broad, rounded. Inner supraorbital angle clearly separated from lateral angle of frontal margin. Outer supraorbital margin tumid dorsally. Anterolateral margin gently convex outward with three spines including postorbital one. Postorbital spine largest, directing forward. Second and 3rd anterolateral spines faintly visible. Anterolateral margin slightly narrower than posterolateral one. Posterolateral margin slightly convex. Posterior margin straight.

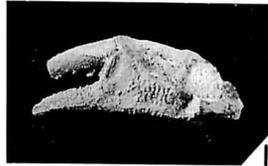
Right cheliped slender. Cutting edge of fixed finger with approximately ten small, blade-shaped teeth. Upper surface of carpus broadly rectangular in dorsal view.

Remarks.—The present species is quite different from the known fossil species of *Carcinoplax* in having a more circular carapace, a broad orbital margin and faintly anterolateral spines. In having a circular carapace, the extant species *C. angusta* Rathbun, 1914 from the South China Sea bears some resemblances to *Carcinoplax* sp., but differs in having a strongly tumid carapace.

Figure 8. 1-7. *Miosesarma nagureense* n. sp. 1: a and b. inner and outer views of right chela. IGPS 103074, Ng-6, $\times 2.5$. 2: paratype, ventral view of male abdomen and thoracic sternum. IGPS 102974, Ng-13, $\times 1.2$. 3: dorsal view of female carapace with chelipeds and walking legs. IGPS 103075, Ng-16, $\times 1.0$. 4: paratype, dorsal view of carapace with walking legs (plaster cast). IGPS 103081, Nk-2, $\times 1.0$. 5: holotype, dorsal view of male carapace with chelipeds and walking legs. IGPS 102976, Ng-9, $\times 1.0$. 6: dorsal view of female carapace with cheliped and walking legs. IGPS 102975, Ng-13, $\times 1.0$. 7: dorsal view of carapace with chelipeds and walking legs. IGPS 103080, Ng-8, $\times 1.2$. 8-9. *Maja morii* sp. nov. $\times 1.0$. 8: paratype, dorsal view of carapace. IGPS 103101, Ng-13. 9: holotype, dorsal view of carapace with cheliped and walking legs. IGPS 103100, Ng-13.



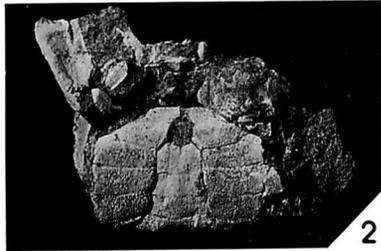
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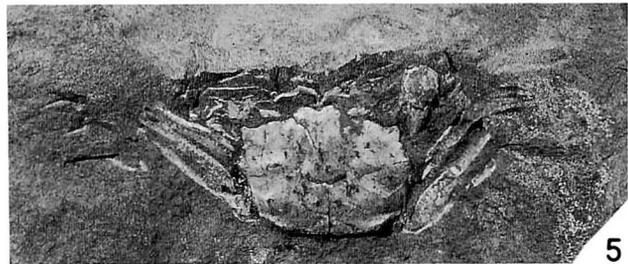
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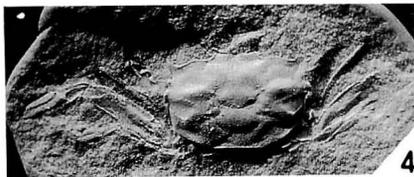
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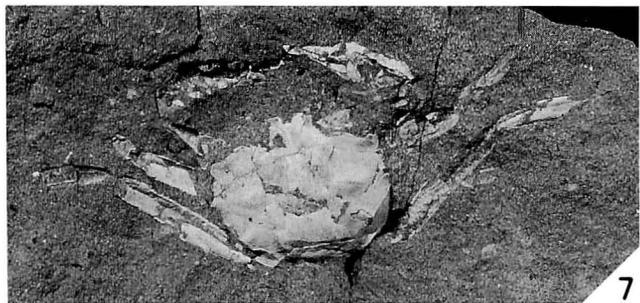
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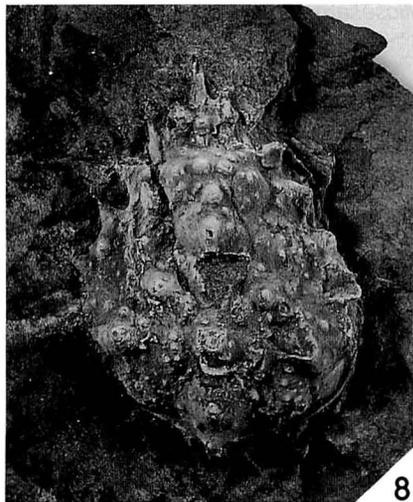
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Subfamily Rhizopinae Miers, 1886
Genus *Typhlocarcinodes* Alcock, 1900

Type species.—By monotypy *Typhlocarcinus integrifrons* Miers, 1881.

Typhlocarcinodes ? sp.

Figure 7-2

Material.—IGPS coll. cat. no. 102973.

Occurrence.—Nagura Formation.

Description.—Carapace oval in outline without any projection or spine along margin; moderately convex; dorsal surface covered all over with irregularly pointed granules. Frontal margin hardly distinguishable. Orbits not recognizable on dorsal surface. Cervical groove shallow. Cardiac region discernible.

Left chela very small. Observable part of chela about half as long as carapace length. Manus swollen, showing irregularly granulated upper surface. Fixed finger with strong keel on lower margin of outer surface. Walking legs also granulated.

Remarks.—The present species may be assigned to *Typhlocarcinodes* by having a granulated carapace which is wider than long, smooth margins of the carapace without projections or spines, and orbits which cannot be observed from the dorsal surface. However, the poor preservation of the present material renders it difficult to determine its exact generic position.

Superfamily Majoidea Samouelle, 1819
Family Majidae Samouelle, 1819
Subfamily Majinae Samouelle, 1819
Genus *Maja* Lamarck, 1801

Type species.—By subsequent designation under the plenary powers; *Cancer squinado* Herbst, 1788 (ICZN opinion 511)

Geologic range.—Miocene to Recent.

Maja morii sp. nov.

Figures 8-8, 9

Material.—Holotype: IGPS coll. cat. no. 103100 (carapace, left chela, merus and carpus of walking legs). Paratype: IGPS coll. cat. no. 103101 (carapace).

Occurrence.—Nagura Formation.

Etymology.—In honor of Professor Kei Mori, who supported the present study and made useful suggestions.

Diagnosis.—*Maja* with moderately long and slightly divergent rostrum. Three orbital spines approximated. Posterior margin of carapace bearing single conical tubercle.

Description.—Carapace pyriform. Rostrum with acute spines slightly divergent. Regions well defined. Median longitudinal, branchial and hepatic regions strongly convex. Protogastric region bearing two longitudinal series of conical tubercles, extending to base of rostrum. Mesogastric region strongly convex with two large, conical tubercles arranged

longitudinally. Metagastric region also highly convex with a large, conical tubercle. Urogastric region with a conical tubercle noticeably smaller than others. Cardiac region marked by broad, plain furrows; strongly convex with a large, conical tubercle in middle part. Intestinal region swelling into conical elevation. Hepatic region narrowly convex; marked by broad, plain furrows. Branchial regions with large numbers of variable sized tubercles. Sinuous swellings consisting of large tubercles extending parallel to branchiocardiac groove. Metabranial region with small tubercles and granules; less developed than mesobranial and intestinal swellings. Supraorbital eave with sparse granules. Antorbital spine acutely triangular, directing laterally. Intercalated spine short (about half length of antorbital and one third length of postorbital spines). Postorbital spine triangular, directed anteriorly; anterior surface excavated. These three spines closely approximated. Propodus of left chela straight; outer surface longitudinally carinated. Fingers thin with acutely pointed tips. Walking legs long, slender. Merus cylindrical. Carpus and manus slightly flattened.

Remarks.—*Maja morii* most resembles the fossil species *Maja biaensis* Lörenthey in Lörenthey and Beurlen, 1929 from the Middle Miocene of Hungary, in the general arrangement of tubercles and lateral spines on the carapace. However *M. morii* is readily distinguished from *M. biaensis* in having a single tubercle on the posterior end of the carapace. The present record documents the first occurrence of a fossil *Maja* species in the northern Pacific region.

Section Thoracotremata Guinot, 1977
Superfamily Grapsoidea MacLeay, 1838
Family Grapsidae MacLeay, 1838
Subfamily Sesarminae Dana, 1851
Genus *Miosesarma* Karasawa, 1989

Type species.—By monotypy *Miosesarma japonicum* Karasawa, 1989.

Geologic range.—Miocene.

Miosesarma nagurense sp. nov.

Figures 8-1a-7

Camptandrium ? sp. Fujiyama, 1982, p. 370, pl. 185, fig. 1840.

Material.—IGPS coll. cat. no. 102974-103095. Holotype: IGPS coll. cat. no. 102976 (carapace with chelipeds and walking legs). Paratypes: IGPS coll. cat. no. 102974 (carapace, thoracic sternum and abdomen); IGPS coll. cat. no. 103081 (carapace with walking legs).

Occurrences.—Nenokami Sandstone Member; Nagura Formation; lower part of the Yokoze Formation.

Etymology.—From the Nagura Formation, which yields abundant specimens.

Diagnosis.—*Miosesarma* with a triangular process on mesobranial region in which mesobranial sharp, oblique ridge terminated. Hepatic region depressed.

Description.—Carapace quadrilateral in outline, about three-fourths as long as wide. Dorsal surface moderately

convex. Frontal region bilobed. A pair of short but strong ridges arranged transversely at boundary between frontal and protogastric regions. Hepatic region depressed. Protogastric region gently convex. Bottle-shaped mesogastric region well defined; surface slightly flattened; tapering anteriorly into median furrow. Cardiac region transversely hexagonal; well marked and convex. Epibranchial lobe transversely tumid with a sharp ridge extending from 3rd anterolateral spine to mesobranchial lobe. Mesobranchial lobe strongly tumid with a sharp ridge extending from 4th anterolateral spine into transversal ridge; terminated in a triangular process. Cardiac and branchio-cardiac furrows distinct. Frontal margin narrow (about 0.24-0.26 of carapace width). Inner orbital margin slightly concave at base of frontal lobe; outer orbital margin sinuous, reaching to postorbital angle. Anterolateral margin bearing four spines including postorbital angle. First largest, thorn-shaped, flattened, directed forward. Second small, directed obliquely anteriorly, with pointed tip. Third large with tip pointing upward. Fourth rudimentary, at lateral end of mesobranchial ridge. Posterolateral margin slightly convergent. Penultimate somite of male abdomen not broad; slightly longer than 3rd to 5th somites. Telson narrow; slightly indented into penultimate somite.

Manus of mature male cheliped elongated, triangular in cross section. Fixed finger with acutely pointed tip, slightly curved downward and inward. Cutting edge of finger poorly preserved. Walking legs long.

Merognath of third maxilliped nearly rectangular. Ischiognath larger than merognath; with nearly right-angled posterointernal angle; external half depressed. Exopodite short.

Remarks.—*Miosesarma nagureense* sp. nov. is readily distinguished from the type *Miosesarma japonicum* Karasawa, 1989 from the Miocene Mizunami Group in having the hepatic region depressed and a triangular process on the mesobranchial region. The dorsal surface of the present new species is more unevenly convex and regions are better defined than are those of *M. japonicum*. The chelipeds of mature specimens show distinct sexual dimorphism. The chelae of mature females are tiny and slender, whereas the male ones are long and stout.

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Early Late Permian (Wordian) non-ammonoid cephalopods from the Hamrat Duru Group, central Oman Mountains

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Received 15 October 1995; Revised manuscript accepted 1 May 1996

Abstract. The Wordian Rustaq Formation is a unit of the Hawasina Nappes in the central Oman Mountains, and contains a diverse pelagic fauna. Four species of non-ammonoid cephalopods are described herein: orthocerids *Brachycycloceras rustaqense* sp. nov. and *Bitauioceras* cf. *zonatum* (Gemmellaro), nautilid *Liroceras* sp. and bactritid *Bactrites*? sp. One of these, *Brachycycloceras rustaqense*, represents the youngest record of the genus, previously known unquestionably only from the Carboniferous. The fauna indicates affinity to the Timor and Sicily faunas.

Key words: Orthocerids, nautilid, bactritid, central Oman Mountains, Wordian

Introduction

During the Late Cretaceous obduction of the Semail Ophiolite, Tethyan margin sediments were thrust onto the Arabian continental margin in the Oman Region (e.g. Glennie *et al.*, 1973; Robertson and Searle, 1990). The allochthonous units of sedimentary origin are called the Hawasina Nappes and subdivided into the following six groups: Ramaq, Al Buda'ah, Hamrat Duru, Al Aridh, Kawr and Umar (Bécheu *et al.*, 1988; Pillevuit, 1993). This report, preceded by a preliminary report in the account of Pillevuit (1993), deals with non-ammonoid cephalopods obtained from reddish cephalopod limestone of the Rustaq Formation of the Hamrat Duru Group. The Permian ammonoid fauna of the formation indicates a close resemblance to those from the west Mediterranean (Sosio fauna, Gemmellaro, 1887–1888) and Timor (Haniel, 1915), suggesting the Hawasina Basin corresponds to a seaway along the northern margin of Gondwana (Blendinger *et al.*, 1992). This faunal exchange between the Hawasina Basin and Timor is also supported by the investigation of the trilobite fauna by Pillevuit (1993).

The Rustaq Formation, defined by Pillevuit (1993), crops out in the vicinity of Rustaq village in the central Oman Mountains (Figure 1). This stratum represents the lowest part of the Hamrat Duru Group, and consists of pillow lavas and carbonate rocks indicating a pelagic environment. The cephalopod limestone containing a thin barren dolomite is 2.6 m thick (Figure 2). Besides cephalopods, the Rustaq

fauna includes conodonts, ostracodes, crinoids, trilobites and serpulids. Blendinger *et al.* (1992) assigned a Wordian (early Guadalupian, early Late Permian) age to the fauna, based on ammonoids, including *Sicanites schopeni* (Gemmellaro), *Agathiceras suessi* Gemmellaro and *Sociocrimites insignis* (Gemmellaro), and conodonts.

The specimens studied are deposited in the paleontological collections of the Geological Museum of Lausanne (MGL), Switzerland.

Systematic paleontology

Class Cephalopoda Cuvier, 1797

Subclass Nautiloidea Agassiz, 1847

Order Orthocerida Kuhn, 1940

Superfamily Orthocerataceae M'Coy, 1844

Family Brachycycloceratidae Furnish, Glenister and Hansman, 1962

Genus *Brachycycloceras* Miller, Dunbar and Condra, 1933

Type species.—*Brachycycloceras normale* Miller, Dunbar and Condra, 1933.

Brachycycloceras rustaqense sp. nov.

Figures 3–1–5

Cycloceratid (? *Brachycycloceras*) Pillevuit, 1993, p. 114.

