

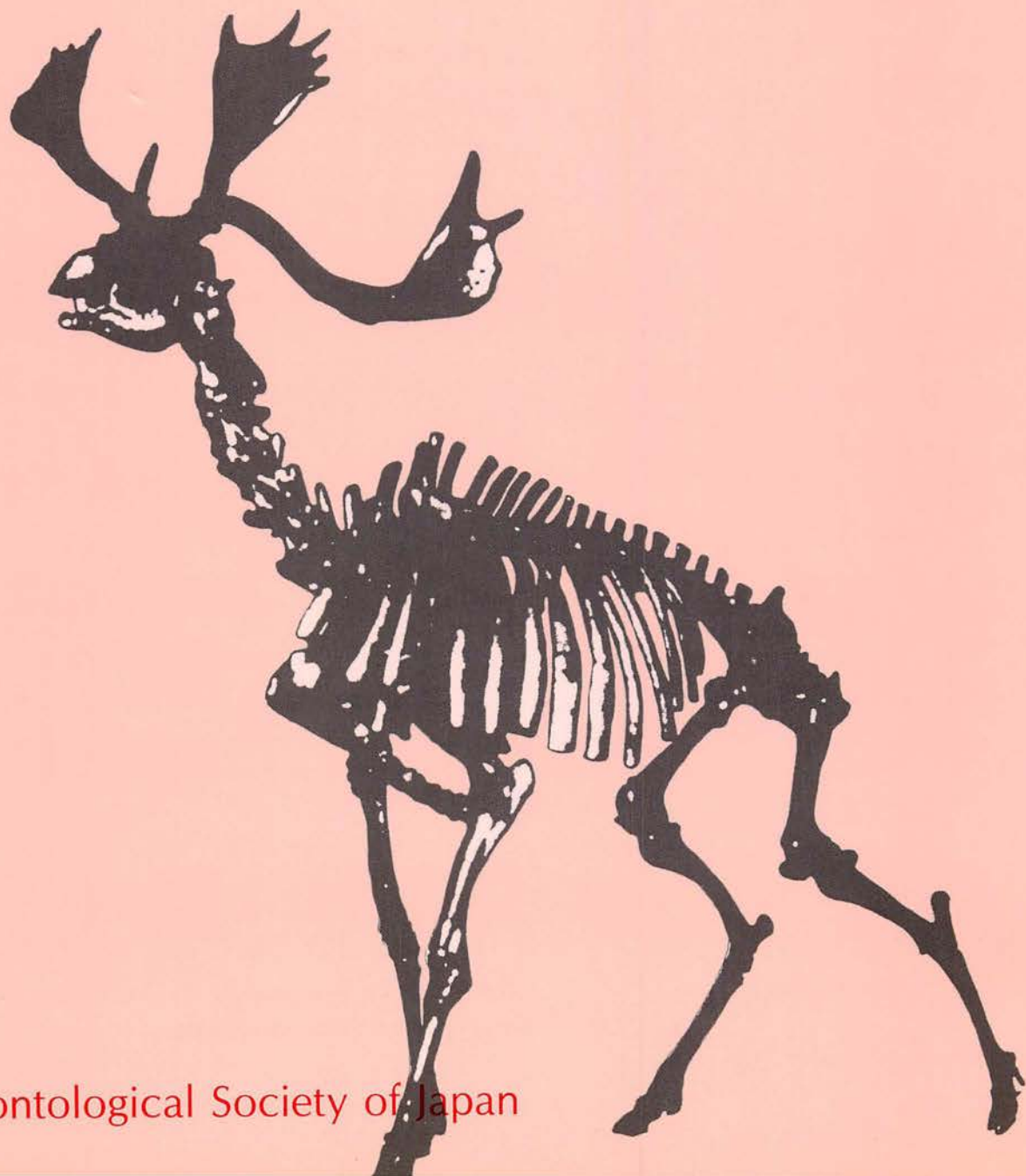
Paleontological Research

Palaeontological
Society of Japan



日本古生物学会

Vol. 6 No. 2 June 2002



The Palaeontological Society of Japan

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Cover: Typical Pleistocene fossils from the Japanese Islands. Front cover: *Sinomegaceros yabei* (Shikama). Back cover: *Paliurus nipponicum* Miki, *Mizuhopecten tokyoensis* (Tokunaga), *Neodenticula seminae* (Simonsen and Kanaya) Akiba and Yanagisawa and *Emiliania huxleyi* (Lohmann) Hay and Mohler.

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Molluscan fauna of the “Miocene” Maéjima Formation in Maéjima Island, Okayama Prefecture, southwest Japan

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Received August 2, 2001; Revised manuscript accepted January 15, 2002

Abstract. Molluscan fauna of the “Miocene” Maéjima Formation is examined from taxonomical, biostratigraphical and paleozoogeographical points of view. It is composed of four gastropods and 14 bivalves including a new species. Two assemblages, the *Isognomon* and the *Megangulus-Acila* assemblage, were discriminated. The *Isognomon* assemblage is autochthonous or para-autochthonous and is composed of elements inhabited the littoral to upper sublittoral gravelly to rocky bottom in a warm sea. The *Megangulus-Acila* assemblage represents a mixed composition between muddy sand and gravelly to rocky bottom elements, and was formed in an upper sublittoral muddy bottom near a rocky shore. Occurrences of *Megangulus maximus* (Nagao), *Isognomon (Hippochaeta) hataii* Noda and Furuichi and *Chlamys (Leochlamys) namigataensis* (Ozaki) indicate the age of the Maéjima Formation as the Paleogene, not the Miocene. The molluscan fauna of the Paleogene Maéjima Formation contains both Tethyan Indo-Pacific elements and Northern Pacific elements. Taxonomy of selected molluscan taxa including a new arcid, *Arca (Arca) uedai* sp. nov., is described or discussed.

Key words: *Arca (Arca) uedai* sp. nov., First Setouchi Series, Maéjima Formation, molluscan fauna, Paleogene

Introduction

The First Setouchi (or Setouti) Series (Kasama and Huzita, 1957) is the generic name for the Miocene strata scattered in the median zone of southwestern Japan (or the Setouchi Geologic Province; Ikebe, 1957), and all of its constituent formations had been regarded as uppermost lower to lower middle Miocene mainly on the basis of the lithology, sedimentary cycle and molluscs (e.g. Huzita, 1962; Itoigawa and Shibata, 1973, 1986, 1992; Ishida, 1979). It has been known that the “Miocene” molluscan assemblages in the coastal area of the eastern Seto Inland Sea (= Setouchi-Éngan Belt; Yano *et al.*, 1995a) are different from those in the neighboring backbone area (= Bihoku Belt; Yano *et al.*, 1995a), both in the western Setouchi Geologic Province (e.g. Huzita, 1962; Itoigawa, 1969, 1971, 1983; Ueda, 1991; Yano *et al.*, 1995a). There are two current interpretations explaining this difference; some paleontologists have postulated the existences of different water masses in the two areas in the late early to early middle Miocene (e.g. Itoigawa, 1983), while others have assumed a paleogeographic barrier between the two areas in the late early to early middle Miocene except during times of maximum transgression (e.g. Ueda, 1991; Takayasu

et al., 1992; Yano *et al.*, 1995a).

On the other hand, it is becoming clear that constituent formations of the First Setouchi Series around the eastern part of the Seto Inland Sea are of Eocene to Oligocene, not Miocene age, as a result of studies during the last fifteen years (Matsuo, 1987; Ozaki and Matsuura, 1988; Suzuki *et al.*, 1995; Ozaki *et al.*, 1996; Yamamoto *et al.*, 2000b; Kurita *et al.*, 2000, 2001). Yamamoto *et al.* (2000b) found latest middle to late Eocene calcareous nannofossils and dinoflagellate cysts from the “Miocene” Iwaya Formation of the Kobe Group in Awajishima Island, and considered that the difference between the “Miocene” molluscan assemblages in the coastal area of the eastern Seto Inland Sea and those from the backbone area in the western Setouchi Geologic Province is due to chronologic difference. However, their opinion conflicts with the previous molluscan data because the Miocene species have often been listed from the First Setouchi Series in the eastern part of the Seto Inland Sea (Huzita, 1962; Saito, 1962; Saito *et al.*, 1970; Bando and Furuichi, 1978; Itoigawa, 1983; Huzita and Maeda, 1984; Mizuno *et al.*, 1990; Okumura and Sato, 1999). However, most of these studies are unaccompanied by either figures or descriptions of molluscan taxa. Thus, it is necessary to reinvestigate the molluscan

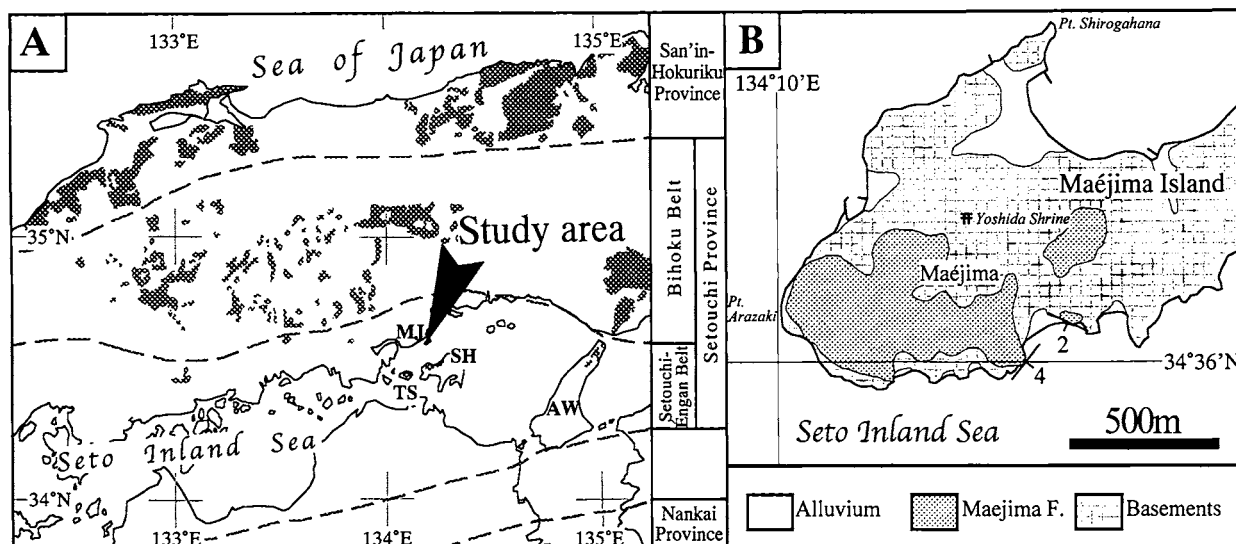


Figure 1. Location and geologic maps of the study area. **A.** Location of study area (arrow) and distribution of the “Miocene” sediments (hatched area; modified from Shibata and Itoigawa, 1980). The geologic province division follows Yano *et al.* (1995a) partly modified after Seto *et al.* (2000). AW: Awajishima Island, MJ: Maéjima Island, SH: Shodoshima Island, TS: Teshima Island. **B.** Geologic map of the western part of Maéjima Island, Okayama Prefecture.

fauna of the area, especially from the taxonomical point of view.

The Maéjima Formation is the Tertiary in the western part of Maéjima Island, Ushimado Town, Oku County, southeastern Okayama Prefecture (Figure 1A, B), and has been regarded as one of the constituents of the Miocene First Setouchi Series (e.g. Itoigawa, 1969, 1983; Itoigawa and Shibata, 1986). The distribution of the Tertiary in this island was for the first time reported by Sato (1938), and the stratigraphy was established recently by Yamamoto (2001). Although molluscan assemblages resembling those from other “Miocene” formations in the coastal areas in the eastern part of the Seto Inland Sea have been reported by Itoigawa (1969, 1971, 1983) and Yamamoto (2001) provisionally, precise constituents and faunal characteristics still remain unclear. In this paper, I taxonomically review the molluscan fauna of the “Miocene” Maéjima Formation and discuss the geologic age and its paleogeographical and paleozoogeographical implications.

Geological setting

The Maéjima Formation (Itoigawa and Shibata, 1986, as Maeshima Formation; revised by Yamamoto, 2001) is distributed in the southwestern part of Maéjima Island, unconformably overlying the pre-Tertiary plutonic rocks (Figures 1B, 2). Although Yamamoto (2001) subdivided the Maéjima Formation into the Lower Conglomerate and Sandstone and the Upper Sandstone Member, they are

treated herein as the lower and the upper part with a revision of the boundary (Figure 2A).

The lower part of the Maéjima Formation is less than 10 m in thickness and is composed mainly of granule to pebble conglomerate with numerous fragments of balanids, brachiopods, calcareous algae and molluscs. This part is well exposed on the southwestern coast of Maéjima Island, which is designated to be the type locality of the formation.

The upper part (30 m+) consists mainly of siltstone to muddy very fine-grained sandstone and is associated with calcareous medium- to coarse-grained sandstone. The upper part abuts on the basement and is conformably underlain by the lower part. Outcrop of the upper part is little exposed because it is distributed only in the hilly area with a low relief.

The age of the Maéjima Formation is not known precisely, which indicates an age of Yamamoto *et al.* (2000a) preliminarily reported a Sr isotope value of about 0.7077, which indicates an age of late Eocene or older.

Material

Molluscan samples were collected from eight localities; five from the lower part and three from the upper part (Figure 2A, B). The preservation of fossil molluscs is quite poor and shell material of most specimens examined was dissolved away except for pectinids and an ostreid. Thus, hydrophilic vinyl polysiloxane impression materials (PROVIL novo, Putty®, regular set, Heraeus Kulzer, Inc.,

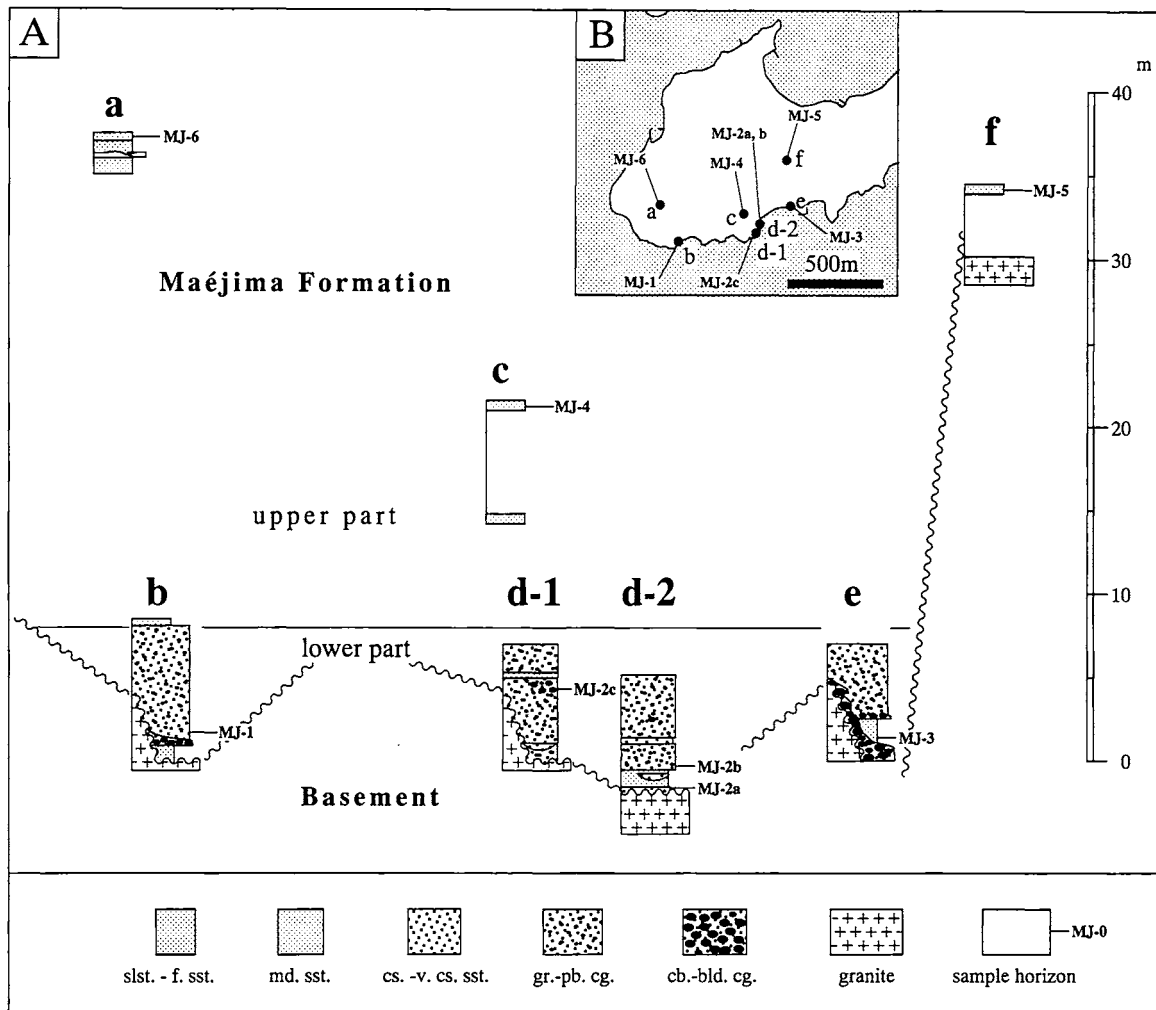


Figure 2. Columnar sections of the Maėjima Formation and locations of measured points and fossil localities. **A.** Columnar sections of the Maėjima Formation. Abbreviations. slst.: siltstone; sst.: sandstone (f.: fine-grained; m.: medium-grained; cs.: coarse-grained; v.cs.: very coarse-grained); cg.: conglomerate (gr.: granule; pb.: pebble; cb.: cobble; bld.: boulder). **B.** Map showing the points where the geologic columns (a through f) were made and fossil localities. Mapped area same as Figure 1B.

Ltd. and EXAFINE® Putty Type, GC Co., Ltd.) were used for the examination of molds.

Molluscan fauna

Four species of Gastropoda and 14 species of Bivalvia including a new species were discriminated as a result of the examination (Table 1). On the basis of the dominant and associated species, the following two assemblages are discriminated (Figure 3).

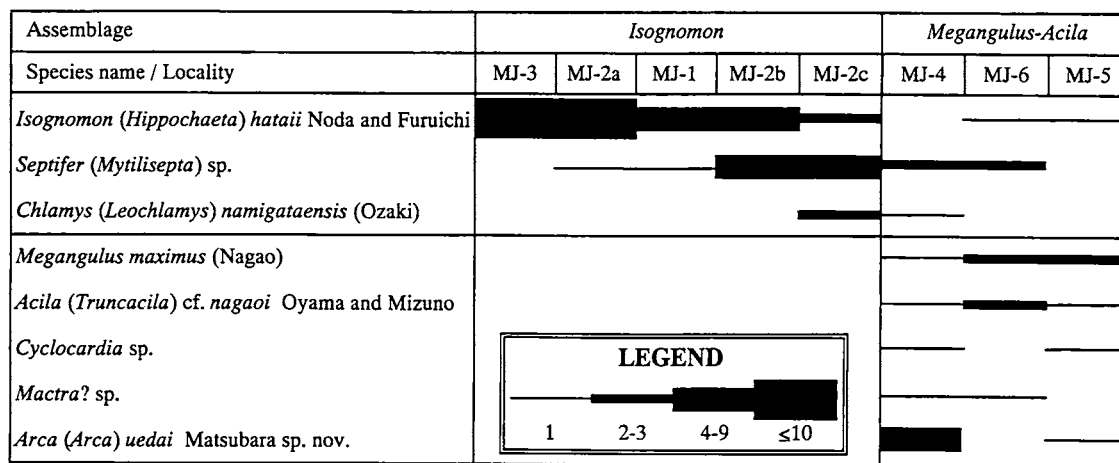
A. *Isognomon* assemblage

This assemblage is characterized by an abundant occurrence of *Isognomon* (*Hippochaeta*) *hataii* Noda and Furuichi, and is generally associated with a few specimens

of *Septifer* (*Mytilisepta*) sp. The *Isognomon* assemblage occurred from conglomerate to conglomeratic sandstone in the lower part of the Maėjima Formation (Locs. MJ-1, 2a, 2b, 2c and 3). At Loc. 3, *I. (H.) hataii* occurs abundantly in the matrix of boulder conglomerate without any associated species, and most of the specimens are articulated. At other localities, although most specimens of this species are disarticulated, they are less broken and a few articulated valves are included. Consequently, this assemblage is regarded to be autochthonous or para-autochthonous in broad sense. Taking the lithology of rocks in which the assemblage occurs and the habitat of the Recent homologues of these two species into account (Higo *et al.*, 1999), this assemblage inhabited littoral to upper sublittoral, gravelly to rocky bottom of an open sea.

Table 1. List of fossil Mollusca from the "Miocene" Maéjima Formation.

Horizon	Lower part					Upper part			
	Species name/Locality	MJ-1	MJ-2a	MJ-2b	MJ-2c	MJ-3	MJ-4	MJ-5	MJ-6
Gastropoda									
Patellogastropoda, fam., gen. et sp. indet.									1
<i>Calyptraea</i> sp.							2		1
Naticidae? gen. et sp. indet.									1
Muricidae? gen. et sp. indet.							1		
Bivalvia									
<i>Acila (Truncacila)</i> cf. <i>nagaoi</i> Oyama and Mizuno							1	1	2
<i>Arca (Arca)</i> <i>uedai</i> sp. nov.							6	1	
<i>Glycymeris (glycymeris)</i> sp.									1
<i>Septifer (Mytilisepta)</i> sp.	1	1	3	4		2			2
<i>Isognomon (Hippochaeta)</i> <i>hataii</i> Noda and Furuichi	6	12	4	2	26			1	1
<i>Delectopecten</i> sp.									1
<i>Chlamys (Leochlamys)</i> <i>namigataensis</i> (Ozaki)				2			1		
<i>Crassastrea</i> sp.			1						
Luchinidae gen. et sp. indet.							1		1
<i>Cyclocardin</i> sp.							1	1	
<i>Glans</i> sp.									2
<i>Megangulus maximus</i> (Nagano)							1	3	3
<i>Mactra?</i> sp.							1		3
<i>Tapes?</i> sp.									2
TOTAL	7	13	8	8	26		17	7	21

**Figure 3.** Molluscan assemblages of the Maéjima Formation. Number in legend indicates that of individuals.

The *Ostrea-Balanus* assemblage of Itoigawa (1969) probably corresponds to the *Isognomon* assemblage. But only a single specimen of *Crassostrea* sp. was collected from Loc. MJ-2c among all the localities examined in the present study. Consequently, the occurrence of the *Ostrea-Balanus* Assemblage from the Maéjima Formation is not supported.