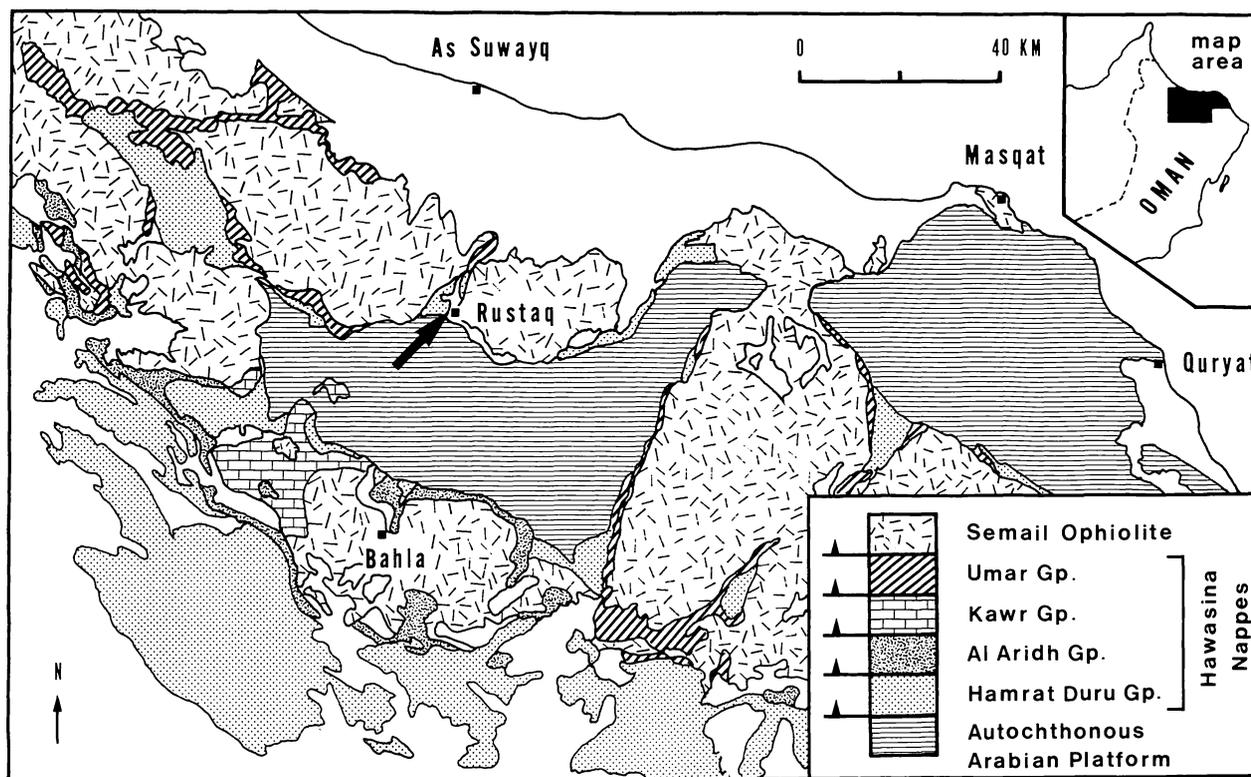


Figure 1. Map showing fossil locality (arrow), and geology of the central Oman Mountains (modified from Béchenec *et al.*, 1990).

Diagnosis.—Species of strongly annulated *Brachycycloceras* with depressed cross section; annulations form adapical lateral sinus; siphuncular position between center and venter.

Description.—Single deciduous phragmocone, 40.8 mm in length, of strongly annulated exogastric shell with depressed cross section, shell diameter of slightly deformed adoral end approximately 28 mm in lateral diameter (breadth) and 21 mm in dorsoventral diameter (height); annulations form deep adapical sinus on lateral side, 2–3 annuli bear in length equal to corresponding dorsoventral diameter; sutures with shallow but broad ventral lobes; septa thin with weak curvature; camerae short, width (max.)/length ratio of camerae approximately 6–8 in dorsoventral section of adoral shell; siphuncle narrow, between center and venter in position with suborthochoanitic short septal necks, length of septal necks ranges from 0.5 to 0.9 mm; connecting rings not preserved; no cameral and/or siphuncular deposits detected.

Discussion.—Although examined specimen is a fragmentary deciduous phragmocone abraded on the apical dorsal side, the distinctive shell shape and siphuncular structure and position confirm generic identification. The known stratigraphic distribution of *Brachycycloceras* was previously restricted to sediments ranging from the Namurian (Phillips, 1985) to the Upper Pennsylvanian (Furnish *et al.*, 1962). Only a questionable record of a Lower Permian species of the genus has been reported from western Australia (Teichert, 1951). This Wordian specimen thus represents the youngest

record of this genus, so this discovery from the Oman Mountains is noteworthy.

Brachycycloceras rustaqense sp. nov. differs from all other described *Brachycycloceras* species in having a depressed shell cross section and the lateral sinus of the annulations.

Etymology.—The specific name is derived from the Rustaq Formation, where the species occurs.

Material.—The holotype, MGL 72026.

Superfamily Pseudorthocerataceae Flower and Caster, 1935

Family Pseudorthoceratidae Flower and Caster, 1935

Subfamily Spyroceratinae Shimizu and Obata, 1935

Genus *Bitauioceras* Shimizu and Obata, 1936

Type species.—*Orthoceras bitauniense* Haniel, 1915.

Bitauioceras cf. *zonatum* (Gemmellaro, 1890)

Figures 3–6—11

cf. *Orthoceras zonatum* Gemmellaro, 1890, p. 45, pl. 11, figs. 9–11, pl. 12, figs. 19, 20.

Bitauioceras sp. Pillecuit, 1993, p. 114.

Description.—Orthocones with gradual shell expansion, angle of expansion approximately 3–4 degrees; cross section circular; largest specimen (MGL 72027) of phragmocone attains 20.0 mm in diameter; surface ornamentation of relatively coarse transverse lirae forming salients;

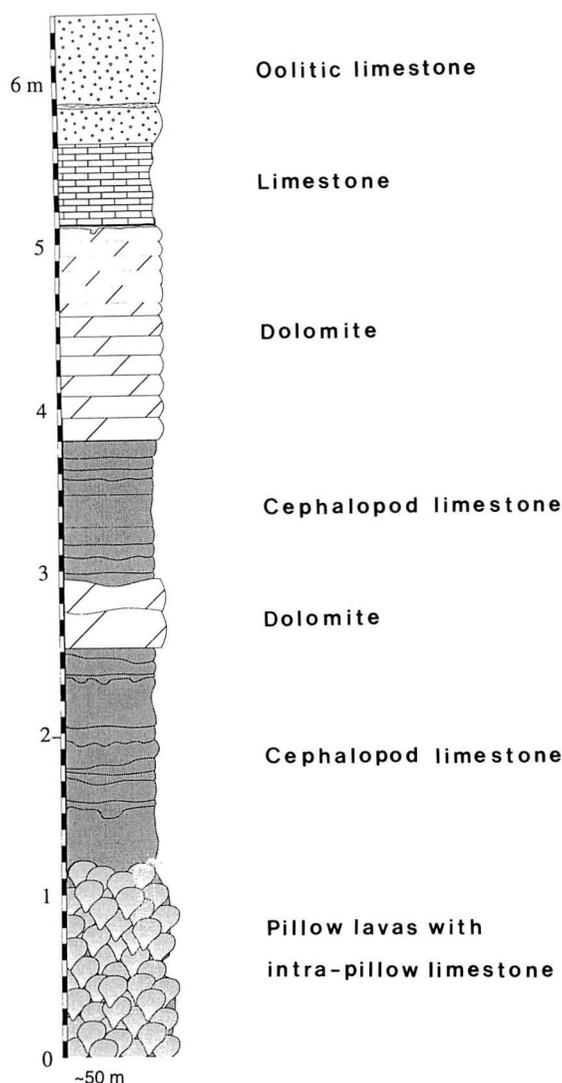


Figure 2. Stratigraphic section of the Rustaq Formation, in the Rustaq area.

length of fragmentary body chamber of immature specimen (MGL 72028) 30.8 mm and adoral shell diameter 15.9 mm; sutures not observed, but obvious obliquity not recognized in dorsoventral section; camerae long, width (max.)/length ratio of camerae ranges from 1.1 to 1.3, septa exhibit considerably strong curvature; siphuncular position subcentral, minimum distance of central axis of siphuncle from shell surface per shell diameter in dorsoventral section ranges

from 0.48 to 0.46, septal necks suborthochoanitic to orthochoanitic, short, 1.1 mm long in well-preserved neck; connecting rings not preserved; internal molds of phragmocone and body chamber bear transverse, shallow constrictions caused by periodic thickenings of shell wall, and transverse, straight to partly zigzag wrinkled layer; no cameral and/or siphuncular deposits detected.

Discussion.—The specimens of *Bitauioceras* cf. *zonatum* from the central Oman Mountains closely resemble *B. zonatum* (Gemmellaro) from the Middle Permian of Sicily in its general shell shape, nature of surface ornamentation and well-developed wrinkled layer. The unknown adoral siphuncular structure of the type specimens leads to the tentative specific assignment of the specimens.

Prior to the present description, *Bitauioceras* had been recorded from Sicily, southern Urals, Timor, Japan, northern Mexico, and Texas (Niko and Nishida, 1987). The genus was widespread in the Tethyan region and the southern margin of the Boreal region during Sakmarian to Guadalupian times.

Material.—Two specimens, MGL 72027, an incomplete phragmocone, 65.7 mm long, and MGL 72028, a fragment of immature body chamber, 30.8 mm long.

Order Nautilida Agassiz, 1847

Superfamily Clydonautilaceae Hyatt in Zittel, 1900

Family Liroceratidae Miller and Youngquist, 1949

Genus *Liroceras* Teichert, 1940

Type species.—*Coloceras liratum* Girty, 1911.

Liroceras sp.

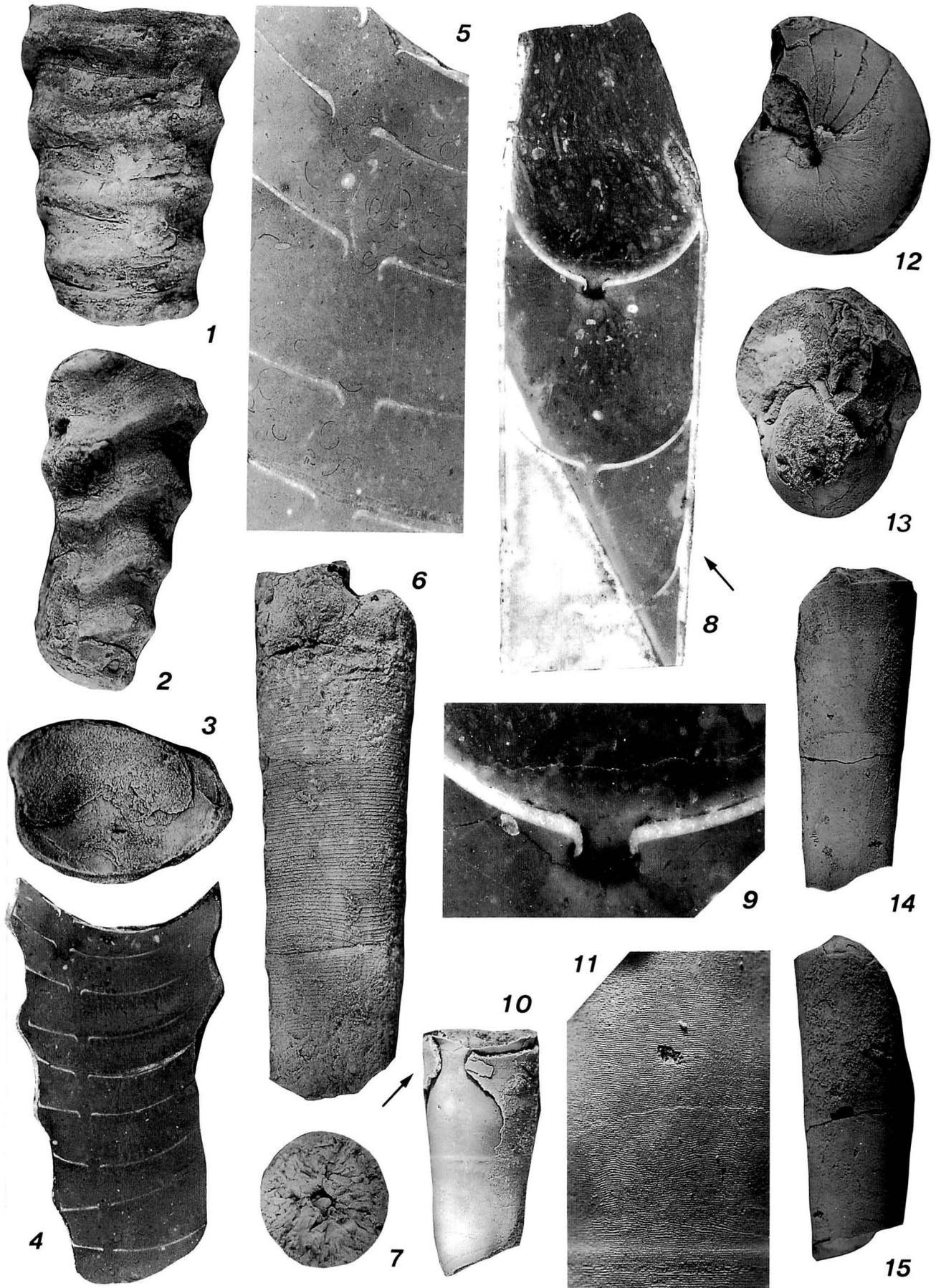
Figures 3-12, 13

Description.—Single subglobose nautilicone with 21.5 mm in shell diameter, whorl breadth/height ratio 1.86; coiling extremely involute with umbilicus comprising less than 10 percent of diameter; whorl section reniform, rounded ventrally and laterally; shell surface smooth, lacking in conspicuous ornament without growth lines; suture simple, nearly straight.

Discussion.—The specimen probably represents an immature portion of the shell. The lack of those diagnostic features which appear in the adult shell precludes specific determination.

Material.—A specimen, MGL 72029.

Figure 3. 1-5. *Brachycycloceras rustaqense* sp. nov., holotype, MGL 72026, 1: ventral view, 2: lateral view, venter on right, 3: septal view of adoral end, venter down, 4: dorsoventral polished section, venter on left, 5: details of siphuncle. 6-11. *Bitauioceras* cf. *zonatum* (Gemmellaro), 6-9, MGL 72027, 6: ventral view, 7: view of apical end, venter down, 8: dorsoventral polished section, venter on left, arrow indicates shell constriction, 9: details of septal neck, 10, 11, MGL 72028, 10: side view, arrow indicates shell constriction, 11: internal mold of body chamber showing wrinkled layer. 12, 13. *Liroceras* sp., MGL 72029, 12: lateral view, 13: apertural view. 14, 15. *Bactrites*? sp., MGL 72030, 14: dorsal view showing dorsal carina, 15: lateral view, venter on right. 4, 8= $\times 2$, 5, 9, 11= $\times 6$, all other figures= $\times 1.5$.



Subclass Bactritoidea Shimanskiy, 1951
 Order Bacritida Shimanskiy, 1951
 Family Bacritidae Hyatt, 1884
 Genus *Bacrites* Sandberger, 1843

Type species.—*Bacrites subconicus* Sandberger, 1843.

***Bacrites* ? sp.**

Figures 3–14, 15

Description.—Single incomplete body chamber of orthoconic shell, 39.8 mm in length, with circular cross-section, weak dorsal carina; angle of shell expansion approximately 9 degrees; surface ornamentation with weak transverse lirae.

Discussion.—The combination of carina and transverse ornamentation of the shell surface, which is characteristic of some bacritids; such as the body chamber of *Bacrites peytonensis* Mapes (1979, pl. 8, figs. 4–14, pl. 9, figs. 2, 3, 6–8, 12, 13, 15, 17–19, pl. 14, figs. 7, 8, 10) and *Ctenobacrites mirus* Shimanskiy (1954, pl. 9, figs. 1, 2), indicates that the specimen can be assigned to the Family Bacritidae. In addition, the lacking of the coarse costae and/or lirae suggests the Oman species belongs to *Bacrites* rather than *Ctenobacrites*.