B. *Megangulus-Acila* assemblage

The *Megangulus-Acila* assemblage occurred from siltstone to medium-grained sandstone in the upper part of

the Maéjima Formation (Locs. MJ-4, 5 and 6). This assemblage is characterized by infaunal Bivalvia species, *Megangulus maximus* (Nagao) and *Acila (Truncacila)* cf. *nagaoi* Oyama and Mizuno. Most shells of these species are disarticulated and are arranging parallel to the bedding plane. However, a few articulated specimens of *M. maximus*, *A. (T.)* cf. *nagaoi*, *Cyclocardia* sp. and *Mactra?* sp. are recognized. This fact indicates that most shells of these species have not been transported a great distance from their original habitat. These species are regarded as shallow burrowers in an upper sublittoral, muddy to sandy

bottom (Higo *et al.*, 1999). On the other hand, *Arca* (*Arca*) *uedai* sp. nov., *Septifer* (*Mytilisepta*) sp. and *Isognomon* (*Hippochaeta*) *hataii* are considered to be epibyssate benthos on a gravelly to rocky bottom. There are no articulated specimens among these species, and thus they are considered to have been transported from their original habitat. These facts suggest that this assemblage represents a mixed composition formed in an upper sublittoral, muddy to muddy sand bottom neighboring a rocky shore in an open sea.

The occurrences of muddy to sandy bottom elements such as *Acila* (*Truncacila*), *Mactra*? and *Cyclocardia* indicate that this assemblage is compared with the *Mactra-Acila* assemblage of Itoigawa (1983) characterizing the molluscan assemblages in the coastal area of the eastern Seto Inland Sea.

Discussion

Geologic age

Among the constituents of the molluscan fauna of the Maéjima Formation, *Megangulus maximus* (Nagao), *Isognomon* (*Hippochaeta*) *hataii* Noda and Furuichi, and *Chlamys* (*Leochlamys*) *namigataensis* (Ozaki) are important for the age estimation (Figure 4). The first species has been recorded from the Paleogene of Kyushu and the other two species are known from the "Miocene" of southwest Honshu around the eastern part of the Seto Inland Sea.

M. maximus occurs from the Funazuan to the Nishisonogian Stages (Mizuno, 1962) of southwest Japan (e.g. Nagao, 1928b; Oyama *et al.*, 1960; Mizuno, 1964; Okamoto and Imamura, 1964; Okamoto, 1970; Shuto and Shiraishi, 1971; Kamada, 1980; Fuse and Kotaka, 1986; Shuto, 1991). Although the precise age of the stratotype of the Funazuan Stage, the Funazu Sandstone Member of the Iojima Formation in the Takashima Coalfield, west Kyushu, is unknown, a calcareous nannofossil biostratigraphy of the correlate Matsushima Group in the Sakito-Matsushima Coalfield (SK-MT in Figure 4) was studied by Okada (1992). Okada (1992) assigned this group to the Subzone CP 15b to CP 16a of Okada and Bukry (1980). In addition, Okada (1992) also correlated the Oniike Formation of the Sakasegawa Group in the Amakusa Coalfield (AM in Figure 4) and the Yotsuyama Formation of the Manda Group in the Miike Coalfield (MK in Figure 4), both of which are referred to the Okinoshiman Stage below the Funazuan Stage (Mizuno, 1964), to CP 14b to CP 15b. These calcareous nannofossil biostratigraphic data suggest that the lower limit of the Funazuan Stage is in CP 15b. According to Berggren *et al.* (1995), this calcareous nannofossil zone ranges from 36.0 to 34.3 Ma or the late Eocene. Okada (1992) also studied the age of the Nishisonogi Group in the Sakito-Matsushima Coalfield

(SK-MT in Figure 4), the stratotype of the Nishisonogian Stage by means of calcareous nannofossil biostratigraphy, and assigned the age of the upper part of the Nishisonogi Group to sometime during CP 17 to CP 19 on the basis of the occurrence of *Dictyococcites bisectus*. According to Berggren *et al.* (1995), the last occurrence of this species (cited as *Reticulofenestra bisecta* in Berggren *et al.*, 1995) is 23.9 Ma or the latest Oligocene. Concerning the Ashiya Group in the Chikuhō Coalfield (CH in Figure 4), one of the correlatives of the Nishisonogian Stage, biostratigraphic studies were carried out by Saito and Okada (1984), Tsuchi *et al.* (1987), Okada (1992) and Ibaraki (1994). According to them, the age of the Ashiya Group is the late early to early late Oligocene. Further, the Taoyama Formation of the Hioki Group in the Yuyawan area (YY in Figure 4), another correlative of the Nishisonogian Stage, contains *D. bisectus* (Fuse and Kotaka, 1986). Ozaki (1999) also reported fission-track ages of 25.2 ± 1.7 Ma and 23.1 ± 1.6 Ma (error: 1σ) from the Hitomaru Formation which overlies the Taoyama Formation in the Yuyawan area. Taking these data into account, the range of *M. maximus* is regarded as late Eocene to Oligocene (Figure 4).

I. (H.) hataii is a species originally described from the "Miocene" Teshima Formation of the Tonosho Group in Teshima Island, northern Kagawa Prefecture (SH-TS in Figure 4; Noda and Furuichi, 1972). Bando and Furuichi (1978) correlated this formation to the Shikai Formation of the Tonosho Group in Shodoshima Island, situated several kilometers east of Teshima Island. This correlation is strongly supported by the occurrence of an endemic bivalve, *Tapes nagahamaensis* Saito, Bando and Noda, 1970, recorded only from the Teshima and Shikai Formations. Saito *et al.* (1970), Noda and Furuichi (1972), Bando and Furuichi (1978), Itoigawa and Shibata (1992) and Okumura and Sato (1999) all regarded the Tonosho Group distributed in Shodoshima and Teshima Islands as of early middle Miocene age. However, Kurita *et al.* (2000) reported the Eocene dinoflagellate cysts from the Shikai Formation. Consequently, the age of the Teshima Formation, which contains *I. (H.) hataii*, is also considered to be Eocene (Figure 4).

C. (L.) namigataensis was originally described from the "Miocene" Namigata Formation in Ibara City, Okayama Prefecture (NM in Figure 4; Ozaki, 1956). The age of the Namigata Formation has been considered to be the lowest middle Miocene (e.g. Shibata and Itoigawa, 1980; Itoigawa, 1983; Yano *et al.*, 1995a, b). Yano *et al.* (1995b) discriminated four benthic foraminiferal assemblages characterized by such species as *Elphidiella momiyamaensis* Uchio, *Pseudonion japonicum* Asano, *Hanzawaia tagaensis* Asano and *Cibicidoides pseudoungerianus* (Cushman) from the Namigata Formation. They pointed out that these assemblages are comparable with

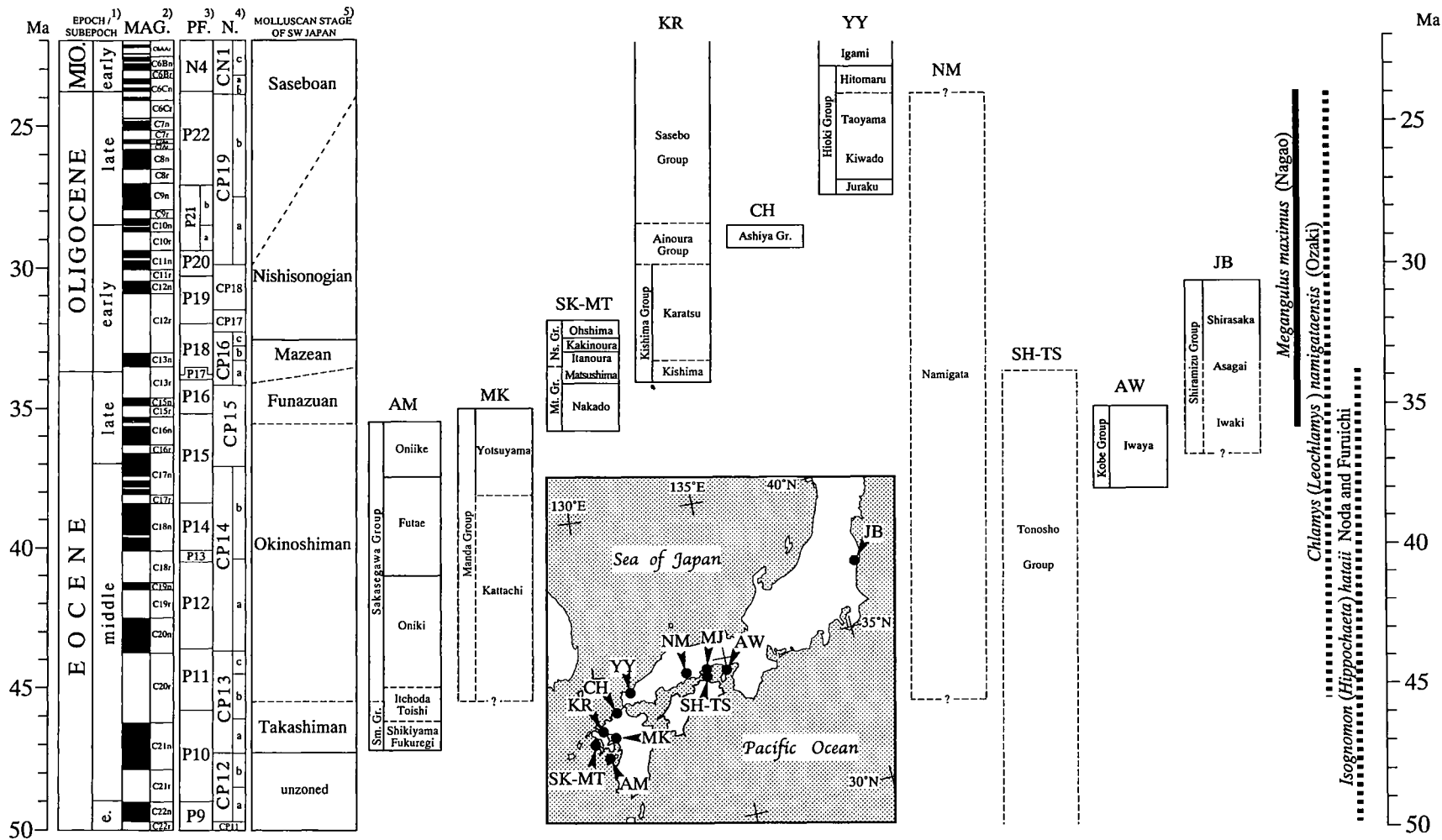


Figure 4. Correlation of the selected Paleogene strata in Japan and chronologic range of molluscan species discussed in the text. Time scale: 1) Berggren *et al.* (1995); 2) Cande and Kent (1995) and Berggren *et al.* (1995); 3) Blow (1969); 4) Okada and Bukry (1980); 5) Mizuno (1962, 1964). e.: early; MAG.: Magnetic polarity; MIO.: Miocene; N.: Calcareous nannofossils; PL.: Planktonic foraminifera. AM: Amakusa Coalfield (Okada, 1992); AW : Awajishima area (Yamamoto *et al.*, 2000b); CH: Chikuho Coalfield (Saito and Okada, 1984; Tsuchi *et al.*, 1987; Okada, 1992; Ibaraki, 1994); JB: Joban Coalfield (Tomida, 1986; Yanagisawa and Suzuki, 1987); KR: Karatsu Coalfield (Sakai *et al.*, 1990; Miyachi and Sakai, 1991; Okada, 1992; Ibaraki, 1994); MK: Miike Coalfield (Okada, 1992); NM : Namigata area (Nishimoto and Itoigawa, 1977; SH-TS: Shidoshima-Teshima area (Kurita *et al.*, 2000); SK-MT: Sakito-Matsushima Coalfield (Okada, 1992); YY: Yuyawan area (Fuse and Kotaka, 1986; Ozaki, 1999). Mt.Gr.: Matsushima Group; Ns.Gr.: Nishisonogi Group; Sm.Gr.: Shimoshima Group.

those of the *Miogypsina kotoi-Operculina complanata* Assemblage Zone of Nomura (1992), being assigned to the latest early to early Middle Miocene. However, *E. momiyamaensis*, *H. tagaensis* and *C. pseudoungerianus* were also reported from the Iwaya Formation of the Kobe Group by Tai (1959), from which Yamamoto *et al.* (2000b) reported Eocene calcareous nannofossils and dinoflagellate cysts. In addition, the benthic foraminiferal assemblages from the Namigata Formation do not include *Ammonia tochiensis* (Uchio) which is one of the representative species in the Miocene benthic foraminiferal zone (Yano *et al.*, 1995b). Consequently, the benthic foraminiferal data do not indicate a Miocene age for the Namigata Formation.

On the other hand, Nishimoto and Itoigawa (1977) preliminarily reported *Carcharodon angustidens* (Agassiz) from the Namigata Formation in addition to the upper lower Oligocene Yamaga Formation of the Ashiya Group and the upper Oligocene Taoyama Formation of the Hioki Group. This fossil shark has very characteristic teeth with distinct anterior and posterior cusps. Yabumoto and Uyeno (1994) indicated that in Japan *C. angustidens* has been restrictedly found from the middle Eocene to the upper Oligocene of southwest Japan. Consequently, the age of the Namigata Formation is regarded to be somewhere during the middle Eocene to the late Oligocene, not the Miocene (Figure 4).

Although *C. (L.) namigataensis* was also recorded from the middle Miocene Kawazu Formation in Shimane Prefecture by Masuda (1962), his figured specimen (Masuda, 1962, pl. 21, fig. 1) is not referred to *Pecten (Chlamys) namigataensis* Ozaki, 1956 (see systematic paleontology to be discussed below). Recently, *C. (L.) namigataensis* was for the first time found from the Paleogene Iwaki Formation of the Shiramizu Group in the Joban Coalfield (JB in Figure 4), northeast Honshu, Japan. Nemoto and O'Hara (2001) figured a right valve of *Chlamys ashियाensis* (Nagao) from this formation, but their figured specimen is, in my opinion, *C. (L.) namigataensis* (see systematic paleontology). The age of the Iwaki Formation of the Shiramizu Group is considered to be the late Eocene or the early Oligocene on the basis of the occurrence of *Entelodon cf. orientalis* Dashzeveg (Tomida, 1986) and the planktonic microfossils age of the Shirasaka Formation (early Oligocene; Yanagisawa and Suzuki, 1987), the uppermost constituents of the Shiramizu Group.

Taking these facts into account, the geologic age of the Maéjima Formation is judged to be Paleogene, somewhere between the middle Eocene and late Oligocene.

Implications of the molluscan fauna of Maéjima Formation

Itoigawa (1983) grouped the "Miocene" molluscan as-

semblages from the First Setouchi Series in the coastal area of the eastern part of the Seto Inland Sea, including the Maéjima Formation, into four types, the *Cyclina-Barbatia*, the "Ostrea", the *Mactra-Acila* and the *Cyclocardia-Nuculana* assemblages. Constituents of these assemblages were considered to have inhabit the intertidal to uppermost sublittoral sandy mudbottom, uppermost to upper sublittoral rocky bottom, upper sublittoral sandy bottom, and upper sublittoral muddy bottom, respectively (Itoigawa, 1983). An assemblage comparable in generic composition to the *Mactra-Acila* assemblage was also recognized in the Maéjima Formation, namely, the *Megangulus-Acila* assemblage. Recent studies on planktonic microfossils (Kurita *et al.*, 2000, 2001; Yamamoto *et al.*, 2000b) indicate that some of the formations yielding these assemblages are of Eocene age, which concords with the results of the present study for age assignment.

It has been known that the four assemblages of Itoigawa (1983) have little similarity in not only specific but also generic compositions to the Miocene molluscan assemblages from the neighboring backbone area (e.g. Huzita, 1962; Itoigawa, 1969, 1971, 1983; Ueda, 1991; Yano *et al.*, 1995a). The latter assemblages are represented by the embaymental arcid-potamid [potamidid] fauna of Tsuda (1965). Yamamoto *et al.* (2000b) preliminarily considered that the difference between the assemblages from the coastal area of the Seto Inland Sea and those from the backbone area is chronological taking account of the Eocene planktonic microfossils from the Iwaya Formation of the Kobe Group, while previous researchers explained it by paleoenvironmental or paleogeographic factors in Miocene time (e.g. Itoigawa, 1983; Ueda, 1991; Takayasu *et al.*, 1992; Yano *et al.*, 1995a). The result of the present study supports the view of Yamamoto *et al.* (2000b), and both indicate that the Miocene First Seto Inland Sea (Ikebe, 1957) was not invaded in the coastal area of today's eastern part of the Seto Inland Sea, and that the "Miocene" shallow marine area in the eastern part of the Seto Inland Sea in the judgment of previous researchers (e.g. Shibata and Itoigawa, 1980; Itoigawa and Shibata, 1992; Takayasu *et al.*, 1992) was in fact of Paleogene age. Consequently, it is necessary to revise the Tertiary paleogeography of southwest Japan on the basis of the precise geochronologic data in near future.

It is notable that the molluscan fauna of the Paleogene Maéjima Formation contains both Tethyan Indo-Pacific elements and Northern Pacific elements of Honda (1991, 1994). The former are represented by such genera as *Isognomon* and *Septifer*, and the latter by, for example, *Cyclocardia* and *Megangulus* (Honda, 1994; Ogasawara, 1996). Honda (1994) revealed the northward migration of the Tethyan Indo-Pacific elements in the middle Eocene and the southward migration of the Northern Pacific ele-

ments during the late early Oligocene to early Miocene. However, the precise timing and mode of migration of the molluscan fauna have not fully been clarified because Paleogene shallow marine sediments were accepted to be almost lacking in the area between Kyushu and the Pacific coast of northeast Honshu. Although the precise geologic age of the Maéjima Formation was not determined by the molluscan evidence in the present study, further geochronological studies of the Paleogene shallow marine sediments in the coastal area of the eastern part of the Seto Inland Sea and taxonomical studies of the molluscan fauna will provide a reliable basis for elucidation of the successive changes of the Paleogene molluscan fauna in the Northwest Pacific region.

Concluding remarks

Until the middle of 1990s, Paleogene marine sediments in southwest Japan had been considered to be restricted mostly to the Southern Shimanto Belt (Taira *et al.*, 1980) in the back arc of the Japanese Islands, except for Kyushu. Honda (1991, 1994) discriminated the North Japan-Western Okhotsk, Central Japan and Taiwan-South Japan Provinces from north to south for the western Pacific Paleogene molluscan faunal provinces. The Central Japan Province, in particular, was proposed on the basis of fragmental molluscan records from the accretionary sediments deposited in the lower sublittoral zone or at greater depths. Consequently, the characteristics of the shallow marine molluscan faunas in this province have been less than clear. The result of the present study strongly supports the age estimation based on planktonic microfossils by Kurita *et al.* (2000, 2001) and Yamamoto *et al.* (2000b) that the constituent formations of the "Miocene" First Setouchi Series in the coastal area of the eastern part of the Seto Inland Sea are in fact Paleogene, not Miocene (Kurita *et al.*, 2000, 2001; Yamamoto *et al.*, 2000b).

Systematic description of selected taxa

All the illustrated specimens are housed at the Museum of Nature and Human Activities, Hyogo (MNHAH). The following institutional abbreviations are also used in this paper: IGPS: Institute of Geology and Paleontology, Tohoku University, Sendai; NSMT: National Science Museum, Tokyo; UMUT: University Museum, the University of Tokyo.

Class Bivalvia
Subclass Paleotaxodonta
Order Nuculoida
Superfamily Nuculoidea
Family Nuculidae

Genus *Acila* H. & A. Adams, 1858
Subgenus *Truncacila* Grant and Gale, 1931,
ex Schenck MS

Acila (Truncacila) sp. cf. *A. (T.) nagaoui*
Oyama and Mizuno, 1958

Figure 5.4

Compare.—

Acila nagaoui Mizuno (MS). Mizuno, 1956, pl. 2, fig. 1.
[*nomen nudum*]

Acila (Truncacila) nagaoui Oyama and Mizuno, 1958, p. 7–8.
pl. 1, figs. 14, 15.

Material.—MNHAH reg. no. D1-018895 (from MJ-5).

Discussion.—The specimens from the Maéjima Formation are comparable with *Acila (Truncacila) nagaoui* Oyama and Mizuno, 1958, in having a small, rather longer than high, posteriorly oblique, oval shell with a beak situated at four-fifths of the shell length from the anterior end and a weak posterior ridge. They are not sufficiently well preserved to allow a precise species assignment.

Subclass Pteriomorpha
Order Arcoidea
Superfamily Arcoidea
Family Arcidae
Subfamily Arcinae
Genus *Arca* Linnaeus, 1758
Subgenus *Arca* Linnaeus, 1758

Arca (Arca) uedai sp. nov.

Figure 5.5, 5.7a-c, 5.12

Type specimens.—MNHAH reg. nos. D1-018896 (Holotype); D1-018897 through D1-018903 (Paratypes).

Type locality.—Loc. MJ-4. A small outcrop exposure on its northern side about 400m south-southeast of Yoshida Shrine, Maéjima Island, Ushimado Town, Oku County, Okayama Prefecture (34° 36' 2" N, 134° 10' 29" E).

Diagnosis.—Rather small-sized *Arca (Arca)* with a low umbonal area, low crescent-shaped ligamental area, narrow hinge plate and shell surface sculptured by fine, low, numerous radial ribs.

Description.—Shell rather small (less than 40 mm in shell length), transversely elongate quadrate, inequilateral, moderately inflated; hinge line straight, long; beak blunt, prosocline, situated about two-fifths anteriorly of shell length; posterior ridge distinct, shell strongly depressed behind it; posteroventral margin obliquely truncated; central part of shell weakly depressed; shell surface sculptured by about 60 fine, low radial ribs; ribs generally with a fine intercalary rib on interspace; growth lines fine, generally

Table 2. Measurements of *Arca (Arca) uedai* sp. nov.

MNHANreg.no.	Length (mm)	Height (mm)
D1-018896*	34.2	18.8
D1-018897**	24.5***	12.3***
D1-018898**	35.0+***	15.2***
D1-018899**	30.9+	15.9

*holotype. **paratype. ***deformed

weak but rather strengthen on central depressed area; ligamental area low crescentic in shape, smooth except for one or a few, rather deep, chevron-shaped ligamental grooves; adductor muscle scars moderate in size, ovate (type A of Noda, 1966), weakly impressed; pallial line shallow, weakly impressed; inner ventral margin not crenated.

Etymology.—The present new species is named in honor of the late Tetsuro Ueda of Niigata University, who contributed to the molluscan paleontology of the First Setouchi Series during the middle 1980s to early 1990s.

Discussion.—*Arca (Arca) uedai* sp. nov. closely resembles *A. (A.) miurensis* Noda, 1966, from the Pleistocene Koshiba Formation in Kanagawa Prefecture. However, the present new species possesses a narrower hinge plate and lower ligamental area.

A. (A.) sakamizuensis Hatai and Nisiyama, 1952, from the Oligocene Sakamizu Formation of the Ashiya Group in Fukuoka Prefecture, Kyushu, is similar to the present new species in having fine radial ribs. The former is discriminated from the latter by having a more produced umbonal area and a higher ligamental area.

A. (A.) washingtoniana Dickerson, 1917, from the Oligocene Gries Ranch Formation of Washington, U.S.A., is another allied species, but is distinguished from *Arca (Arca) uedai* sp. nov. by having coarser radial ribs on the younger shell and stronger teeth.

The Recent *A. (A.) boucardi* Jousseume is easily distinguished by having a larger shell with a stronger posterior ridge, coarser, less numerous radial ribs, and a higher umbonal area.

Measurements.—Table 2.

Order Mytiloida
 Superfamily Mytiloidea
 Family Mytilidae
 Genus *Septifer* Récluz, 1848
 Subgenus *Mytilisepta* Habe, 1951

Septifer (Mytilisepta) sp. indet.