Material.—A specimen, MGL 72030.

Acknowledgments

This study was supported by Swiss National Science Foundation, Foundation Georgine Claraz and Lausanne University. We thank Dr. Hilal Bin Mohd Al Azry for assistance in the field.

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Middle Triassic (Anisian) foraminifers from the Kaizawa Formation, southern Kanto Mountains, Japan

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Received 21 December 1995 ; Revised manuscript accepted 20 May 1996

Abstract. This paper concerns the systematic paleontology and faunal comparison of newly found Anisian foraminifers in the Kaizawa Formation distributed in the Iwai-Kanyo area, southern Kanto Mountains. The Nishitama Group including the Kaizawa Formation in the northern part of Itsukaichi is a coherent stratigraphic unit ranging in age from the latest Permian to possibly Early Jurassic. The formation shows many diagnostic lithologic characters indicating shallow shelf deposits, and is quite different from those of the surrounding Jurassic formations containing numerous exotic blocks of oceanic origin.

The foraminiferal fauna consists of 25 species assignable to 16 genera having a close Tethyan faunal affinity. Among them, *Glomospira densa* (Pantić) and *Meandrospira dinarica* Kochansky-Devidé and Pantić are especially important stratigraphically as well as biogeographically, because they are zonal indicators restricted to the Anisian of the Muschelkalk and contemporaneous limestones in Europe to West Asia. Most of the other species are common to those reported from the Middle Triassic of the Tethyan Realm.

Key words : Anisian foraminifers, Tethyan faunal affinity, Kaizawa Formation, Iwai-Kanyo area, Kanto Mountains

Introduction

Triassic strata with ammonoid, various pelecypod and gastropod fossils are narrowly distributed in the Iwai area, one of the classical and important fields for the study of Japanese Triassic stratigraphy and paleontology (e.g. Ichikawa and Kudo, 1951). In the southern part of the Kanto Mountains, isolated distribution of Upper Triassic strata with pelecypods is also known in the west of Ome (Takagi, 1944 ; Ozawa and Hayami, 1969). These strata show many lithologic characters diagnostic of shallow shelf deposits, and are in striking contrast to the surrounding formations composed of Jurassic sandstone and shale including numerous exotic blocks. No invertebrate megafossils have been found in these Jurassic terrigenous clastic rocks.

Recently, I have found Middle Triassic foraminifers from oolitic limestone and conglomeratic limestone in the Iwai-Kanyo area, the northern part of Itsukaichi. The limestone had been thought to be referable to the uppermost Permian Oguno Formation by Ozawa and Kobayashi (1986). The uppermost Permian to Upper Triassic stratigraphy in this area is re-examined in detail, and the Anisian Kaizawa Formation is newly proposed for the limestone and associated conglomeratic limestone, sandstone, and black shale (Kobayashi and Ozawa, in press).

Although several hundreds of papers on the Japanese Upper Paleozoic foraminifers, mostly fusulinaceans, have been published and over a century has passed since Naumann (1881, 1885) first reported Triassic fossils from Japan, Triassic foraminifer research is exceedingly scarce. Only two papers on the Triassic foraminifers have been published. One is a brief note by Goto (1986) on the occurrence of *Meandrospira* from the Kozuki-Tatsuno Belt, Southwest Japan. The other is concerned with the composition and characteristics of the Late Triassic fauna contained in the exotic limestone blocks of the Southern Chichibu Belt by Kristan-Tollmann (1991).

The distinguished foraminifers from the Kaizawa Formation consist of 25 species assignable to 16 genera and show an intimate Tethyan faunal affinity. Some of them are thought to be stratigraphically important, and have been described or illustrated from the Middle Triassic limestones of the various regions of the Tethyan Realm.

This paper focuses on the systematic paleontology of the Middle Triassic (Anisian) foraminifers of the Kaizawa Formation. Faunal composition and its comparison with other regions of the Tethyan Realm are discussed.

All the specimens illustrated and listed in this paper are stored in the collection of the Division of Earth Sciences, Museum of Nature and Human Activities, Hyogo.

Geologic setting

The Nishitama Group was originally introduced by Ozawa and Kobayashi (1986) for Middle Carboniferous to Lower Jurassic shelf deposits in the southern Kanto Mountains. The group in the Iwai-Kanyo area is composed of six formations in ascending order: the Oguno (Dorashamian), Iwai (Scythian), Kaizawa (Anisian), Arai (Carnian), Kayakubo (Norian), and Kanyo (Norian possibly ranging up to Lower Jurassic) (Kobayashi and Ozawa, in press). The surrounding formations are composed of upper Lower to Middle Jurassic terrigenous clastic rocks and oceanic exotic blocks of basaltic rocks, limestone and chert ranging in age from late Early Carboniferous to Late Triassic. Geologic structure, litho- and bio-facies of limestone and sandstone are quite different between the two. Moreover, diverse tectonostrati-

graphic subdivision of these Jurassic accretionary complexes has been offered by various authors (Takashima and Koike, 1984; Ozawa and Kobayashi, 1986; Sakai, 1987)

Remarkable lithologic characters of the Nishitama Group in the Iwai-Kanyo area are intercalations of impure limestone containing detrital quartz grains, molluscan- and plant-bearing sandstone and shale, intraformational conglomerate with acidic to intermediate igneous rock pebbles and lack of basaltic rocks and chert. These features are strongly indicative of a deposit in shallow shelf environments. Although these six formations are now fault bounded on each other, it is considered that each younger formation had originally rested unconformably upon the older one. The geologic map of the Iwai-Kanyo area is shown in Figure 1.

The Kaizawa Formation, typically exposed in the south of Kaizawa, is narrowly distributed from Iwai to Arai trending NW

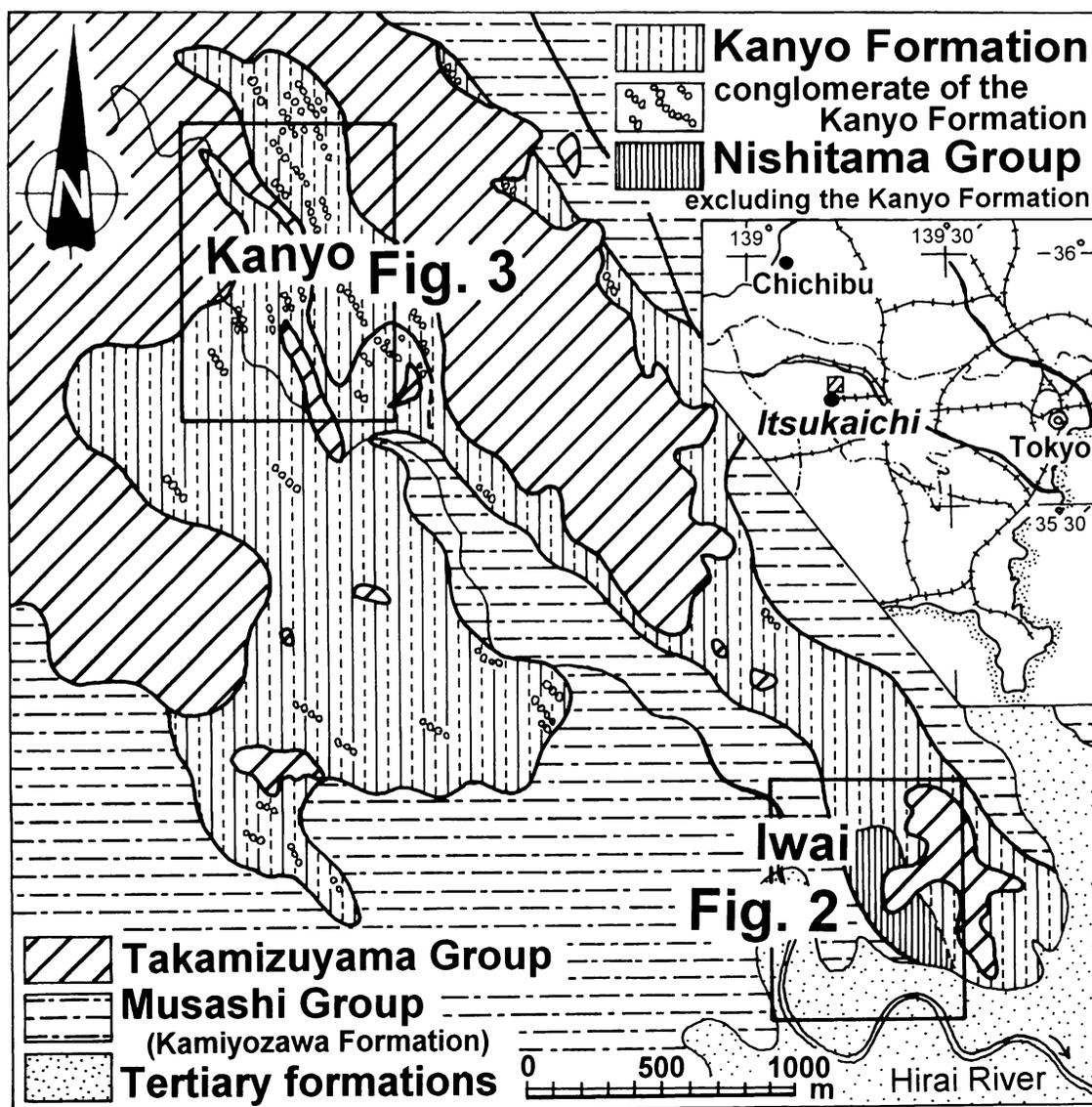


Figure 1. Geologic map of the Iwai-Kanyo area.

to SE (Figure 2). It is isolatedly distributed near Kanyo (Figure 3). The Kaizawa Formation attains more than 20 m in thickness, and is composed of limestone, conglomeratic limestone, sandstone, and black shale, but their frequencies are variable in places. Sandstone and shale less dominantly crop out due to differential erosion. Limestone cobbles to

pebbles of the conglomeratic limestone are exclusively of Dorashamian and Anisian age. All the limestone and most of the cobbles to pebbles of Anisian age are dark gray and are classified into oöid grainstone cemented with sparry calcite. They contain large quantities of well-sorted quartz grains both in the matrix and nucleus of oöids. Anisian

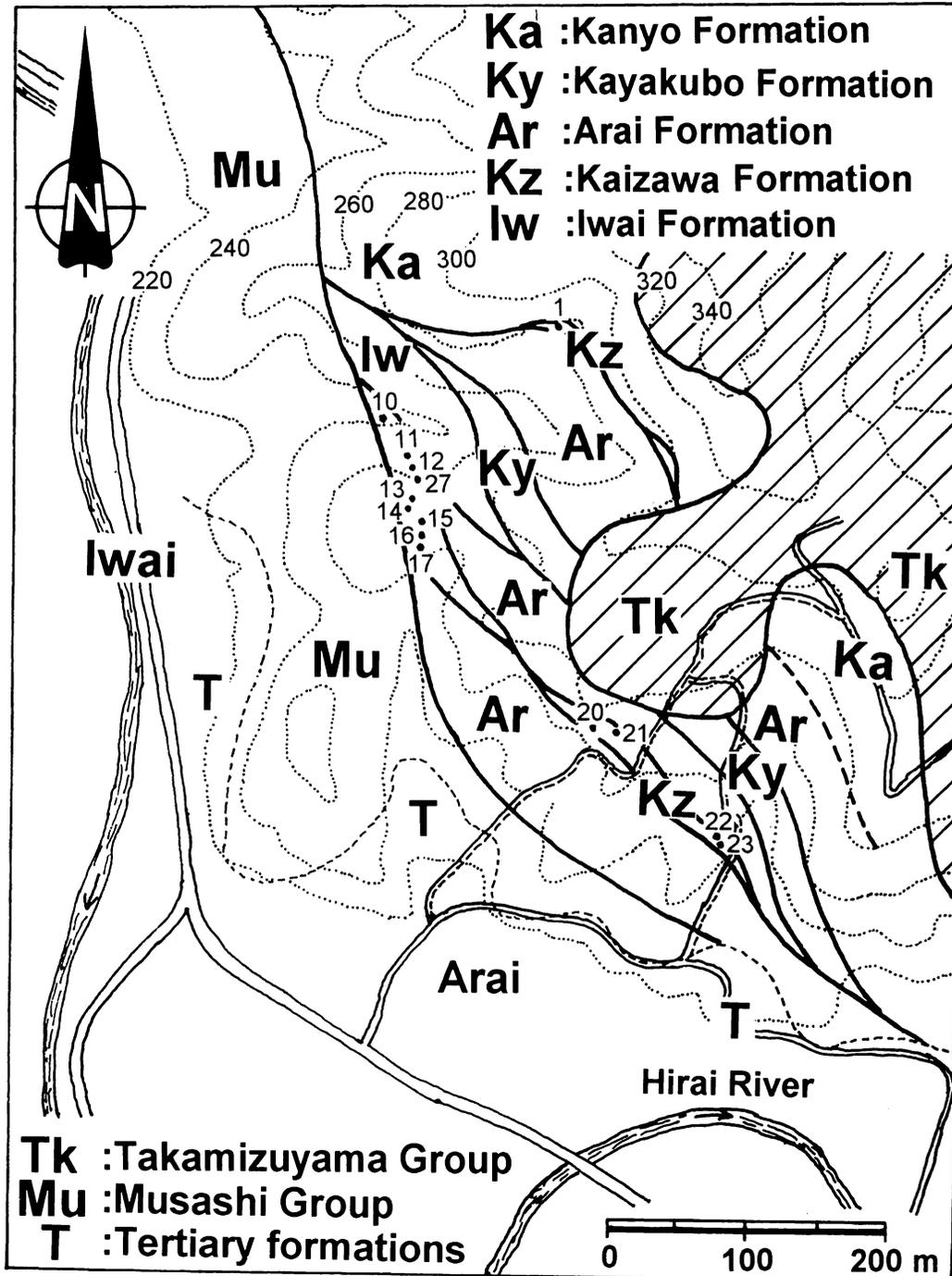


Figure 2. Geologic and topographic map of the Iwai area. 1, 10-17, 20-23, and 27 are foraminifer fossil localities in this area.

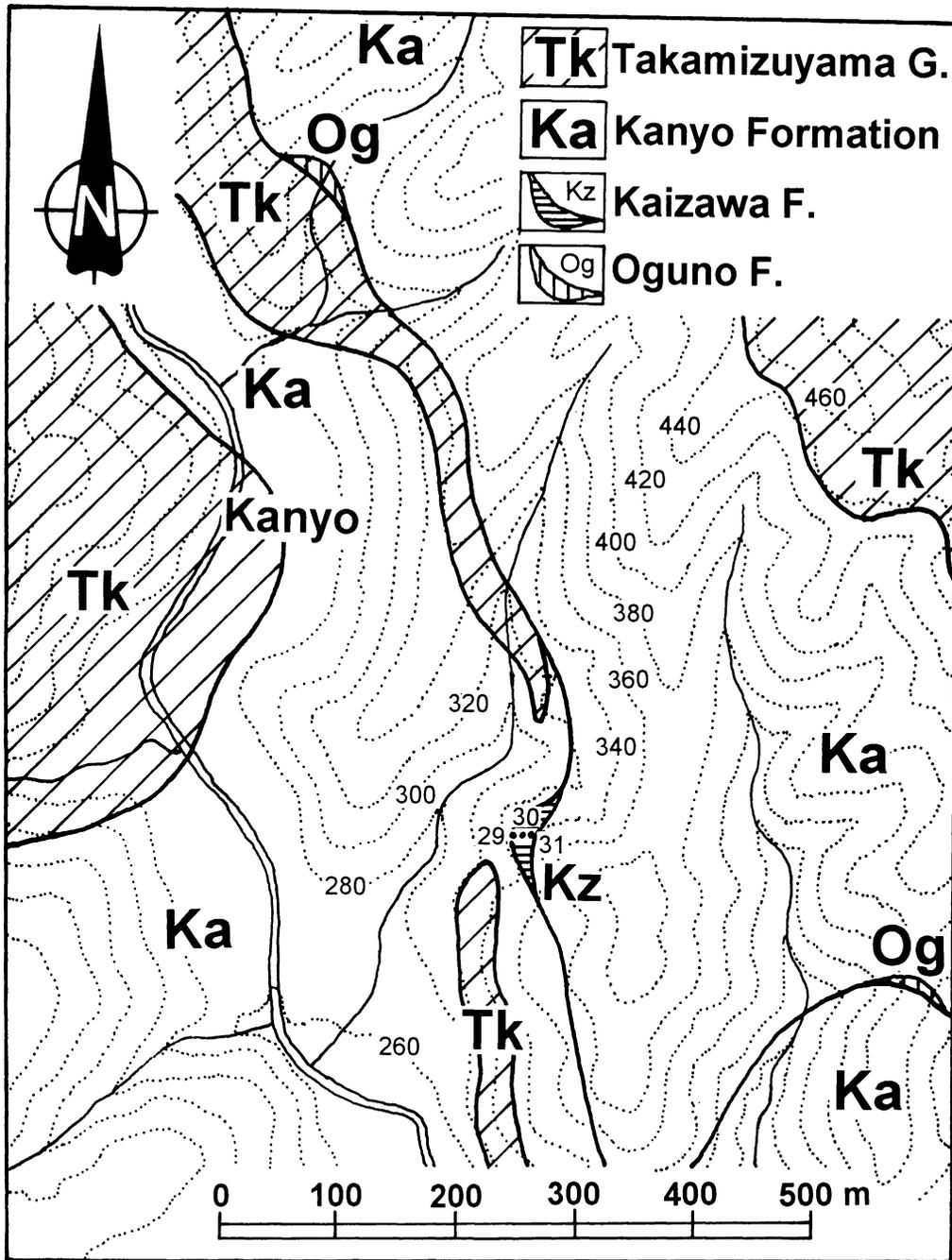


Figure 3. Geologic and topographic map of the Kanyo area. 29-31 are foraminifer fossil localities in this area.

pebbles to cobbles of algal grainstone and algal packstone are also observable in places. Those of Dorashamian age are gray to light gray and mostly of algal grainstone. Detrital quartz grains are characteristically contained in almost all of the limestone and conglomeratic limestone.

Limestones, especially algal limestones, of this formation are highly fossiliferous. They yield algae, foraminifers, bryozoans, sponges, crinoids, pelecypods, gastropods, ostracods, conodonts, and others. Foraminifers are com-

mon to rare in algal limestones. In almost all foraminifers scattered in oöid grainstone the outer whorls of the tests are worn.

Composition and comparison of foraminifer fauna

Foraminifers occur at several levels of the limestone and conglomeratic limestone of the Kaizawa Formation. Localities yielded them in the Iwai and Kanyo areas are shown in

Figures 2 and 3, respectively. Distinguished 25 taxa from 17 localities are shown in Table 1. The present fauna exhibits a striking Tethyan affinity. Although the faunal composition and number of taxa occurring are variable, significant differences in composition are not recognizable.

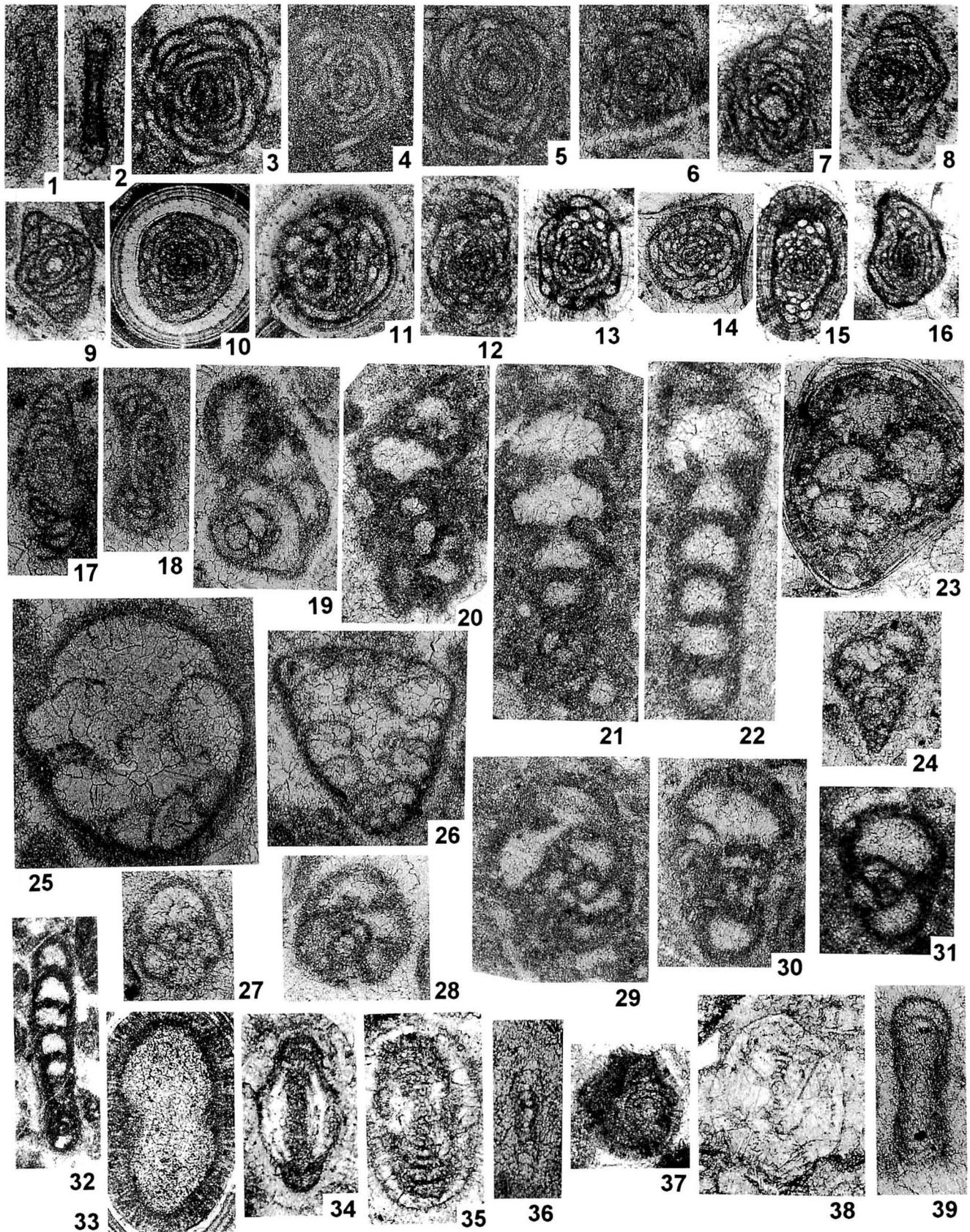
Among the foraminifer species, *Glomospira densa* (Pantić) is the most dominant species. *Meandrospira dinarica* Kochansky-Devidé and Pantić is also common in the present fauna. The occurrence of these two species in the Kaizawa Formation is worthy of note, because they are consid-

ered to be stratigraphically important and restricted to the Anisian of the Muschelkalk and contemporaneous limestones widely distributed in Europe to West Asia (e.g., Premoli Silva, 1971; Zaninetti *et al.*, 1972; Gaździcki *et al.*, 1975; Zaninetti, 1976; Trifonova, 1978a). In Southeast to East Asia, *Glomospira densa* and species allied to *Meandrospira dinarica* are reported from the Anisian limestones of Peninsular Malaysia (Gaździcki and Smit, 1977), Guizhou (He, 1984), Hubei (Lin and Zheng, 1978) and others. Although the taxonomic treatment of the genus *Arenovidalina* has been

Table 1. Anisian foraminifers from the Kaizawa Formation. Locality numbers correspond to those in Figures 2 and 3.

	1	10	11	12	13	14	15	16	17	20	21	22	23	27	29	30	31
<i>Ammodiscus</i> sp.		X												X			
<i>Glomospira densa</i>	X	X		X	X	?	X			X	X		X	X	X	X	X
<i>Glomospira</i> sp.		X		X											X	X	
<i>Glomospirella irregularis</i>		?		X										X			
<i>Rectoglomospirella</i> sp.	X																
<i>Malayspirina</i> cf. <i>fontainei</i>		X		X										X			
<i>Duotaxis</i> sp.		?		X													
<i>Gaudryina</i> cf. <i>triadica</i>		X	?	X									?				
" <i>Endothyra</i> " cf. <i>kuepperi</i>		X		X		?								X			
Endothyridae gen. et sp. indet.		X		X													
<i>Triadodiscus</i> sp.	X																
<i>Triadodiscus</i> ? sp.	X										X						
<i>Arenovidalina amyvolvoluta</i>	X	X	X				X	X	X	X	X	X	X		X		
<i>Arenovidalina</i> sp.	?	X		?				X		X							X
<i>Aulotortus</i> ? sp.	X																
Involutinidae gen. et sp. indet.	X								?					X	X		
<i>Meandrospira dinarica</i>	X	X	X	X	?								X	X	X		
" <i>Meandrospira</i> " <i>deformata</i>		X		X						X							
<i>Austrocolomia</i> cf. <i>marschalli</i>		X															
<i>Austrocolomia</i> sp.		X									X						
<i>Cryptoseptida</i> ? sp.		X		X													
<i>Nodosaria expolita</i>			X	X													
<i>Nodosaria</i> spp.			X	X										X			
<i>Diplotremina astrofimbriata</i>	X			X	X									X			
<i>Diplotremina</i> sp.														X			

Figure 4. 1, 2. *Ammodiscus* sp., 1: Loc. 10, D2-02926a, 2: Loc. 27, D2-02947a, $\times 120$. 3-14. *Glomospira densa* (Pantić), 3: Loc. 10, D2-02923a, 4: Loc. 10, D2-02926b, 5: Loc. 12, D2-02867, 6: Loc. 12, D2-02869a, 7: Loc. 10, D2-02921a, 8: Loc. 27, D2-02949a, 9: Loc. 10, D2-02917a, 10: Loc. 15, D2-13247, 11: Loc. 10, D2-02925a, 12: Loc. 27, D2-02949b, 13: Loc. 31, D2-02882, 14: Loc. 30, D2-02879, 3, 4 = $\times 70$; 5-14 = $\times 80$. 15, 16. *Glomospira* sp., 15: Loc. 29, D2-02874, 16: Loc. 30, D2-02878, $\times 80$. 17, 18. *Glomospirella irregularis* (Moeller), 17: Loc. 12, D2-02869b, 18: Loc. 27, D2-02946a, $\times 80$. 19. *Rectoglomospirella* sp., Loc. 1, D2-02952a, $\times 80$. 20-22. *Malayspirina* cf. *fontainei* Vachard, 20: Loc. 10, D2-02923b, 21: Loc. 10, D2-02926c, 22: Loc. 12, D2-02866a, $\times 80$. 23, 24. *Gaudryina* cf. *triadica* Kristan-Tollmann, 23: Loc. 23, D2-13162, 24: Loc. 10, D2-02918, $\times 80$. 25, 26. *Duotaxis* sp., 25: Loc. 12, D2-02871a, 26: Loc. 12, D2-02868a, $\times 80$. 27-31. "*Endothyra*" cf. *kuepperi* Oberhauser, 27: Loc. 10, D2-02921b, 28: Loc. 10, D2-02917b, 29: Loc. 10, D2-02926d, 30: Loc. 10, D2-02920a, 31: Loc. 12, D2-02871b, $\times 80$. 32. Endothyridae gen. et sp. indet., Loc. 12, D2-02866b, $\times 80$. 33, 35. *Triadodiscus* ? sp., 33: Loc. 21, D2-13178, 35: Loc. 1, D2-02950, $\times 100$. 34. *Triadodiscus* sp., Loc. 1, D2-02952b, $\times 100$. 36, 37. *Arenovidalina* sp., 36: Loc. 10, D2-02927, $\times 120$, 37: Loc. 31, D2-02882c, $\times 80$. 38. *Aulotortus* ? sp., Loc. 1, D2-02951a, $\times 80$. 39. Involutinidae gen. et sp. indet., Loc. 1, D2-02951b, $\times 120$.



widely different among authors (Loeblich and Tappan, 1964; Zaninetti, 1976; Trifonova, 1978a; Pillar, 1983), this genus is also an excellent stratigraphic indicator of the Anisian. *Arenovidalina amylovoluta* He, originally described from southern Sichuan, was distinguished from *A. chialingchian-gensis* He, the type species of the genus, by larger numbers of whorls and larger tests (Ho, 1959). This species is characteristic of the present fauna, and mostly associated with *Glomospira densa* and *Meandrospira dinarica*.

In addition to these three species, this formation yields some diagnostic species showing longer geologic ranges, and also described and illustrated in various regions of the Tethyan Realm. *Endothyra kuepperi* was originally described from the Carnian of the Eastern Alps (Oberhauser, 1960), but it is also reported from the Anisian of the western Carpathians (Salaj *et al.*, 1967) and southern Poland (Gaździcki and Zawidzka, 1973). *Diplotremina astrofimbriata* was established in the Ladinian of the Eastern Alps (Kristan-Tollman, 1964). Later, it was ascertained that the species is also obtainable from the Pelsonian, biostratigraphically equivalent to the *Glomospira densa* Zone in the lower part of the Muschelkalk, of southern Poland (Gaździcki *et al.*, 1975) and also from the Anisian of Guizhou (He, 1984).

The above foraminifers of the Kaizawa Formation are safely assignable to an Anisian age. This age assignment is not in conflict with the occurrence of *Neogondolella bulgarica* (Budurov and Stefanov) in the lenticular conglomeratic limestone in association with *Meandrospira dinarica* and others. This conglomeratic limestone was formerly regarded as part of the Arai Formation by Ozawa and Kobayashi (1986).

The present foraminifer fauna also contains forms morphologically similar to well known species in Europe that are not always indicative of the Anisian. The chronostratigraphic distribution of *Gaudryina triadica* Kristan-Tollman and *Austrocolomia marschalli* Oberhauser has been considered to be limited to the Upper Triassic (Carnian to Rhaetian).

"*Meandrospira*" *deformata* Salaj is probably identical with the original materials from the Upper Anisian of the western Carpathians (Salaj *et al.*, 1967) and those from the Lower Anisian of the Muschelkalk of southern Poland (Gaździcki *et al.*, 1975). In East and Southeast Asia, *Glomospirella irregularis* (Moeller) is known from the Anisian of southern Sichuan (Ho, 1959) and eastern Burma (Brönnimann *et al.*, 1975). Materials from these two localities are similar to almost all of those referable to the genus *Glomospirella* from

the Kaizawa Formation. The genus *Malayspirina* proposed from the Upper Ladinian to Carnian of Peninsular Malaysia by Vachard (Fontaine *et al.*, 1988) is diagnostic in its thick agglutinated wall and planispirally to plectospirally coiled early stage continued by biserially to nearly uniserially uncoiled second stage with an abrupt change of coiling. The present materials are closely similar to the Malaysian ones, but the former seem to have smaller tests and a more distinguishable early stage than the latter.