Figure 5.8, 5.9, 5.14

Material.—MNHAH reg. nos. D1-18905 through D1-018907 (from MJ-2b), D1-018908 and D1-018909 (from

MJ-2c), D1-018910 (from MJ-4), and D1-018911 (from MJ-6).

Discussion.—Several poor specimens have been obtained. The occurrence of a septum in the subumbonal region and inner ventral margin lacking fine crenations indicate this species is referred to the subgenus *Mytilisepta* Habe, 1951.

Septifer (Mytilisepta) sp. from the Maéjima Formation is similar in general shell shape to *Septifer (Septifer) nagaio* Oyama, 1951, which was introduced as a new name for *Mytilus hirsutus* Lamarck of Yokoyama, 1927 from the Oligocene Nishisonogi Group in Nagasaki Prefecture. However, the holotype designated by Oyama (1951) (UMUT reg. no. CM24987) has a very finely crenated inner ventral margin, as Mizuno (1952) described.

The present species is easily distinguished from the Recent species, *Septifer (Mytilisepta) keenae* Nomura, 1936 distributed in southern Hokkaido and southward, in having a larger shell with finer radial ribs and weakly curved anteroventral margin.

Order Pterioida
 Superfamily Pterioidea
 Family Isognomonidae
 Genus *Isognomon* [Lightfoot, 1786]
 Subgenus *Hippochaeta* Philippi, 1844

Isognomon (Hippochaeta) hataii
 Noda and Furuichi, 1972

Figures 5.15-5.17, 6.13, 6.14

Isognomon (Isognomon) hataii Noda and Furuichi, 1972, p. 120, text-fig. 1.

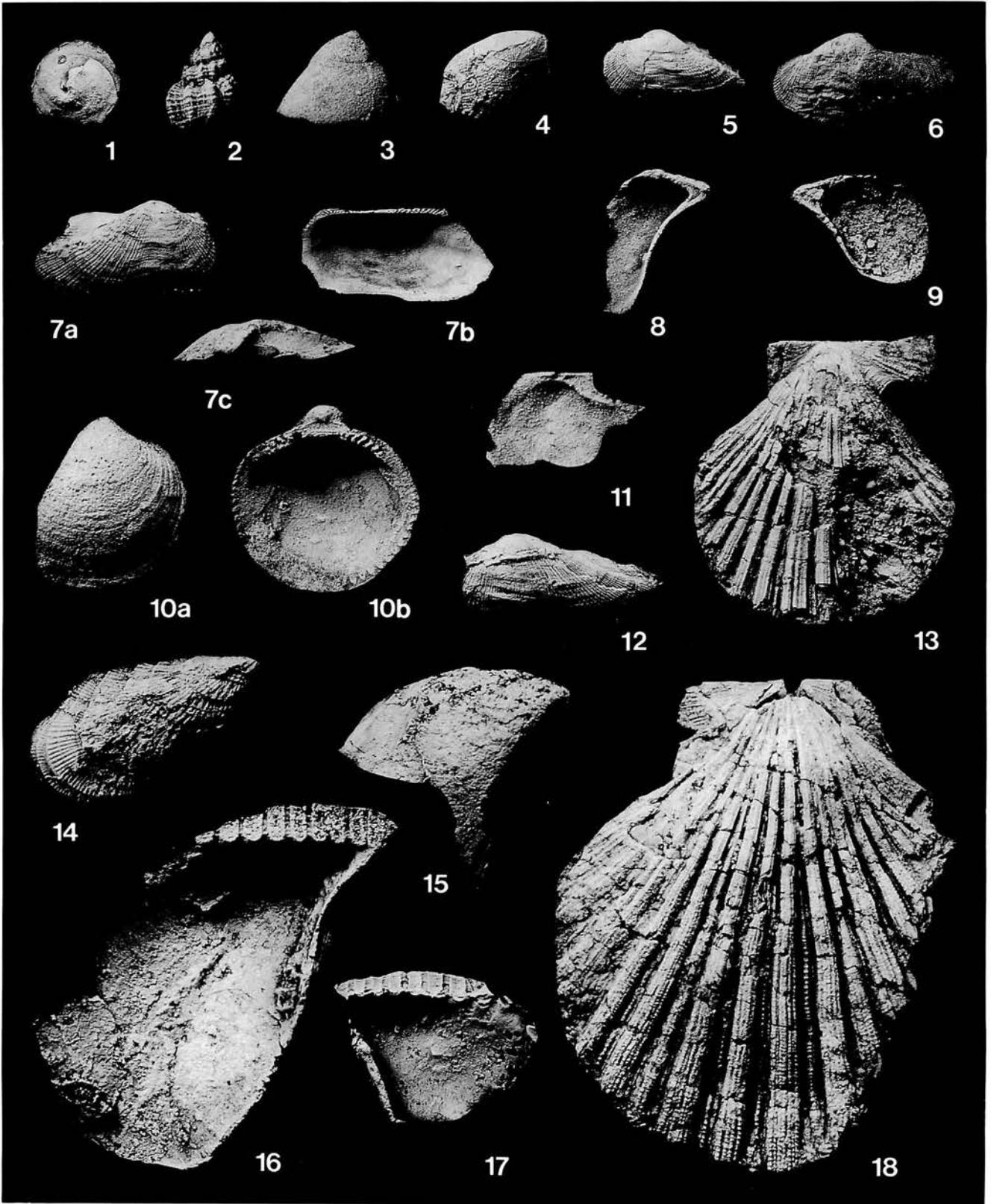
Isognomon (Isognomon) hataii Noda and Furuichi. Kaikiri and Nishimoto, 1995, p. 204.

Type specimen.—IGPS coll. cat. no. 91766 (Holotype).

Material.—MNHAH reg. nos. D1-018912 through D1-018918 (from MJ-1), D1-018919 through D1-018924 (from MJ-2a), D1-018925 through D1-018941 (from MJ-3), and D1-018942 (from MJ-6).

Emended diagnosis.—Shell of large size, mytiliform, rather thin except for ligamental area, moderately inflated; shell surface nearly smooth except for very fine, irregular, dense growth lines; byssal sinus roundly depressed; ligamental part rather thick; ligamental area rather broad, with 8 to 12 deeply concave resilifer grooves; lamellar ligament attachment area broader than groove, weakly depressed, surrounded by a fine ridge.

Description.—Shell rather large in size for the genus, mytiliform, rather thin except for ligamental area, moderately inflated; apical angle about 60°; byssal sinus rather depressed; posterodorsal margin nearly straight or weakly



curved; posteroventral margin nearly parallel to anterior one, weakly curved; centroventral margin arcuate and smoothly continuing to antero- and posteroventral margin; shell surface nearly smooth, sculptured only by very fine, irregular, dense growth lines; ligamental part thick; ligamental area rather broad, weakly annulated, with 8 to 12 resilifer grooves on fully grown individuals; resilifer grooves subequal, perpendicular to posterodorsal margin; lamellar ligament attachment areas weakly depressed, broader than resilifer grooves, surrounded by a fine ridge, with U-shaped inner margin; three byssal-pedal retractor muscle scars on subligamental part of internal shell; pallial line shallow, coarse, irregularly dotted near beak; adductor muscle scar indistinct.

Discussion.—The broad and shallow lamellar ligament attachment areas, narrow resilifer grooves and three byssal-pedal retractor muscle scars on the inner dorsal area indicate the Maéjima specimens are referred to the subgenus *Hippochaeta*. The ligamental area of the type species, *Perna maxillata* Lamarck, is well figured in Cox (1969) and Savazzi (1995).

The examined specimens from the Maéjima Formation can be referred to *Isognomon (Isognomon) hataii* Noda and Furuichi, 1972. This species was originally described from the Teshima Formation of the Tonosho Group in Teshima Island, Kagawa Prefecture, on the basis of a single incomplete left valve. Unfortunately, the shell features such as shape, thickness and surface sculpture are unknown because the holotype (IGPS coll. cat. no. 91766) is an internal mold lacking both shell material and the posterior half of the ventral area. Comparison with the holotype shows that apical angle and ligamental features are identical. Consequently, *I. (I.) hataii* is transferred here to the subgenus *Hippochaeta*, and the holotype is a fragmental juvenile specimen having less diagnostic characters.

Earlier Matsubara (2001) preliminarily identified *Isognomon* from the Maéjima Formation as *Pedalion murayamai* Yokoyama, 1932, originally described from the "Bed III" (= ? middle Eocene Krasnopolievskaya Forma-

tion, after Kafanov and Amano, 1997) in the Dorogawa-Hishitori Region, south Sakhalin. However, it becomes clear that the Maéjima specimens have deeper resilifer grooves, less depressed lamellar ligament attachment areas, coarser pallial line, and a much more indistinct adductor muscle scar than *P. murayamai*. In addition, the byssal area of *P. murayamai* is rather distinctly bent, while that of the Maéjima specimens is gently curved. Consequently, the Maéjima specimens are not referred to this species. It may be noted that the holotype of *P. murayamai* (UMUT reg. no. CM27020) is missing.

The present species is also similar in shell shape to *Pedalion tomiyasui* Nagao, 1928a, from the middle Eocene Iojima Formation of the Okinoshima Group of Kyushu. However, it is easily distinguished from the latter species by having a larger shell with narrower resilifer grooves and weakly compressed lamellar ligament attachment areas.

Pedalion clarki Effinger, 1938, originally described from the Oligocene Gries Ranch Formation of Washington, U.S.A., is another allied species, but differs in having more numerous resilifer grooves.

Pedalion tugaruense Nomura, 1935a, originally described from the lower middle Miocene Tanosawa Formation in Aomri Prefecture, northeast Japan, is easily distinguished from *I. (H.) hataii* by its thicker, much more longitudinally elongate shell with higher ligamental area and much blunter umbonal angle.

Distribution.—Teshima Formation of the Tonosho Group in Kagawa Prefecture, Eocene; Maéjima Formation in Okayama Prefecture, Eocene or Oligocene.