Other foraminifers are rather poorly oriented and sufficient numbers of materials are not prepared. However, they are illustrated herein so that they can be compared with the Triassic fauna of other regions and the entire aspect of the present fauna shown. Although specific and generic identifications are difficult, they resemble materials described or illustrated from Triassic limestones in many places of the Tethyan Realm.

As mentioned above, the conglomeratic limestone of the Kaizawa Formation consists of Upper Permian as well as Anisian pebbles. The Anisian fauna is quite distinctive, and is easily distinguished from the Upper Permian one in its composition. The Anisian foraminifers have smaller tests and lower frequency of occurrence in comparison with the Upper Permian ones. Limestone lithofacies and composition of other invertebrate fossils are also different between the Upper Permian and Anisian.

Systematic paleontology

Descriptive remarks based on the materials from the Kaizawa Formation are given of nine important taxa. The taxonomic arrangement of the species principally follows the classification by Loeblich and Tappan (1988), with slight modification.

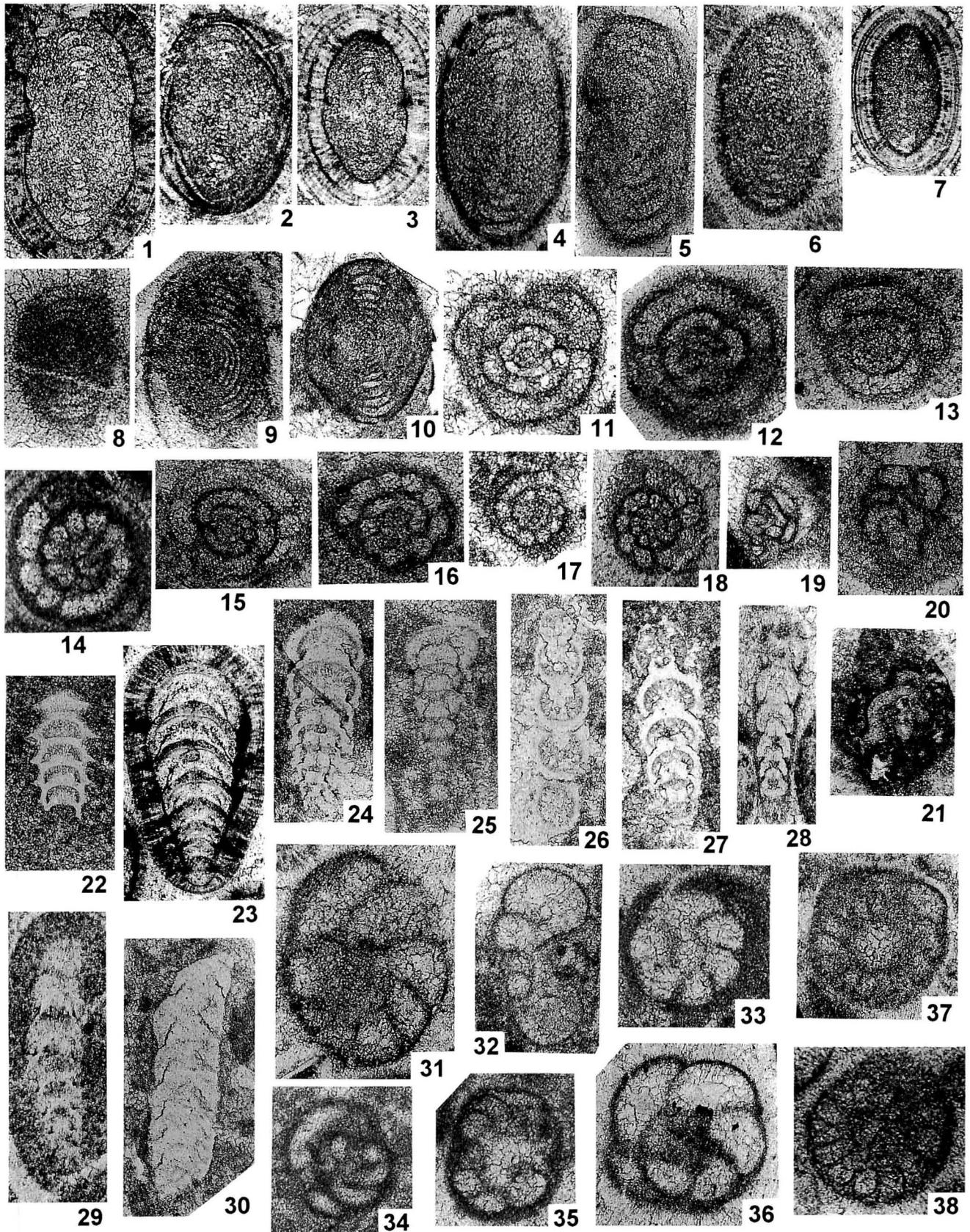
Order Foraminiferida Eichwald, 1830
Suborder Textulariina Delange and Hérouard, 1896
Superfamily Ammodiscacea Reuss, 1862
Family Ammodiscidae Reuss, 1862
Genus *Glomospira* Rzehak, 1885

Glomospira densa (Pantić)

Figures 4-3-14

Pilammia densa Pantić, 1965, p. 189, pl. 1, figs. 1, 2, pl. 2, figs. 1-9; Salaj, Biely and Bystricky, 1967, pl. 1, fig. 7; Premoli

Figure 5. 1-10. *Arenovidalina amylovoluta* Ho, 1: Loc. 29, D2-02874a, 2: Loc. 20, D2-13204, 3: Loc. 10, D2-02924a, 4: Loc. 21, D2-13185, 5: Loc. 23, D2-02885, 6: Loc. 21, D2-13184, 7: Loc. 10, D2-02921c, 8: Loc. 11, D2-13277a, 9: Loc. 15, D2-13246, 10: Loc. 10, D2-02925b, 1-3 = $\times 100$; 4-6 = $\times 120$; 7-10 = $\times 80$. **11-18.** *Meandrospira dinarica* Kochansky-Devidé and Pantić, 11: Loc. 11, D2-13278, 12: Loc. 12, D2-13299, 13: Loc. 27, D2-02946b, 14: Loc. 29, D2-02874b, 15: Loc. 1, D2-02951c, 16: Loc. 10, D2-02920b, 17: Loc. 11, D2-13277b, 18: Loc. 27, D2-02947b, $\times 120$. **19-21.** "*Meandrospira*" *deformata* Salaj, 19: Loc. 10, D2-02924b, 20: Loc. 12, D2-13300, 21: Loc. 20, D2-13208, $\times 80$. **22.** *Austrocolomia* cf. *marschalli* Oberhauser, Loc. 10, D2-02926e, $\times 80$. **23.** *Austrocolomia* sp., Loc. 21, D2-13180, $\times 80$. **24, 25.** *Cryptoseptida* ? sp., 24: Loc. 10, D2-02922, 25: Loc. 12, D2-02869c, $\times 80$. **26, 27.** *Nodosaria expolita* Trifonova, 26: Loc. 12, D2-02868b, 27: Loc. 11, D2-13279a, $\times 100$. **28-30.** *Nodosaria* spp., 28: Loc. 27, D2-02948a, 29: Loc. 27, D2-02949c, 30: Loc. 11, D2-13279b, $\times 80$. **31-36.** *Diplotremina astrofimbriata* Kristan-Tollmann, 31: Loc. 27, D2-02948b, 32: Loc. 10, D2-02920c, 33: Loc. 12, D2-02869d, 34: Loc. 12, D2-02866c, 35: Loc. 12, D2-02870, 36: Loc. 1, D2-02953, $\times 80$. **37, 38.** *Diplotremina* sp., 37: Loc. 27, D2-02947c, 38: Loc. 27, D2-02947d, $\times 80$.



Silva, 1971, p. 325, 326, pl. 21, figs. 1-3, pl. 22, figs. 3, 4.

Glomospira cf. *densa* (Pantić). Zaninetti, 1969, p. 27-29, pl. 4, figs. A, B, C.

Glomospira densa (Pantić). Brönnimann *et al.*, 1973a, p. 307, 308, figs. 1-7, 10, 11; Brönnimann *et al.*, 1973b, p. 466, pl. 47, figs. 3, 4; Gaździcki *et al.*, 1975, pl. 2, figs. 5-9; Zaninetti, 1976, p. 89-91, pl. 2, figs. 17, 21; Gaździcki and Smit, 1977, pl. 3, figs. 4-9; Trifonova, 1978a, pl. 2, fig. 3; He, 1984, p. 422, pl. 1, figs. 1-7.

Descriptive remarks.—Although Pantić (1965) proposed a new genus *Pilamina* with *P. densa* from the Anisian of Montenegro as the type species, it is considered generally to be a junior synonym of *Glomospira* Rzehak. The present species has been described or illustrated from various regions of the Tethyan Realm, and is one of the most reliable indicators of an Anisian age. The present materials are identical with them. Compared with the specimens found in algal limestone, those contained in oöid grainstone have a smaller test and a rather irregular test outline. These differences are evidently due to abrasion of the outer test.

Occurrence.—Common to rare at Locs. 15 and 31, and rare at Locs. 1, 10, 12, 13, 14 (?), 20, 21, 23, 27, 29, and 30.

Genus *Glomospirella* Plummer, 1945

Glomospirella irregularis (Moeller)

Figures 4-17, 18

Glomospirella irregularis (Moeller). Ho, 1959, p. 398, 412, pl. 4, figs. 14-23; Brönnimann *et al.*, 1975, p. 10, pl. 3, figs. 7-10, 12-14, 16, 18.

Descriptive remarks.—The present specimens are characterized by a thick biumbonate test consisting of an undivided tubular chamber streptospiral in the early stage and later becoming planispirally enrolled. They are similar to *Glomospirella irregularis* (Moeller) described from the Anisian of southern Sichuan (Ho, 1959) and eastern Burma (Brönnimann *et al.*, 1975) in size and morphology of the test. The amount of material is insufficient for thorough comparison with previous descriptions of the species.

Occurrence.—Rare at Locs. 10 (?), 12 and 27.

Superfamily Lituolacea de Blainville, 1827

Family Lituolidae de Blainville, 1827

Subfamily Ammomarginulinae Podobina, 1978

Genus *Malayspirina* Vachard, 1988

Malayspirina cf. *fontainei* Vachard

Figures 4-20—22

Compared.—

Endothyranella sp. Zaninetti and Brönnimann, 1975, pl. 35, figs. 13-15.

Earlandinita ? sp. Gaździcki and Smit, 1977, pl. 7, figs. 6, 9.

Earlandinita cf. *soussii* Salaj. Gaździcki and Smit, 1977, pl. 7, fig. 7.

Earlandinita soussii Salaj. Gaździcki and Smit, 1977, pl. 7, fig. 8.

Endothyranella sp. Altiner and Zaninetti, 1981, pl. 85, figs. 4-8.

Malayspirina fontainei Vachard in Fontaine *et al.*, 1988, p. 157, 158, figs. 5a-d, i, j, o, figs. 6e, h.

Descriptive remarks.—Generic identification of *Malayspirina* requires longitudinal sections, because its chambers are coiled nearly planispirally in the early stage, then uncoiled and arranged linearly in the second stage. A randomly cut section of this genus is similar to that of *Earlandinita*, *Endothyranella* or *Endothyra*, depending on the orientation of the section.

The present materials closely resemble the following forms illustrated from West and Southeast Asia: *Endothyranella* sp. associated with *Meandrosira pusilla* (He) and others from the Anisian of Pakistan (Zaninetti and Brönnimann, 1975); *Endothyranella* sp. from the Carnian to Norian of Turkey (Altiner and Zaninetti, 1981); *Earlandinita soussii* Salaj, *E. cf. soussii* Salaj and *E. ?* sp. from the Anisian to Ladinian of Peninsular Malaysia (Gaździcki and Smit, 1977). These forms closely resemble *Malayspirina fontainei* newly proposed by Vachard (Fontaine *et al.*, 1988) from the Ladinian to Carnian of Peninsular Malaysia. The present materials have, however, a smaller test and more distinctive early stage than the original ones of *Malayspirina fontainei*.

Occurrence.—Rare at Locs. 10, 12 and 27.

Suborder Fusulinina Wedekind, 1937

Superfamily Endothyracea Brady, 1884

Family Endothyridae Brady, 1884

Subfamily Endothyrinae Brady, 1884

Genus *Endothyra* Phillips, 1846

"*Endothyra*" cf. *kuepperi* Oberhauser

Figures 4-27—31

Compared.—

Endothyra kuepperi Oberhauser, 1960, p. 16, pl. 3, figs. 7, 14, 22; Gaździcki and Zawidzka, 1973, pl. 1, fig. 14; Zaninetti, 1976, p. 126, 127, pl. 8, figs. 20-25; Gaździcki and Smit, 1977, pl. 8, figs. 7, 8; Trifonova, 1978b, pl. 2, fig. 8.

Neoendothyra kuepperi (Oberhauser). Salaj *et al.*, 1967, pl. 1, fig. 11.

"*Endothyra*" *kuepperi* Oberhauser. Zaninetti, 1969, p. 41-43, fig. 7, pl. 6, fig. c.

"*Endothyra*" aff. *kuepperi* Oberhauser. Premoli Silva, 1971, p. 337, pl. 27, fig. 4.

Endothyra malayensis Gaździcki and Smit, 1977, p. 324, pl. 8, figs. 1-3.

Endothyranella ? sp. Gaździcki and Smit, 1977, pl. 8, figs. 4, 5.

Endothyranella sp. Gaździcki and Smit, 1977, pl. 8, fig. 9.

Descriptive remarks.—*Endothyra keupperi* was originally proposed for "*Endothyra*" characterized by having a calcareous agglutinated wall, plectospirally coiled inner whorls and nearly planispirally coiled last whorl from the Carnian of the Eastern Alps (Oberhauser, 1960). Triassic species assigned to *Endothyra*, including this species, by previous authors can not be easily distinguished from Late Paleozoic ones by their morphologic differences except for the composition and thickness of the wall. The wall of the former group is much thicker than that of the latter in comparison with test size,

and is composed of calcareous agglutinated materials instead of microgranular calcite. Although the generic assignment of this species is uncertain, it is tentatively included in "*Endothyra*" with a query as most previous authors have done.

Four forms described or illustrated from the Anisian to Ladinian of Peninsular Malaysia by Gaździcki and Smit (1977), *Endothyra kuepperi*, *E. malayensis* Gaździcki and Smit, *Endothyranella* sp. and *E. ?* sp. resemble each other. They are thought to be conspecific, because the last whorl of "*E. kuepperi*" expands rapidly as compared with the inner ones, and is not completely coiled planispirally. Therefore, a lesser number of chambers in the last whorl and seemingly uncoiled or evolute terminal chamber as shown in excentric sections of the Malaysian forms may be ascribed to different orientations of thin sections.

Occurrence.—Common to rare at Loc. 10, and rare at Locs. 12, 14 (?), and 27.

Suborder Involutinina Hohenegger and Piller, 1977

Family Involutinidae Butschli, 1880

Genus *Arenovidalina* Ho, 1959

Arenovidalina amylovoluta Ho

Figures 5-1—10

Arenovidalina amylovoluta Ho, 1959, p. 401, 415, 416, pl. 7, figs. 10-17.

Ophthalmidium ? amylovoluta (Ho). Zaninetti, 1976, p. 141, pl. 3, figs. 12, 13.

Aulotortus amylovoluta (Ho). Lin and Zheng, 1978, p. 48, pl. 10, figs. 28, 29.

Descriptive remarks.—Ho (1959) erected the genus *Arenovidalina* from the Anisian of southern Sichuan, and discriminated four species by slight differences in test size and shape and degree of expansion of the second tubular chamber. However, comparison of their corresponding whorls indicates that the significant differences which Ho (1959) insisted on are not clear among the four Chinese forms. Smaller forms like *Arenovidalina chialingchiangensis* may merely represent incomplete or immature specimens of larger forms like *A. amylovoluta*. *Aulotortus chialingchiangensis* (Ho) and *A. amylovoluta* (Ho), described from the Lower Triassic of Hubei by Lin and Zheng (1978), closely resemble each other, and are hardly distinguishable by slight differences in their size and shape of tests.

The present materials are tentatively assigned to *A. amylovoluta* until the validity of the four Chinese species is examined in the type locality.

Occurrence.—Rare at Locs. 1, 10, 11, 15-17, 20-23, and 29.

Suborder Miliolina Delage and Hérouard, 1896

Superfamily Cornuspiracea Schultze, 1854

Family Cornuspiridae Schultze, 1854

Genus *Meandrospira* Loeblich and Tappan, 1946

Meandrospira dinarica Kochansky-Devidé and Pantić

Figures 5-11—18

Meandrospira dinarica Kochansky-Devidé and Pantić. Salaj *et al.*, 1967, pl. 1, figs. 13a, 19; Brönnimann *et al.*, 1973a, p. 313, 314, pl. 20, figs. 8, 11, 12; Brönnimann *et al.*, 1973b, p. 469, pl. 46, figs. 11, 15, pl. 47, fig. 10; Gaździcki *et al.*, 1975, pl. 9, figs. 5-9; Zaninetti, 1976, p. 133-135, pl. 1, figs. 12-14; Gaździcki and Smit, 1977, pl. 4, fig. 7; Trifonova, 1978a, pl. 2, fig. 7; He, 1984, p. 427, pl. 3, figs. 4-9.

Meandrospira ? dinarica Kochansky-Devidé and Pantić. Zaninetti, 1969, p. 47-49, pl. 4, figs. E, F.

Citaella dinarica (Kochansky-Devidé and Pantić). Premoli Silva, 1971, p. 324, pl. 20, figs. 2, 4-8.

Descriptive remarks.—Zigzag bends of the tubular second chamber are not so markedly recognizable in the present materials as in previously described ones. However, they are closely similar to the European materials and safely identified with this species in many respects, though very few completely axial and equatorial sections were prepared.

Occurrence.—Common to rare at Loc. 10, and rare at Locs. 1, 11, 12, 13 (?), 23, 27, and 29.

"*Meandrospira*" *deformata* Salaj

Figures 5-19—21

Meandrospira deformata Salaj. Salaj *et al.*, 1967, p. 122, pl. 2, figs. 3a-3d.

Meandrospira ? deformata Salaj. Gaździcki *et al.*, 1975, p. 290, pl. 7, figs. 9-16.

"*Meandrospira*" *deformata* Salaj. Zaninetti, 1976, p. 138, pl. 1, figs. 20-22; Resch, 1979, pl. 4, fig. 20.

Descriptive remarks.—The present materials are common in appearance to the originally and subsequently described ones in a meandrospherical coiling restricted to inner whorls, followed by irregular coiling in outer ones. Detailed reconstruction of test characters needs more specimens.

Occurrence.—Rare at Locs. 10, 12, and 20.

Suborder Lagenina Delage and Hérouard, 1896

Superfamily Robuloidacea Reiss, 1963

Family Ichthyolariidae Loeblich and Tappan, 1946

Genus *Austrocolomia* Oberhauser, 1960

Austrocolomia cf. *marschalli* Oberhauser

Figure 5-22

Compared.—

Austrocolomia marschalli Oberhauser, 1960, p. 38, pl. 1, figs. 42-46, 52.

? *Austrocolomia marschalli* Oberhauser. Trifonova, 1978b, pl. 3, fig. 4.

? *Austrocolomia* aff. *marschalli* Oberhauser. Fontaine *et al.*, 1988, fig. 5q.

Descriptive remarks.—A few distinctive specimens obtained have straight sutures, with distinct abrupt shoulders perpendicular to the long axis of an elongate test with more than 6 chambers. The upper surface of each chamber is

smooth and domed posteriorly. From these features, they are possibly referable to this species, but have smaller and slenderer tests in comparison with the type material from the Carnian of the Eastern Alps (Oberhauser, 1960). Abrupt shoulders diagnostic to the original materials are indistinct or absent in single specimens illustrated from Bulgaria (Trifonova, 1978b) and Peninsular Malaysia (Fontaine *et al.*, 1988). Further examination of more materials are necessary to exactly identify them with the original ones.

Occurrence.—Rare at Loc. 10.

Superfamily Duostomineacea Brotzen, 1963
Family Duostominidae Brotzen, 1963
Genus *Diplostromina* Kristan-Tollmann, 1960

Diplostromina astrofimbriata Kristan-Tollmann

Figures 5-31—36

Diplostromina astrofimbriata Kristan-Tollmann, 1964, p. 64, 65, pl. 14, figs. 1-4; Premoli Silva, 1971, p. 340, 341, pl. 27, figs. 1, 5, 6, pl. 28, figs. 1, 2; Gaździcki *et al.*, 1975, pl. 6, figs. 4-7; Zaninetti, 1976, p. 186, 187, pl. 17, fig. 5; Gaździcki and Smit, 1977, pl. 10, fig. 9; He, 1984, p. 426, pl. 4, figs. 1-7; Skoutsis-Coroneou *et al.*, 1990, pl. 2, figs. 11, 12.

Descriptive remarks.—Several horizontal and oblique sections and an oblique vertical section are obtained. Although details of test construction and the test characters are unknown because of insufficient numbers of individuals and no free specimens, such structural patterns as convex spiral side, opposite side with deeply lobed umbilicus, chambers gradually increasing in size, fimbriated sutural end toward umbilicus and calcareous finely granular wall seem to be essentially the same as those of the type material from the Ladinian of the East Alps (Kristan-Tollman, 1964). However, it is difficult to compare apertural characters between the two.

The general aspects of the present materials closely resemble the illustrations shown by Gaździcki *et al.* (1975) from the Illyrian (upper Anisian) of the Muschelkalk of southern Poland. *Diplostromina* sp. in this paper is distinguished from the present species by having more chambers and the indistinctive fimbriated suture of the former.

Occurrence.—Rare at Locs. 1, 12, 13 and 27.

Acknowledgments

I would like to express my cordial thanks to Dr. Koichiro Ichikawa, Professor Emeritus of Osaka City University, Dr. Hisayoshi Igo, Professor of the University of Tsukuba and Dr. Tomowo Ozawa, Associate Professor of Nagoya University for their critical reading of the manuscript. Deep appreciation is due to Dr. Chikao Kurimoto, Geological Survey of Japan for his kind cooperation in collecting the literature on foraminifers. A part of this study was financially supported by a Grant-in Aid for Scientific Research (C) of the Japanese Ministry of Education, Science and Culture (Project No. 05640521).

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SHORT NOTES

34

A little known species of *Inoceramus* (Bivalvia) from the Turonian (Cretaceous) of Hokkaido

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Received 10 January 1996; Revised manuscript accepted 20 May 1996

Inoceramus kamuy Matsumoto and Asai has been recently established on a number of specimens from the Lower Turonian of Hokkaido (Matsumoto and Asai, 1996). There is, furthermore, another little known species from the lower part of the Turonian in Hokkaido. A short note is given here on it.

Paleontological description

Genus *Inoceramus* Sowerby, 1814

Type species.—*Inoceramus cuvierii* Sowerby, 1814.

Inoceramus aff. *I. tuberosus* Keller, 1982

Figures 1 A-F

Material.—The description below is based primarily on GK. H8320 collected by K. Tanabe, H. Hirano and T.M. in 1973 from the siltstone exposed at loc. R4519 in the lower course of the Nakakinenbetsu River of the Obira [Obirashibe] area, northwestern Hokkaido. GK. H8320 is a medium-sized individual of conjoined left and right valves. It is associated with several imperfect smaller (probably young) shells. There are also a few other specimens which are referable to this species.

Repositories of the described specimens are as follows:

GK=Type Room, Department of Earth and Planetary Sciences, Kyushu University, Fukuoka 812-81
IGPS=Institute of Geology and Palaeontology, Tohoku University, Sendai 980-77

Terminology.—For the terms to describe morphological characters and their abbreviations, I follow generally those of recent papers, except for β =beak angle or apical angle instead of angle of umbonal inflation (see Matsumoto and

Asai, 1996, table 1).

Description.—The shell is medium-sized, inequilateral and somewhat inequivalve, with the left valve more inflated than the right. The beak is prosogyrous; the left beak is more strongly incurved over the hinge line than the right. The apical angle is less than 90° and may be measured as 85° to 65° in accordance with the curved outline of the apical part. The growth axis is nearly straight, forming an angle of about 55° with the hinge line, and divides the disk in half. The left valve is much inflated and the right valve is moderately so. The umbonal part, which is demarcated by a constriction from the main part, is especially inflated; hence the left umbo appears to be hemispherical and the right one dome-like in lateral and posterior views. The anterior side of the valve is steeply inclined, partly vertical to the plane of commissure, and is somewhat concave below the umbo. The anterior margin is, thus, gently sinuous and bent rather abruptly to the semicircular ventral margin, which in turn passes to the moderately to gently convex posterior margin. The hinge line is fairly long, with s/l about 3/4, and forms the angle (γ) of 100° (in youth) to 125° (later) with the posterior margin. The posterodorsal wing is narrow and inclined in youth, but later it becomes broader and flatter. The anterior hinge angle (α) is roughly 100°, if the sinuosity of the anterior margin is ignored. The ratio L/H decreases gradually with growth in the young stage and becomes nearly constant (about 0.8) in the middle and late growth stages.

The comarginal major ribs are normally moderately strong, but some of them are rather weak. They are more distinct when associated with deeper grooves which occur at periodic intervals. The grooves are disposed on both the left and right valves at corresponding positions and accordingly can be interpreted as marking periodic arrests of growth; hence they can be called constrictions. Some of the major ribs are bifurcated or intercalated. Minor rings are discernible even on some parts of the internal mould. They are

Figure 1. *Inoceramus* aff. *I. tuberosus* Keller. GK. H8320 from loc. R4519. A: lateral view of the left valve (LV) with posterodorsal view of the right valve (RV), B: lateral view of RV with posterodorsal view of LV, C: dorsal view of both valves (BV) with LV below, D: dorsal view of BV with LV above, E: anterior view of BV, F: posterior view of BV, with the external mould of a small RV in a broken part of the nodule. Figures are natural size. Photos by courtesy of M. Noda without whitening.

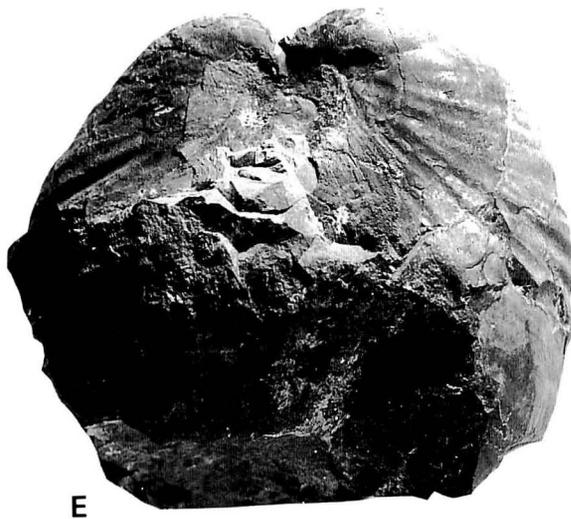
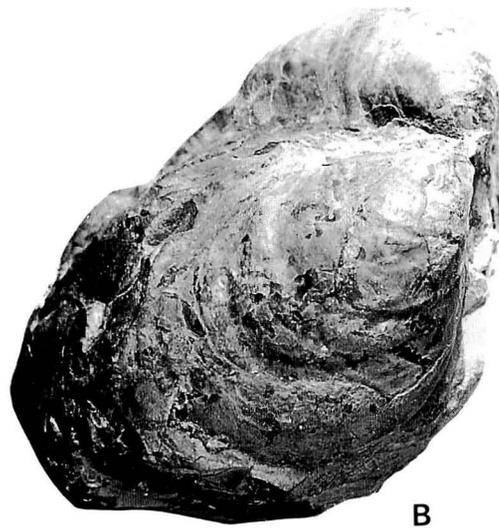
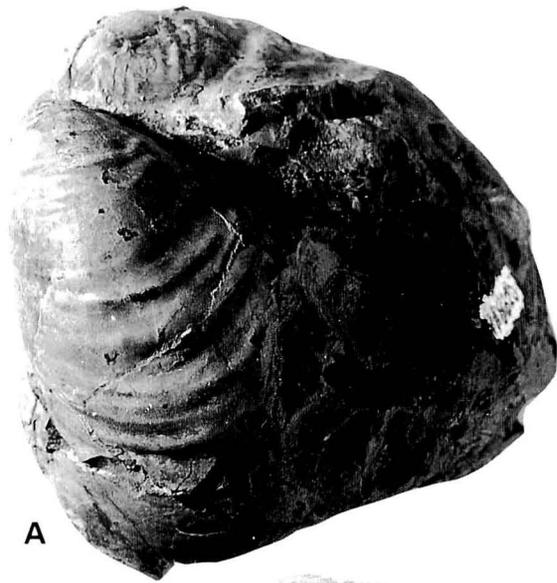


Table 1. Measurements of *Inoceramus* aff. *tuberosus*

Valve	h	l	l/h	H	L	L/H	b	b/l	b/H	s	s/l	γ	δ
Left	65	57	.89	72	58	.80	30	.50	.42	43	.74	125°	55°
Right	63	55	.87	70	52	.80	25	.45	.36	43	.78	125°	55°

Linear dimensions are in mm. Outline of the shell is partly restored.

impressed more clearly on the external mould. On the anterior side they are much crowded and become fine lamellae or lirae.

In the last part (with H=55–75 mm) the major ribs tend to weaken, the interspaces somewhat broaden and the minor rings become faint. This probably indicates the adult to old stage.

IGPS. 22725 from the Obira area (though without a pinpointed locality) was described as an example of *Inoceramus concentricus* var. *costatus* Nagao and Matsumoto (1939, p. 270, pl. 27, fig. 2). It consists of both valves and is different from *I. costatus* (lectotype [*ibid.*, pl. 24, fig. 1] and some other examples) as redefined by Tamura and Matsumura (1974, p. 49) in its more rounded shell shape, stronger and coarser ribs, and distinct posterior wing. It closely resembles the middle-aged part of the above described GK. H8320 and is probably an example of this species. The ribs are more distinct in the right valve of IGPS. 22725 than in that of GK. H8320, but this is due to the secondary abrasion of the latter. Even in the latter the ribs remain more clearly on the less abraded anterolateral and posterolateral portions. Also the ribs of moderate intensity are impressed on the external mould of a smaller shell which is associated with GK. H8320 in the same nodule.

Measurements.—See Table 1.