Order Ostreoida

Superfamily Pectinoidea

Family Pectinidae

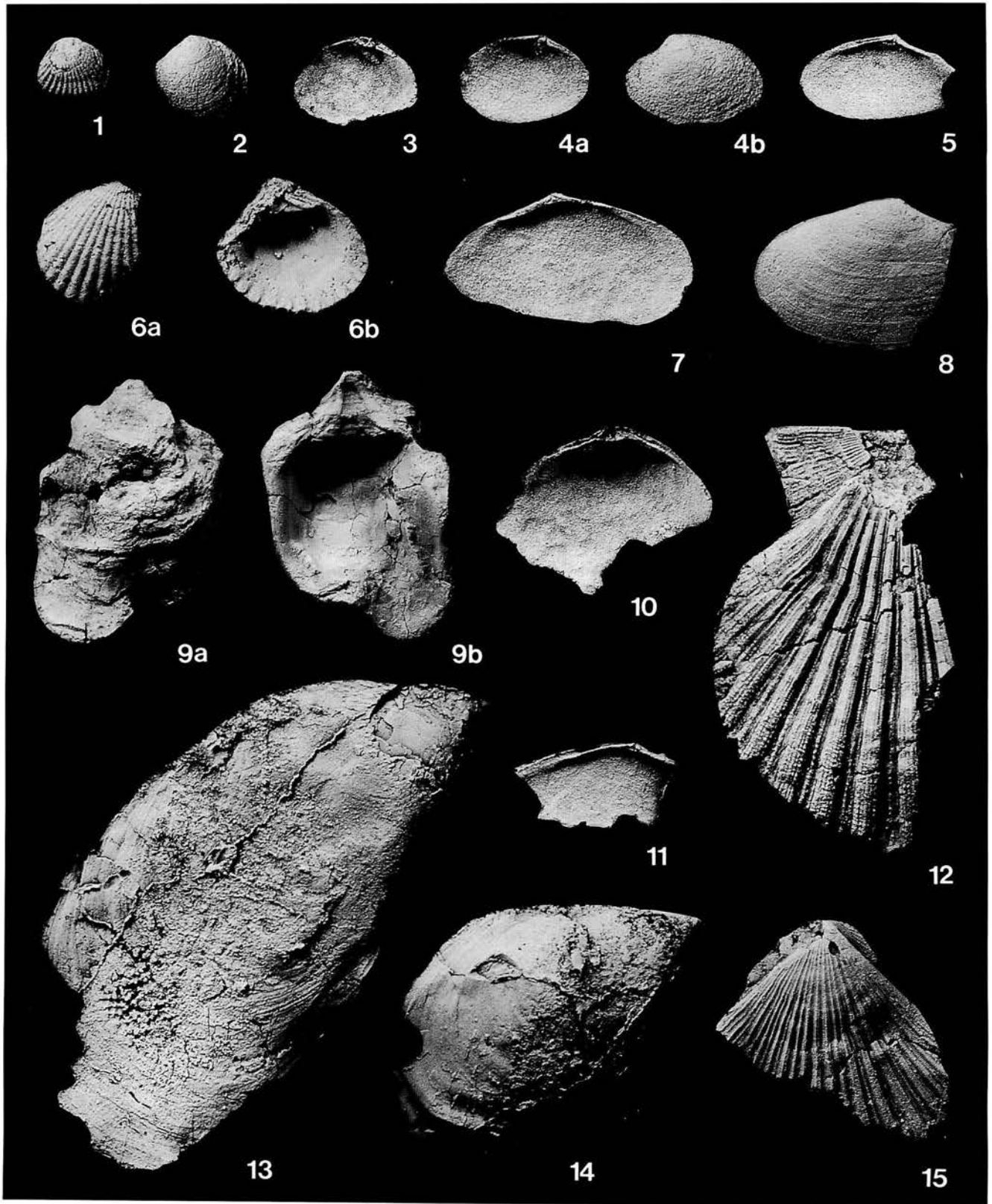
Subfamily Chlamydiae

Tribe Chlamidini

Genus *Chlamys* [Röding, 1798]

Subgenus *Leochlamys* MacNeil, 1967

← **Figure 5.** Mollusca from the Maéjima Formation (1). All specimens in natural size, unless otherwise stated. All specimens whiten by magnesium oxide. **1.** *Calyptrea* sp. Dorsal view of internal mold, MNHAH reg. no. D1-018890, ×1.5. **2.** Muricidae? gen. and sp. indet. Dorsal view, MNHAH reg. no. D1-018893, silicon rubber cast, ×1.5. **3.** Naticidae? gen. and sp. indet. Dorsal view, rather compressed, MNHAH reg. no. D1-018891, silicon rubber cast, ×1.5. **4.** *Acila (Truncacila)* cf. *nagaoi* Oyama and Mizuno. Left valve, MNHAH reg. no. D1-018895, silicon rubber cast. **5, 6, 7a-c, 12.** *Arca (Arca) uedai* sp. nov. **5.** Left valve, MNHAH reg. no. D1-018897 (paratype). **6.** Left valve, MNHAH reg. no. D1-018899, ×1.5. **7a-c.** Right valve, MNHAH reg. no. D1-018896 (holotype), silicon rubber cast. **7a.** External view. **7b.** Internal view. **7c.** Umbonal view. **12.** Left valve MNHAH reg. no. D1-018898 (paratype), compressed umbonal-ventrally. All specimens silicon rubber casts. **8, 9, 14.** *Septifer (Mytilisepta)* sp. **8.** Internal view of left valve, MNHAH reg. no. D1-018911. **9.** Internal view of right valve, MNHAH reg. no. D1-018905. **14.** Right valve, MNHAH reg. no. D1-018908. All specimens silicon rubber casts. **10a-b.** *Glycymeris (Glycymeris)* sp. Left valve. MNHAH reg. no. D1-018904, silicon rubber cast. **10a.** External view. **10b.** Internal view showing especially strong teeth and ligamental area with chevron sculpture. **11.** *Delectopecten* sp. Internal view of left valve, MNHAH reg. no. D1-018943, silicon rubber cast, ×2. **13, 18.** *Chlamys (Leochlamys) namigataensis* (Ozaki). **13.** Right valve, MNHAH reg. no. D1-018945. **18.** Left valve, MNHAH reg. no. D1-018944. **15, 16, 17.** *Isognomon (Hippochaeta) hataii* Noda and Furuichi. **15.** Right valve lacking ventral part. MNHAH reg. no. D1-018929. **16.** Internal view of left valve. MNHAH reg. no. D1-018926. **17.** Internal view of right valve, showing ligamental area. MNHAH reg. no. D1-018916. All specimens silicon rubber casts.



Leochlamys MacNeil, 1967, p. 9–10.

Azumapecten Habe, 1977, p. 82.

Type species.—*Chlamys* (*Leochlamys*) *tugidakensis* MacNeil, 1967, by original designation. Unnamed "Pliocene" in Tugidak Island, Alaska, U.S.A.

Discussion.—Habe (1977) proposed the subgenus *Azumapecten* on the basis of the following description: "Shell of small to moderate size; right valve rather inflated, with irregular, spiny radial ribs; left valve rather compressed; anterior and posterior auricles intercalating a beak between them, rather large; posterior auricle rather oblique; byssal notch on anterior part of right valve" (translated from Japanese by the present writer). *Pecten* (*Chlamys*) *farreri* Jones and Preston, 1904, living in the Northwest Pacific was designated as the type species.

The original description of *Azumapecten* involves several obscurities in the diagnosis and is not associated with any comparison to allied genera or subgenera. However, many malacologists have treated *Azumapecten* as a valid genus or subgenus (e.g. Habe, 1981; Waller, 1993; Hayami and Matsumoto, 1995; Wang, 1996; Higo *et al.*, 1999; Hayami, 2000).

On the other hand, MacNeil (1967) proposed the subgenus *Leochlamys* which was typified by *Chlamys* (*Leochlamys*) *tugidakensis* MacNeil, 1967. MacNeil (1967) and Sinelnikova (1975) also referred "*Chlamys nipponensis* Kuroda" (= *P. (C.) farreri*) to the subgenus *Leochlamys*. Indeed, the large anterior auricle, deep byssal notch, relatively strong ctenolium, irregular spiny radial ribs on shell surface, shagreen microsculpture at least on interspaces of ribs, and absence of distinct crenulations on the inner ventral margin are common to both subgenera. Consequently, *Azumapecten* Habe, 1977, is a junior synonym of *Leochlamys* MacNeil, 1967.

Chlamys (*Leochlamys*) *namigataensis* (Ozaki, 1956)

Figures 5.13, 5.18, 6.12, 6.15

Pecten (*Chlamys*) *namigataensis* Ozaki, 1956, p. 7–8, pl. 2, fig. 4.

Chlamys (*Mimachlamys*) *namigataensis* (Ozaki). Kaikiri and

Nishimoto, 1995, p. 204.

Chlamys ashiyaensis (Nagao). Nemoto and O'Hara, 2001, pl. 2, fig. 2. [not of Nagao, 1928b]

not *Chlamys* (*Mimachlamys*) *namigataensis* (Ozaki). Masuda, 1962, p. 188, pl. 21, fig. 1. [*Chlamys* sp.]

Type specimens.—NSMT reg. no. P1-4379 (Holotype and paratypes). Although Ozaki (1956) noted a specimen registered under this number as the holotype, two unfigured specimens are also registered under the same number. They are paratypes.

Material—MNHAH reg. nos. D1-018944 through D1-018951 (from MJ-2c), and D1-018952 (from MJ-4).

Emended diagnosis.—Moderate-sized *Chlamys* (*Leochlamys*) with 15 to 19 highly elevated radial ribs; fine radial threads appearing above ribs on ventral half of disc; left valve with an intercalary rib; radial sculptures densely imbricated; anterior auricle large, with a deep byssal notch and strong byssal fasciole on right valve; shell surface sculptured by a shagreen microsculpture.

Description.—Shell moderate in size, slightly higher than long, suborbicular, rather thin; apical angle between 85° and 95°; both valves with a shagreen microsculpture; lacking internal rib carinae.

Right valve weakly inflated; radial ribs 18 to 19, rather irregular, highly elevated, with three radial striations making ridges; ribs on both dorsal parts finer than those on center, finely imbricated; interspace of ribs rather deep, with or without an intercalary rib; anterior auricle large, sculptured by 6 to 7 fine radial ribs; byssal notch deep; ctenolium several in number, strong; byssal fasciole broad, strongly annulated; posterior auricle about half the length of the anterior one, with 7 to 8 radial ribs, weakly oblique anteriorly; resilifer pit moderate in size, with a weak resilifer tooth on both dorsal flanks; anterior dorsal tooth weak, long.

Left valve also weakly inflated; radial ribs 15 to 18, highly elevated, rather regular, with three sharp primary striations; an intercalary rib on each interspace; postero-dorsal part sculptured by fine, imbricated, radial striations; secondary radial striations appearing at about 40 mm from

← **Figure 6.** Mollusca from the Maéjima Formation (2). All specimens natural size, unless otherwise stated. All specimens whitened by magnesium oxide. **1, 6a–b.** *Cyclocardia* sp. 1. Left valve, MNHAH reg. no. D1-018956, $\times 2$. 6a–b. Right valve. MNHAH reg. no. D1-018955. 6a. External view lacking umbonal and antero-ventral parts. 6b. Internal view, especially showing transported cardinal teeth, both of $\times 1.5$. Both specimens silicon rubber casts. 2. Lucinidae gen. and sp. indet. Left valve, MNHAH reg. no. D1-018954, silicon rubber cast, $\times 2$. **3, 10.** *Mactra*? sp. 3. Internal view of left valve, MNHAH reg. no. D1-018969, 10. Internal view of right valve, MNHAH reg. no. D1-018968. Both specimens silicon rubber casts, $\times 2$. **4a–b.** *Tapes*? sp. MNHAH reg. no. D1-018971, $\times 2$. 4a. Internal view. 4b. External view. Silicon rubber cast. **5, 7, 8, 11.** *Megangulus maximus* (Nagao). 5. Internal view of right valve, MNHAH reg. no. D1-018965, $\times 2$. 7. Internal view of left valve, MNHAH reg. no. D1-018964, $\times 1.5$. 8. Left valve lacking posterior part of shell, MNHAH reg. no. D1-018961, $\times 1.5$. 11. Internal view of right valve lacking ventral part, MNHAH reg. no. D1-018962, $\times 2$. All specimens silicon rubber casts. **9a–b.** *Crassostrea* sp. Left valve. MNHAH reg. no. D1-018953. 14a. External view. 14b. Internal view. **12, 15.** *Chlamys* (*Leochlamys*) *namigataensis* (Ozaki). 12. Left valve lacking posterior half of shell. MNHAH reg. no. D1-018946. 15. Left valve lacking ventral part and anterior auricle. MNHAH reg. no. D1-018947. **13, 14.** *Isognomon* (*Hippochaeta*) *hataii* Noda and Furuichi. 13. Right valve, slightly compressed. MNHAH reg. no. D1-018928. 14. Right valve. MNHAH reg. no. D1-018925. Both specimens silicon rubber casts.

beak; striations on radial ribs and internal ribs tending to become imbricated ventralward with growth; anterior auricle sculptured by 10 to 14 fine, imbricated radial ribs; posterior auricle as in right valve.

Discussion.—Masuda (1962) considered the present species to be a member of the subgenus *Mimachlamys* Iredale, 1929, as a result of examination of a single right valve collected from the middle Miocene Kawazu Formation in Shimane Prefecture. However, his specimen has lower radial ribs, a shallower byssal notch and a broader apical angle, and is not referred to the present species.