Comparison and discussion.—The specimens from Hokkaido described above are similar to the holotype of *Inoceramus tuberosus* Keller (1982, p. 69, pl. 2, fig. 5), from the Lower Turonian of Germany, in the inflated and rounded valve and the general configuration of the ornament. One specimen of *Inoceramus striatus* Mantell illustrated by Geinitz (1872, p. 41, pl. 13, fig. 10 only) is regarded by Keller as another example of *I. tuberosus*, but it is also a left valve. Keller has stressed the knobby shape of the umbonal part. As the anterior or dorsal view was not illustrated, the character cannot be exactly compared with ours. Geinitz' figure shows an imperfect preservation of the beak. Even in the figure of the holotype, a partly eroded state of the knobby umbo seems to be shown. In our specimens the umbonal part is much inflated and appears to be hemispherical or dome-like in lateral and posterior views, but the beak is pointed at its apex. In the German papers the apical end is not shown and I doubt that the knobby feature might have been produced secondarily from the much inflated umbonal part. At any rate, without examining the actual specimens, I cannot decide the specific identity or difference between the specimens from Japan and Germany. Moreover, the number of samples in the available material is too small in both regions to get a proper concept of a species. For the time being, I have to call our species *Inoceramus* aff. *I. tuberosus* or simply *I. aff. tuberosus*. This means that our

species is closely allied to *I. tuberosus*, but that, in this case, it may or may not be identical with *I. tuberosus*.

I. aff. tuberosus is certainly related with *Inoceramus reduncus* Pergament from the Middle and Upper Cenomanian of the Pacific region of Russia and Hokkaido (see Matsumoto *et al.*, 1988, p. 383), but the former has more rounded and more inflated valves than the latter. *I. reduncus* tends to grow along the growth axis to form a very high outline. Such a form (morphotype) is commonly found in a fairly high level (if not at the top) of the Cenomanian sequence in Hokkaido, as shown by several examples from the Oyubari and Ikushunbetsu areas (Nishida *et al.*, 1993, pl. 6, fig. 3, pl. 7, fig. 1; unfigured specimen from Ikushunbetsu). The younger part of this morphotype resembles *I. aff. tuberosus* in shell shape but has much weaker ornament. In later growth stages *I. reduncus* has smaller ratios of L/H and b/H than those of *I. aff. tuberosus*, although there is some variation within the species.

I interpret that *I. aff. tuberosus* of a later geological age is probably a descendant of *I. reduncus*. As described above, GK. H8320 has the characters of the adult stage. It is not a young shell of *I. reduncus*. *I. aff. tuberosus* may be so to speak a relict of the *I. reduncus* group.

Occurrence.—The siltstone exposed at loc. R4519 is referred to Member Mj (Lower Turonian) by Tanaka (1963), but Tanabe *et al.* (1977) referred it to "Mjk", because Members Mj and Mk are hardly discriminated in that portion of the Obira area. A fairly well-preserved ammonite occurred in the same stratum. It is identified with *Damesites laticarinatus* Saito and Matsumoto, which is rather long-ranging from late Cenomanian to somewhere in mid-Turonian. More accurate age indicators (ornate ammonites or *Mytiloides*) were not found there. Hence, the siltstone of loc. R4519 is either Lower Turonian or early Middle Turonian.

The rare occurrence of *I. tuberosus* in the Lower Turonian of Germany and that of *I. aff. tuberosus* in the lower part of the Turonian in Hokkaido is in high contrast to the abundance of *Mytiloides* spp. The group of *I. reduncus* may have declined in early Turonian time for environmental reasons. In fact, there was a marked event (the so-called OAE) at the end of the Cenomanian, as is observed on the excellent outcrops along the Shirakin River [=Hakkinzawa] route of the Oyubari area (see Hasegawa, 1995; Toshimitsu *et al.*, 1995, fig. 1). Also in the Taki-no-sawa route I observed the black mudstone above the *I. nodai* bed and not far below the bed with *Pseudaspidoceeras flexuosum* Powell (see route map of Nishida *et al.*, 1993, fig. 5).

Acknowledgments

I thank Drs. Kazushige Tanabe and Hiromichi Hirano for

their cooperation with me in field work, Dr. Masayuki Noda for his fine photography and valuable discussion on relevant inoceramids, Drs. Ireneusz Walaszczyk (Warsaw) and Haruyoshi Maeda (Kyoto) for their kind information about Geinitz' paper, and Dr. Kunihiro Ishizaki and Miss Kazuko Mori for their help in preparing the manuscript.

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Hakkin-zawa 白金沢, Hokkaido 北海道, Nakakinenbetsu 中記念別, Obira [Obirashibe] 小平 [オビラシベ], Oyubari 大夕張, Shirakin 白金, Taki-no-sawa 滝の沢.

SHORT NOTES

35

Triassic aulacocerid (Mollusca : Cephalopoda) from the central Oman Mountains

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Received 3 December 1995 ; Revised manuscript accepted 10 May 1996

The aulacocerid cephalopod species *Atractites arabicus* sp. nov. was discovered from a limestone conglomerate exposed in the "Rustaq Ouest" area, approximately 5 km west of Rustaq village, central Oman Mountains. This area is characterized by the presence of the thrust sheets, called Hawasina Nappes, of Tethyan origin formed during the Late Cretaceous obduction of ophiolite complex onto the Arabian continental margin (e.g., Robertson and Searle, 1990). The limestone conglomerate overlies siliciclastic sequences containing *Halobia*, and is situated in the basal portion of the Hawasina Nappes (Pillevuit, 1993).

The specimens studied are deposited in the Paleontological collections of Geological Museum of Lausanne (MGL), Switzerland.

Systematic paleontology

Order Aulacocerida Stolley, 1919
Family Xiphoteuthidae Naef, 1922
Genus *Atractites* Gümbel, 1861

Type species.—*Atractites alpinus* Gümbel, 1861.

Atractites arabicus sp. nov.

Diagnosis.—Species of *Atractites* with nearly symmetrical rostra, position of phragmocone slightly shifts to ventral side from central axis of rostrum ; angle of phragmocone expansion approximately 5 degrees.

Description.—Nearly symmetrical rostra of alveolar region with smooth surface ; profile conical to cylindrical, angle of expansion approximately 2 degrees in apical part of holotype, paratype exhibits subparallel sides, outline cylindrical ; cross section of rostrum slightly compressed in lateral direction, lateral/dorsoventral ratio of rostrum approximately 0.94 ; largest specimen (holotype) attains 12.5 mm in dorsoventral rostrum diameter ; rostra mostly composed of coarse crystal of carbonates caused by recrystallisation, but mammillary growth pattern partly recognized ; alveolus pen-

etrates throughout preserved rostrum ; phragmocone orthoconic with approximately 5 degrees of angle of expansion, slightly compressed in cross section, slightly shifts venter from central axis of rostrum in position, lateral/dorsoventral ratio of phragmocone approximately 0.93 ; surface of conotheca smooth ; septa convex adapically with moderately strong curvature ; width/length ratio of camerae somewhat variable, ranges from 1.9 to 3.4 ; siphuncle position at ventral margin, cylindrical with weak constrictions at septal neck, small, its maximum diameter/phragmocone diameter in dorsoventral section approximately 0.12 ; septa of ventral side of siphuncle very small, low simple mound-like in dorsoventral section ; septal necks short, 0.49 mm in length in apical paratype (corresponding dorsoventral diameter of phragmocone 5.1 mm), prochoanitic with retrochoanitic projections, connected by laminated and well-calcified connecting rings ; inner surface of siphuncle coated with organic membrane (conchiolinic ?) ; no cameral and/or siphuncular deposits detected.

Discussion.—Fischer (1951) reported an aulacocerid possessing a holochanitic siphuncle from the Norian (Upper Triassic) of Nevada. He proposed the genus *Choanoteuthis* on the basis of its unique siphuncle. In contrast, Jeletzky (1966) stated that *Atractites ausseanus* (Mojsisovics, 1871) and Fisher's specimen have prochoanitic and feebly retrochoanitic septal necks, and that the holochanitic appearance is caused by strong calcification of the connecting rings. The connecting rings of the present specimens are also strongly calcified and layered, thus its structure is apt to mislead. However, detailed observations, mentioned in the above description, support Jeletzky's view that the genus *Choanoteuthis* is regarded as a synonym of the genus *Atractites*. The siphuncular tube of the present specimens is double-layered (connecting ring and inner layer of organic membrane), but lacks an intercalated porous prismatic layer in contrast to belemnoids (Obata *et al.*, 1980) and the apical shell of *Dictyocorites* (Bandel, 1985).

Atractites sp. described from the Anisian (Middle Triassic) of Afghanistan by Kummel and Erben (1968) is externally

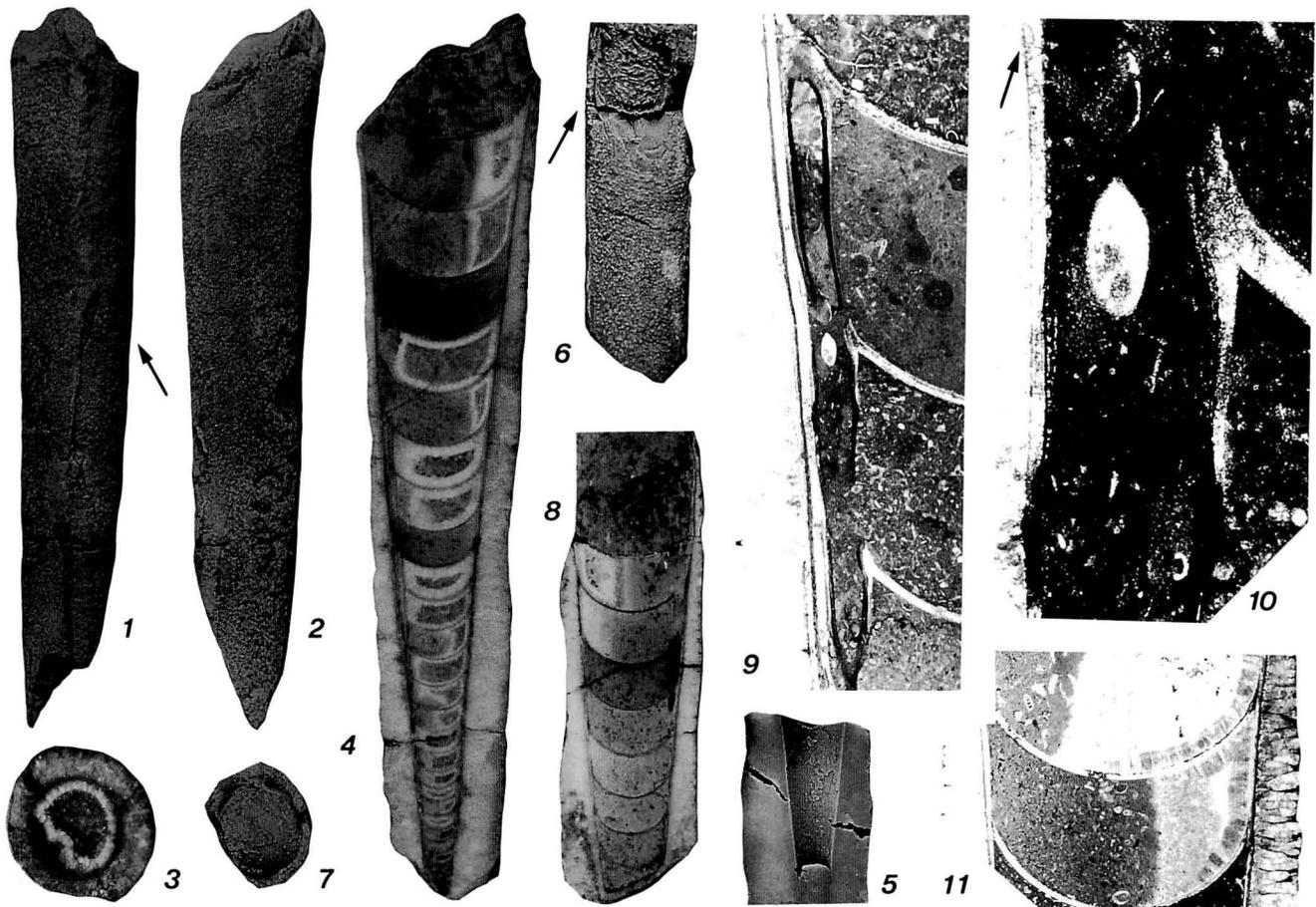


Figure 1. *Atractites arabicus* sp. nov. from the Matbat Formation. 1-5. holotype, MGL 72031, 1: dorsal outline, $\times 1.5$, 2: left profile, $\times 1.5$, 3: cross section at position indicated by arrow given in 1, $\times 2$, 4: dorsoventral polished section, venter on left, $\times 2$, 5: external mold of phragmocone showing smooth surface of conotheca, $\times 2$. 6-11. paratype MGL 72032, 6: left profile, $\times 1.5$, 7: septal view at position indicated by arrow given in 6, $\times 1.5$, 8: dorsoventral polished section, venter on right, $\times 2$, 9: dorsoventral thin section showing siphuncular structure, $\times 12$, 10: details of septal neck and connecting rings, arrow indicating ventral septum, $\times 50$, 11: longitudinal thin section showing mammillary growth pattern of rostrum, $\times 6$. 1, 2, 5-7, coated with ammonium chloride.

similar to *A. arabicus* sp. nov., but apparently differs in distinctly orthochoanitic septal necks, larger apical angle of phragmocone (6-9 degrees vs. approximately 5 degrees in *A. arabicus*) and centrally located phragmocone. Previously there were no records of aulacocerids from Arabia (Doyle, 1990).

Etymology.—The specific name is derived from Arabia.

Material.—The holotype, MGL 72031, is an incomplete rostrum and phragmocone, 66.6 mm in length. The paratype, MGL 72032, is an incomplete rostrum and phragmocone, 33.0 mm in length.

Occurrence and age.—The two specimens were collected from a reddish limestone boulder (up to 2 m in diameter) in a limestone conglomerate bed. The sequence is correlative with the Unit III of the Matbat Formation in the Hawasina Window. Based on the associated ammonoids, Krystyn (personal communication) considers the age of the boulder to be

late Ladinian to early Carnian.

Acknowledgments

Thanks to Dr. L. Krystyn (University of Vienne) for identification and information of the "Rustaq Ouest" ammonoids. Dr. P. Doyle (University of Greenwich) read the original manuscript.

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SHORT NOTES

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Preliminary note on the rediscovery of “*Neoschwagerina* (*Sumatrina*) *multiseptata* Deprat” from Akasaka, Japan

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Received 28 December 1995 ; Revised manuscript accepted 5 May 1996

Deprat (1912) first introduced and described a new neoschwagerinid species with specialized morphologic characters from the Sisophon Limestone of Cambodia as *Neoschwagerina* (*Sumatrina*) *multiseptata* which was later allocated variously: some workers assigned it to the genus *Yabeina* Deprat (1914), and others who follow Lee (1933) to his genus *Lepidolina* Lee. In 1914, Deprat further reported the occurrence of this species from the Akasaka Limestone of Japan. According to him, this species in the Akasaka came from the limestone horizon which is stratigraphically above the limestone division characterized by *Neoschwagerina* (*Yabeina*) *globosa* (Yabe).

Later, the Akasaka Research Group (1956) reported the occurrence of a possible specimen of this missing fusuline from the Akasaka Limestone in association with *Yabeina igoi*. Using the materials collected by the group, Morikawa and Suzuki (1961) described and conferred that specimen to *Yabeina multiseptata* (Deprat). Unfortunately, as their specimen and illustration were not good enough, it was very difficult to make any clear-cut diagnosis and most fusuline workers are not convinced of their identification and description. Honjo (1959) also carried out a paleontological study of this limestone unit but could not confirm any occurrence of *multiseptata*.

From that time onward, most paleontologists believed that Deprat (1914) might have described this species based on his specimens from Cambodia having mistaken them as being of Akasakan derivation. They concluded that *multiseptata* constitutes a fauna or bioseries different from that of *Yabeina globosa* and that there is no possibility that *multiseptata* occurs together with the *Yabeina globosa* fauna. Even though Yamagiwa and Saka (1972) reported the co-occurrence of *multiseptata* with *Yabeina* aff. *globosa* in sandstone lenses within argillaceous rocks exposed along the Toya coast of the Shima Peninsula, Mie Prefecture, Japan, most workers viewed it as an exceptional case.

These situations described above led most fusuline workers to regard the species *multiseptata* as a species of the genus *Lepidolina* rather than of the genus *Yabeina*. These workers believed that *Lepidolina* and *Yabeina* respectively occur in different lithofacies on account of their different ecological traits and, consequently, never occur

together. This way of thinking resulted in the faunal provinciality of *Lepidolina* and *Yabeina*.

The so-called “*Lepidolina*” *multiseptata*, treated as *Yabeina* (*Lepidolina*) *multiseptata* in the present article and represented by specimens showing sufficient morphologic features for specific diagnosis, was discovered from an isolated limestone outcrop in the Akasaka area, the type locality of the genus *Yabeina* (Figures 1 and 2). A few doubtful specimens of *multiseptata* were also detected from the northeastern part of the limestone plateau.

The spirotheca of the present specimens is composed of a tectum and very thin keriotheca, ranging in thickness from 0.01 to 0.03 mm. Secondary transverse septula are short, thin and somewhat irregular in shape, but a few of them are club-shaped. Generally one, or rarely two, secondary transverse septula are present between the adjacent primary ones. These secondary transverse septula are seen starting from the third or fourth volution to the outermost one. Three to five axial septula are present between the adjacent septa. The largest proloculus noticed among the present specimens is 0.4 mm in diameter.

This species occurs in the dark gray, massive to poorly bedded bioclastic micritic limestone that exhibits apparent nodular structure. Petrographically, this limestone is algal-foraminiferal wackestone-packstone composed of abraded bioclasts of dasycladacean algae, fusulines, bryozoans and other unidentifiable shells encased in a micrite matrix.

This species occurs together with *Yabeina igoi* and *Yabeina* aff. *globosa* within an approximately 5 cm-thick zone fairly crowded with fusulines. *Yabeina igoi* which, according to Morikawa and Suzuki (1961), may be synonymous with *Y. ozawai* of Honjo (1959) is the leading faunal constituent among the fusulines, and *multiseptata* follows as the second. A few specimens of *Neoschwagerina minoensis* are also noted.

On the basis of its fossil assemblage, this *Yabeina igoi*-*Yabeina* (*Lepidolina*) *multiseptata* fauna is assignable to the *Yabeina igoi* subzone of Morikawa and Suzuki (1961). According to them and the present field observation, this subzone is situated stratigraphically below the *Yabeina katoi* and *Yabeina globosa* subzones.

It is now necessary to reconsider the previous views of

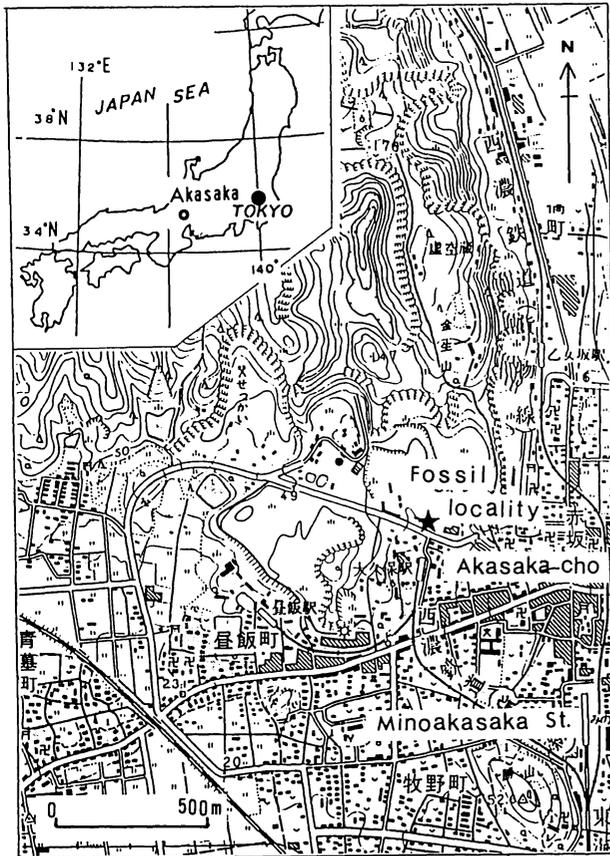


Figure 1. Index map showing locality of *Yabeina* (*Lepidolina*) *multiseptata* bearing limestone outcrop. (part of 1: 25,000 scaled topographic map of Ōgaki City by Geographical Institute of Japan)

biostratigraphic position and biogeographic distribution of *multiseptata*, and its taxonomic position in the light of the present discovery. It obviously shows that the species *multiseptata* represents the lowest part of the *Yabeina* zone in the Akasaka area, but not the same or higher level than the *Yabeina globosa* subzone as previously inferred by most authors. This discovery thus supports the view of Hanzawa and Murata (1963) who placed the *multiseptata* zone below the *Yabeina globosa* zone.

Contrary to the previous general notion of some fusuline provincialists, the present discovery also clearly points out that *multiseptata* can be found in association with some members of the *Yabeina* fauna. Even though further confirmation is probably necessary, it can be said that the paleobiogeographic provinciality of these latest neoschwagerinids does not seem so prominent as previously thought.

The species *multiseptata* was once assigned to the genus

Yabeina Deprat, but now to the genus *Lepidolina* Lee by most students. Originally, Lee (1933), using Deprat's illustrations of *multiseptata* as the type specimen, defined *Lepidolina* as a new genus almost entirely devoid of keriotheca in its wall. However, Skinner and Wilde (1954) and Ishii and Nogami (1964) disapproved of Lee's diagnosis because of the fact that their topotype specimens do possess an unusually thin, but distinct, keriotheca both in the wall and septula as in the case of *Yabeina*.

Although the validity of "*Lepidolina*" should have been automatically null and void since that time, Ozawa (1970) advocated its validity. He stated "This difference in ecological habitat and chronological prosperity between both subfamilies (Neoschwagerininae and Lepidolininae) is noteworthy. This is one of the main reasons I separate *Colania* and *Lepidolina* from the Neoschwagerininae. . . .". However, as a result of the present discovery, it is now evident that the so-called *Lepidolina* occurs together with *Yabeina* in a single limestone sample regardless of inferred ecological factors.

Conclusively, the present discovery is a step toward a solution of the generic status problem of "*Lepidolina*". Concerning its taxonomic position, we advocate, at least for the present, the view of Yabe (1964a, b, 1965, 1966a, b) who discussed this taxonomic problem in detail and concluded that "*Lepidolina*" with the type species *multiseptata* should be reserved as a subgenus of *Yabeina* Deprat. Apart from its taxonomic problem, the present discovery points out that the species *multiseptata* is found in the Akasaka area from the limestone in association with *Yabeina igoi*, but not from the limestone typical of the *Yabeina globosa* subzone.

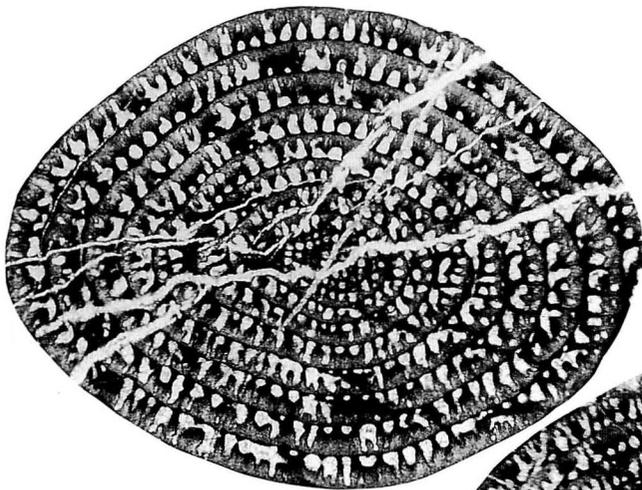
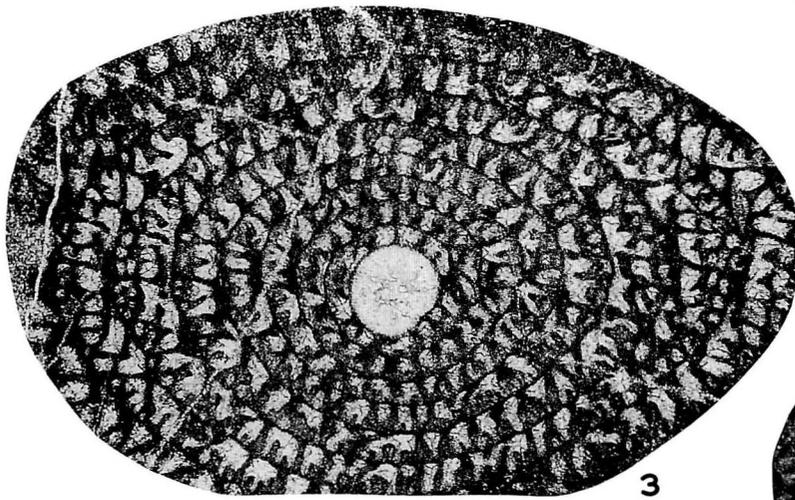
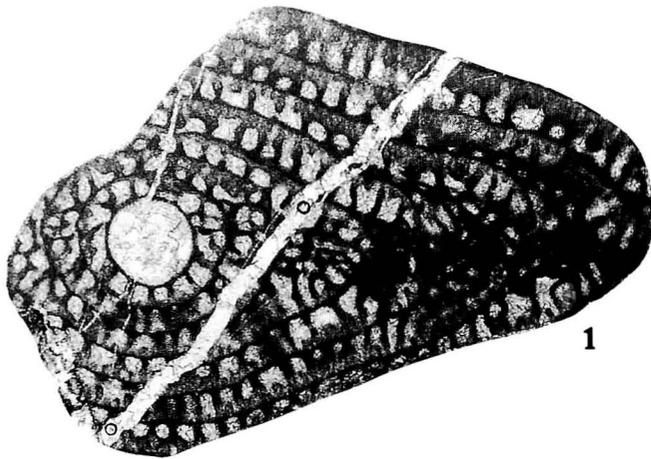
Acknowledgments

The authors are deeply indebted to Yoshiaki Kimata of the Gifu-ken Sekkai Kōgyō Kyodō Kumiai, Ōgaki City, Japan, for his kind permission of trespassing on the limestone-quarry sites of the Akasaka area, and favorable arrangement for carrying out field survey. Special thanks are also due to Takashi Sato of the Kinsho-zan Sekkaiseki Kōzan who accompanied and kindly assisted the first author in the field. The authors would like to extend their sincere thanks to Dr. Yoshihiro Mizuno, Department of Earth Sciences, Faculty of Science, Chiba University, for his kind help in various ways and constructive comments. The first author wishes to express his sincere thanks to Professor Toshiyuki Yamaguchi, Department of Earth Sciences, Faculty of Science, Chiba University, for giving constructive comments, and also to the Ministry of Education, Science and Culture of Japan for providing a scholarship grant.

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Figure 2. *Yabeina* (*Lepidolina*) *multiseptata* (Deprat) and associated neoschwagerinids. 1-4. *Y. (L.) multiseptata*, all figures are $\times 30$ except 4 which is $\times 40$, slide nos. 3-1C-26, 3-1C-2, 3-1C-1 and 3-1C-25. 5. *Yabeina igoi* Morikawa and Suzuki, slide no. 3-1C-8, $\times 15$. 6. *Y. aff. globosa*, slide no. 3-1C-3, $\times 20$.



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日本古生物学会 第 145 回例会

個人講演

日本古生物学会第 145 回例会が、6 月 29 日～30 日に新潟大学で開催された（参加者 147 名）。

シンポジウム

「東アジアの中・古生代生物地理とテクトニクス」

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夜間小集会

第8回化石クニダリア・海綿国際会議組織委員会

.....世話人：森 啓

Palaeontological Society of Japan (PSJ) Standing Committee Actions

During its meetings on April 20, and June 15, 1966, the PSJ Standing Committee enacted the following changes to its membership, according to the new rule.

New members elected (April 20, 1966) ;

Yasuko Fukuda,	Hiroki Hayashi,	Kayuri Nagaoka,
Tsutomu Sato,	Eriko Satou,	Takehisa Tsubamoto,
Mahito Watanabe,	Titima Charoentitirat.	

New members elected (June 15, 1966) ;

Takaomi Hamada,	Kazuyoshi Moriya,	Ryosuke Nakamura,
Kazuyuki Nozu,	Chinatsu Sanada,	Chiharu Shimizu,
Tetsuya Tanaka,	Takumi Tsujino,	Mikiko Ukita,
Shigetaka Yamaguchi,	Kensuke Yasui,	David Chesanow,
Paul G. Davis,	Gurung Damayanti.	

New Patron member (June 15, 1966) ;

Kanagawa Prefectural Museum of Natural History.

Resigned members (April 20, 1966) ;

Tomio Arakawa,	Eiichi Uchida,	Ryuichi Uchimura.
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Resigned members (June 15, 1966) ;

Hitoshi Nakagawa,	Yoshito Nakashima,	Yoshihisa Nohmi,
Hiroko Suzuki.		

Change to overseas member ;

Tamaki Sato.

行事予定

◎1997年年会は、1997年1月30日～2月1日に、京都大学理学部で開催の予定です。講演申し込みは12月5日(必着)締め切りです。なお4月刊行の181号において、この講演申し込み締切日が10月5日となっておりますが、12月5日が正しい日付です。おわびして訂正致します。

◎1997年例会は、1997年6月に、豊橋市自然史博物館で開催の予定です。

◎日本地質学会第104年学術大会(於 福岡; 1997年10月10日-12日)は、日本古生物学会ほかの参加した連合学術大会となります。日本古生物学会は会期中にシンポジウムを実施いたします。シンポジウム企画案は1997年3月までにお申し込み下さい。

◎1998年年会・総会及び同年の第147回例会の開催地を募集しております。

申込先(予稿集原稿・シンポジウム企画案送付先): 〒169-50 東京都新宿区西早稲田1-6-1
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本誌の発行に要する費用は、会員の会費以外に、文部省科学研究費補助金ならびに賛助会員からの会費が当てられています。現在の賛助会員は下記の通りです。

インドネシア石油株式会社
北九州市立自然史博物館
ダイヤコンサルタント
三井石油開発株式会社

関東天然ガス株式会社
ジャパンエナジー石油開発株式会社
帝国石油株式会社
ミュージアムパーク茨城県自然博物館

奇石博物館
石油資源開発株式会社
兵庫県立人と自然の博物館
(アイウエオ順)

○文部省科学研究費補助金(研究成果公開促進費)による。

1996年9月25日 印刷
1996年9月30日 発行

ISSN 0031-0204
日本古生物学会報告・紀事
新篇 183号

2,500円

発行者 日本古生物学会
〒113 東京都文京区本駒込5-16-9
日本学会事務センター内
電話 03-5814-5801
編集者 森 啓・石崎国熙
編集幹事 島本昌憲
印刷者 〒984 仙台市若林区六丁の目西町8-45
笹氣出版印刷株式会社 笹氣 幸緒
本社 022-288-5555 東京 03-3455-4415

Transactions and Proceedings of the Palaeontological Society of Japan

New Series No. 183

September 30, 1996

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