The specimens from the Maéjima Formation have a large anterior auricle, deep byssal notch with strong ctenolium, and distinct shagreen microsculpture. The shagreen microsculpture is one of the diagnostic features of the tribe Chlamidini (Waller, 1993). Thus, the present species is referred to the subgenus *Leochlamys* MacNeil, 1967. The diagnosis of the present species is emended as above, adding the right valve features.

Recently, Nemoto and O'Hara (2001) figured a right valve specimen identified as *Chlamys ashiyaensis* (Nagao, 1928b) from the upper Eocene or lower Oligocene Iwaki Formation of the Shiramizu Group in the Joban Coalfield, northeast Honshu, Japan. Their figured specimen (Nemoto and O'Hara, 2001, pl. 2, fig. 2) is, however, unmistakably referred to the present species. *Pecten (Chlamys) ashiyaensis* Nagao, 1928b is distinguished from *Chlamys (Leochlamys) namigataensis* (Ozaki) by having a more compressed shell with more numerous, lower, more irregular radial ribs lacking dense imbrications.

Distribution.—Namigata Formation in Okayama Prefecture, Paleogene; Iwaki Formation of the Shiramizu Group in Fukushima Prefecture, late Eocene or early Oligocene; Maéjima Formation in Okayama Prefecture, Eocene or Oligocene.

Subclass Heterodonta
Order Veneroida
Superfamily Carditoidea
Family Carditidae
Subfamily Venericardiinae
Genus *Cyclocardia* Conrad, 1867

Cyclocardia sp. indet.

Figure 6.1, 6.6a–b

Material—MNHAH reg. nos. D1-018955 (from MJ-4), D1-018956 and D1-018957 (from MJ-5).

Description.—Shell small, ovate, longer than high, inequilateral, oblique anteriorly, weakly inflated; radial ribs 19 to 23, rather low, round-topped, less curved; radial ribs on anterior two-thirds of shell subequal to their interspaces and broader than them on posterior part; pallial line dis-

tinct; anterior adductor muscle scar ovate, distinct; posterior adductor muscle scar oblong, weakly impressed; inner ventral margin crenated.

Discussion.—A single articulated specimen and two right valves have been obtained. It is interesting that one specimen has a transposed hinge (Figure 6.6b).

Cyclocardia sp. from the Maéjima Formation closely resembles *Cyclocardia takedai* (Honda, 1980) (new name for *Venericardia elliptica* Takeda, 1953), from the middle to upper Eocene Poronai Formation of Hokkaido. However, the former species has round-topped radial ribs while those of the latter species are flat-topped.

Cyclocardia tokunagai (Yokoyama, 1924) from the lower Oligocene Asagai Formation in Fukushima Prefecture is another allied species. However, this species is distinguished from *Cyclocardia* sp. from the Maéjima Formation by having a more triangular, more inequilateral shell with longer posterodorsal margin, less curved ventral margin and more numerous radial ribs. The present species differs from *Cyclocardia siogamensis* (Nomura, 1935b), recorded from the lower-middle Miocene of Japan and Korea, in having a less inflated shell with lower and broader radial ribs.

Superfamily Tellinoidea
Family Tellinidae
Subfamily Tellininae
Genus *Megangulus* Afshar, 1969

Megangulus maximus (Nagao, 1928) comb. nov.

Figure 6.5, 6.7, 6.8, 6.11

Tellina maxima Nagao, 1928b, p. 80, pl. 4, figs. 8–10.

Angulus (Tellinides) maximus (Nagao). Oyama *et al.*, 1960, p. 200–201, pl. 61, fig. 6; Kamada, 1980, p. 333, pl. Pg–18, fig. 7; p. 334, pl. Pg–19, figs. 15, 16; p. 335, pl. N–93, fig. 4; Fuse and Kotaka, 1986, pl. 18, figs. 20, 21.

? *Angulus (Tellinides) maxima* (Nagao). Matsumoto, 1964, p. 106, pl. 1, fig. 14.

Type specimens.—IGPS coll. cat. nos. 36412 (Holotype) and 36452 (Paratypes).

Material.—MNHAH reg. nos. D1-018960 (from MJ-4), D1-018961 through D1-018963 (from MJ-5), and D1-018964 through D1-018965 (from MJ-6).

Description.—Shell rather small, transversely elongate subelliptical, thin, slightly inequilateral, compressed; anterodorsal margin weakly curved; anterior dorsoventral margin rounded; posterodorsal margin nearly straight, narrowly depressed along ligament; posterior end oblique, narrow, subtruncated; beak low, pointed, weakly opisthoclinal, situated slightly posterior to middle of shell; posterior ridge weak; shell surface nearly smooth, sculptured by faint, very

fine, commarginal growth lines which are periodically strengthened; growth lines also rather strengthened on ventral part; hinge plate narrow; both valves with two small cardinal teeth and a weak, thin, long lateral tooth; posterior tooth of right valve and anterior tooth of left valve weakly bifid; nymph low; adductor muscle scars and pallial line indistinct.

Discussion.—Oyama *et al.* (1960) transferred the generic position of *Tellina maxima* Nagao, 1928b to *Angulus* (*Tellinides*) without discussion. Indeed, a thin, compressed shell with small cardinal teeth and weak posterior ridge of the present species could well be identical with those of the type species of *Tellinides*, *Tellina timorensis* Lamarck. However, the anterolateral tooth of the present species is much longer and less oblique than that of the latter. *Tellina nitidula* Dunker (= *Fabulina hokkaidoensis* Habe, 1961), the type species of *Nitidotellina* Scarlato, 1961, also resembles *T. maxima* in having a thin, compressed shell, but the anterior end of the anterolateral tooth on the right valve is angularly pointed ventralward (see Habe, 1977, pl. 41, fig. 5). The most appropriate genus for *T. maxima* is *Megangulus* Afshar, 1969. Although the members of this genus generally have a larger and thicker shell with surface sculptured by commarginal grooves, I assign *Tellina maxima* Nagao, 1928b to it on the basis of the cardinal properties (see Matsukuma *et al.*, 1988 for precise internal shell features of the Recent species).

Megangulus maximus (Nagao, 1928b) is closely similar to *Peronidia ochii* Kamada, 1962, originally described from the upper Eocene or lower Oligocene Iwaki and Asagai formations in Joban Coalfield, Fukushima Prefecture, northeast Japan. However, the former species presents a shorter shell with a more rounded posteroventral margin than the latter one.

Angulus okumurai Taguchi, 1992, from the lower Miocene Yoshino Formation in Okayama Prefecture, also resembles the present species. However, the former species is distinguished from it in having a larger, more equilateral shell with orthogyrous beak and more rounded posterior margin. The precise generic position of *A. okumurai* is also dubious because the cardinal properties have not been sufficiently examined.

Tellina (*Peronidea*) *lutea t-matsumotoi* Otuka, 1940, originally described from the Miocene "Wakkauenbetu Formation" of northern Hokkaido is distinguished from the present species in having a larger shell with a beak situated more anteriorly, and longer, more produced posterior dorsoventral margin.

Tellina vestalioides Yokoyama, 1920 is easily distinguished from the present species by having a more inflated shell with a stronger posterior ridge, weakly concave posteroventral margin behind a posterior ridge, more distinctly truncated posteroventral margin, and stronger cardi-

nal teeth.

Although Matsumoto (1964) reported *Angulus* (*Tellinides*) *maximus* (Nagao) from the lower Miocene Ôga Formation in Shizuoka Prefecture, his figured specimen has a more inflated shell with a beak situated slightly anterior to the middle of the shell, and is not referred to the present species. The specimen from the Ôga Formation of Matsumoto (1964) is probably conspecific with *Hiatula minoensis* (Yokoyama) sensu Shibata and Kato (1988).

Distribution.—Funazu Sandstone Member of the Iojima Formation of the Okinoshima Group in Nagasaki Prefecture, late Eocene; Kishima Formation in Saga Prefecture, latest late Eocene to earliest early Oligocene; Yamaga Formation of the Ashiya Group in Fukuoka Prefecture, latest early to early late Oligocene; Kiwado and Taoyama Formations of the Hioki Group in Yamaguchi Prefecture, late Oligocene; Maéjima Formation in Okayama Prefecture, Eocene or Oligocene.

Superfamily Mactroidea
Family Mactridae
Subfamily Mactrinae
Genus *Mactra* Linnaeus, 1767

Mactra? sp. indet.

Figure 6.3, 6.10

Material.—MNHAH reg. nos. D1-018967 (from MJ-4), and D1-018968 through D1-018970 (from MJ-6).

Description.—Shell rather small, roundly subtrigonal, slightly longer than high, moderately inflated; hinge plate narrow; cardinal and lateral teeth rather weak; anterior and posterior lateral teeth thin; resilifer small, shallowly depressed.

Discussion.—On the basis of cardinal properties, this species is unmistakably referred to the family Mactridae. Unfortunately, the presence or absence of a lamellar plate between resilifer and nymph, and the mode of pallial sinus were not examined in the present material due to poor preservation. Thus, the generic assignment is provisional.

"*Mactra* sp." was regarded as one of the characteristic elements of the *Mactra-Acila* assemblage from the "Miocene" around the eastern part of the Seto Inland Sea (Itoigawa, 1983).

Acknowledgments

I would like to express my appreciation to Y. Yamamoto (Okayama University) for his valuable suggestions on the fossil localities and stratigraphy of the Maéjima Formation. Acknowledgments are also due to T. Kase (National Science Museum, Tokyo), J. Nemoto (Tohoku University), T. Sasaki (University Museum, University of Tokyo) and

H. Kato (Natural History Museum and Institute, Chiba) for their kind assistance in examining specimens. I am indebted to H. Saegusa (Museum of Nature and Human Activities, Hyogo Himeji Institute of Technology) and Y. Suzuki (National Science Museum, Tokyo) for their cooperation in collecting references. I am grateful to G. J. Vermeij (University of California at Davis) and K. Amamo (Joetsu University of Education) for reviewing the manuscript and providing valuable comments. This study was supported by a Grant-in-Aid for Scientific Research from the Japan Society for the Promotion of Sciences (no. 12740293).

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Eocene shallow marine foraminifera from subsurface sections in the Yufutsu-Umaoi district, Hokkaido, Japan

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Received March 26, 2001; Revised manuscript accepted January 29, 2002

Abstract. In subsurface sections of the Yufutsu-Umaoi district, Hokkaido, northern Japan, three Eocene benthic foraminiferal assemblage zones were defined in the Ishikari Group and the overlying Poronai Formation. They are in ascending order: *Evolutinella subamakusaensis-Haplophragmoides crassiformis* Assemblage Zone, *Globocassidulina globosa-Criboelphidium sorachiense* Assemblage Zone, and *Bulimina schwageri-Angulogerina hannai* Assemblage Zone. Assemblages characterizing each zone indicate the littoral to the inner sublittoral, middle sublittoral, and outer sublittoral paleobathymetric zones, respectively. A foraminiferal fauna in the upper bathyal zone was also identified based on reinterpretation of previous studies. It is composed of calcareous species such as *Gyroldina yokoyamai* and *Plectofrondicularia packardii*. Abundant occurrences of agglutinated foraminifera in shallower paleoenvironment suggest brackish and related stratified-water paleoenvironments caused by freshwater input into an embayment called the “Poronai Sea”. Such stratified conditions in coastal shallow marine areas may have formed oxygen-depleted zones as suggested in the previous study. These data and their paleoenvironmental implications are expected to furnish a basis for further consideration on geohistory of the Paleogene formations and also on the Eocene foraminiferal fauna of the northwestern Pacific.

Key words: Eocene, foraminifera, Ishikari Group, paleoenvironment, Poronai Formation

Introduction

The purpose of the present paper is to delineate the Eocene shallow marine foraminiferal assemblages from borehole sections in the Yufutsu-Umaoi district, southern Ishikari Plain, Hokkaido, northern Japan; to consider depositional environments; and to describe paleobathymetric distributions of benthic foraminifera.

Studies of the Japanese Paleogene smaller foraminifera began with the report of Yokoyama (1890). Following him, studies have been conducted mainly on the fossils from the Ishikari Group and the overlying Poronai Formation in the coalfield regions of Hokkaido and from the Kyoragi Formation of the Hondo Group in the Amakusa Islands, Kyushu, southwestern Japan (e.g. Asano, 1952, 1954, 1958, 1962; Asano and Murata, 1957; Fukuta, 1962). Paleogene foraminiferal faunas at various localities in Hokkaido were studied by Kaiho (1983, 1984a, b, c) who reported on their stratigraphic and paleogeographic distributions. Kaiho (1992b) also conducted a com-

parative taxonomic study of the Paleogene foraminiferal faunas from Hokkaido with other regions of the world, and recognized some species from the Poronai Formation as an “intermediate-water” fauna. His “intermediate-water” has a depth range of 100–1000 m (Kaiho, 1992b). This range almost corresponds to three bathymetric zones in the modern northwestern Pacific coast of Japan according to the compilation of Akimoto and Hasegawa (1989). They are the outer sublittoral zone (approximately 70 to 180 m), upper bathyal zone (180 to 550 m) and upper middle bathyal zone (550 to 900 m). However, correlation of each paleobathymetric zone with the foraminiferal fauna was not discussed in the report.

Deep marine foraminiferal assemblages generally include elements transported from shallower marine environments by bottom currents and/or gravity currents (Zalesny, 1959; Ingle, 1980). This means that the deep marine fauna can be recognized only after the shallower marine fauna has been identified. However, little is known about the Paleogene shallow marine foraminiferal faunas in

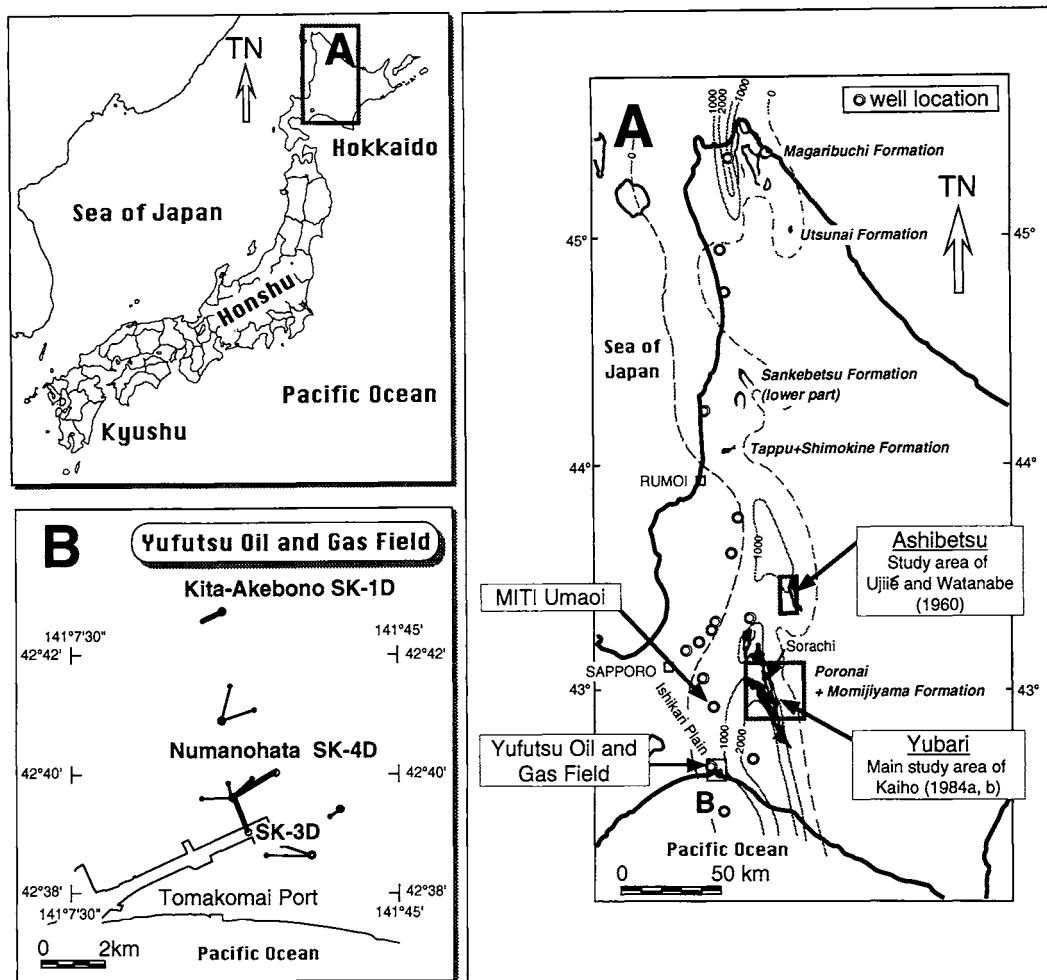


Figure 1. Index map showing the well sections studied. A = Dashed lines denote isopachs of the Poronai Formation and its equivalents drawn in a 500-meter thickness interval (Japan Natural Gas Association and Japan Offshore Petroleum Development Association, 1992). Double circles indicate the sites of the wells controlling the isopachs. Dark areas show surface distribution of the Poronai Formation, Momijiyama Formation, and their equivalents after Yamada *et al.* (1982). B = Location of the wells in the Yufutsu oil and gas field. Double circles indicate the sites of the wells, and small dots indicate the bottom of the wells. Thick lines indicate wells used in this study.

Hokkaido. The material I examined in the present study is from marine strata (Poronai Formation) which grades from nonmarine coal-bearing formation (Ishikari Group), representing a transgressive phase, and thus provides an opportunity to study the shallow marine fauna. Moreover, because paleoenvironments of the Paleogene in Hokkaido and the northwestern Pacific region have not been well studied, data on paleobathymetric distribution of foraminifera examined in the present study are expected to provide a basis for further studies in the region.

Japan Petroleum Exploration Co. Ltd. (JAPEX) has been exploring oil and natural gas in the southern Ishikari Plain. Since the discovery of the Yufutsu oil and gas field, whose reservoir is in the Cretaceous granitoids and Paleogene conglomeratic formations, many wells have been drilled

penetrating the Paleogene rocks, namely, the Ishikari Group and the overlying Poronai Formation (Yufutsu Research Group of JAPEX Sapporo *et al.*, 1992; Fujii and Moritani, 1998; Kurita and Yokoi, 2000). The present study was conducted on three well sections in the Yufutsu oil and gas field, Numanohata SK-3D, Numanohata SK-4D and Kita-Akebono SK-1D. In addition, the well MITI Umaoi, drilled in the Umaoi Hills about 25 km north of the Yufutsu oil and gas field, was also investigated (Figure 1; MITI = Ministry of International Trade and Industry). The present study refers to the area including these wells as the "Yufutsu-Umaoi district".

Geological setting

The middle Eocene Ishikari Group crops out in the hilly areas of the Yubari and Sorachi coal fields (Kaiho, 1983; Iijima, 1996). It is composed of alternating marine and nonmarine formations. Thick coal beds are present in the nonmarine part.

The Poronai Formation, which overlies the Ishikari Group, outcrops in the Yubari and Ashibetsu districts (Figure 1). It is composed mainly of massive siltstone that intercalates with acidic tuff beds in the middle to upper part (Kaiho, 1983). The geologic age of the Poronai Formation in the Yubari district was determined by calcareous nannofossils to be late Middle Eocene to Late Eocene in age (Okada and Kaiho, 1992). Broad distribution of the Poronai Formation and its equivalents in the subsurface of the Ishikari Plain is confirmed by boreholes (Figure 1A: Japan Natural Gas Association and Japan Offshore Petroleum Development Association, 1992; Japanese Association for Petroleum Technology, 1993).

Many researchers have discussed the stratigraphic relationship between the Ishikari Group and the overlying Poronai Formation since Yabe (1951) proposed their heteropic facies (synchronous) relationship (Asano, 1952, 1954; Saito, 1956; Sasa, 1956; Sasa *et al.*, 1953; Yabe and Asano, 1957; Uchio, 1961, 1962), although no conclusive interpretation has yet been drawn. The present study assumes a conformable contact between them in the borehole sections studied here. This interpretation is based on transitional characteristics of lithology as discussed later.

Lithostratigraphy of study sections

Lithologic columns of the study wells are presented in Figure 2. Lithologic descriptions of each section are based on the wellsite survey of ditch cuttings. Numbers shown on the left of each column are drilling depths from the surface. All study wells of the Yufutsu oil and gas field are deviated, therefore drilling length differs from true thickness of formation. In addition, formation contacts are placed on the basis of wireline logs whose depths may not match the drilling depths measured by the length of drill pipes.

Interpretations of wireline logs prove that the uppermost part of the Poronai Formation is missing because of a fault in Numanohata SK-3D. Also because of a fault, an interval from the lowermost Poronai Formation through the upper part of the Ishikari Group is repeated in Numanohata SK-4D.

After correcting for well deviations and formation dips, the true thickness of the Poronai Formation in the Yufutsu oil and gas field is estimated as approximately 450 m to 500 m, while in the vertical well MITI Umaoi, it is approxi-

mately 780 m.

Lithology of the Ishikari Group and the Poronai Formation in the study well sections is similar. Its vertical changes are as follows in ascending order; basal conglomerate bed, medium to finer sandstones with siltstone beds, and finally siltstones and mudstones. The basal conglomerate of the lowermost part of the Ishikari Group grades upward, intercalating with finer-grained sediments, into an alternation sequence of medium to fine sandstone beds and olive-black to olive-gray siltstone beds. Coal beds are frequent. The sandstone and siltstone beds of the uppermost Ishikari Group grade upward into the siltstone and mudstone of the Poronai Formation, which contains marine fossils such as foraminifera, ostracods, dinoflagellates, and fragments of mollusks. The Poronai Formation consists mainly of olive-gray or dark gray siltstone and mudstone. Tuff and sandstone beds intercalate in the upper part of the formation in Kita-Akebono SK-1D and MITI Umaoi, where the formation is thicker than in the other well sections. The Upper Oligocene Minaminaganuma Formation unconformably overlies the Poronai Formation in the Yufutsu-Umaoi district (Kurita and Yokoi, 2000). The Lower Oligocene Momijiyama Formation (Kaiho, 1983; Kurita and Miwa, 1998), which overlies the Poronai Formation in the Yubari district, is not present in the study area.

The upward fining of the sediments without any break from the Ishikari Group to the lower part of the Poronai Formation in the Yufutsu-Umaoi district suggests a transgressive sequence.

Samples and methods

All borehole samples used in the present study are ditch cuttings. Borehole conditions during drilling were good, and contamination caused by the caving was negligible. Samples were taken every 20 m; additional samples were taken from the siltstones in the coal-bearing formation. In the Kita-Akebono SK-1D well, samples were collected at every 10 m for most of the studied interval. A total of 173 samples were examined.

All samples were oven-dried. Subsamples of about 100 g were soaked in boiled sodium sulfate supersaturated solution for about three hours. After removing excess solution, soaked samples were left more than three days. Then they were wet sieved through a 125 μm -opening screen. All specimens in the residues were picked and identified under a binocular microscope.

Percentages of planktonic species, agglutinated species, and calcareous benthic species, and total populations were determined for these samples. Diversity, species richness (number of species) as well as "Simpson's Index for Diversity" (SID; Simpson, 1949) were used to analyze the

South

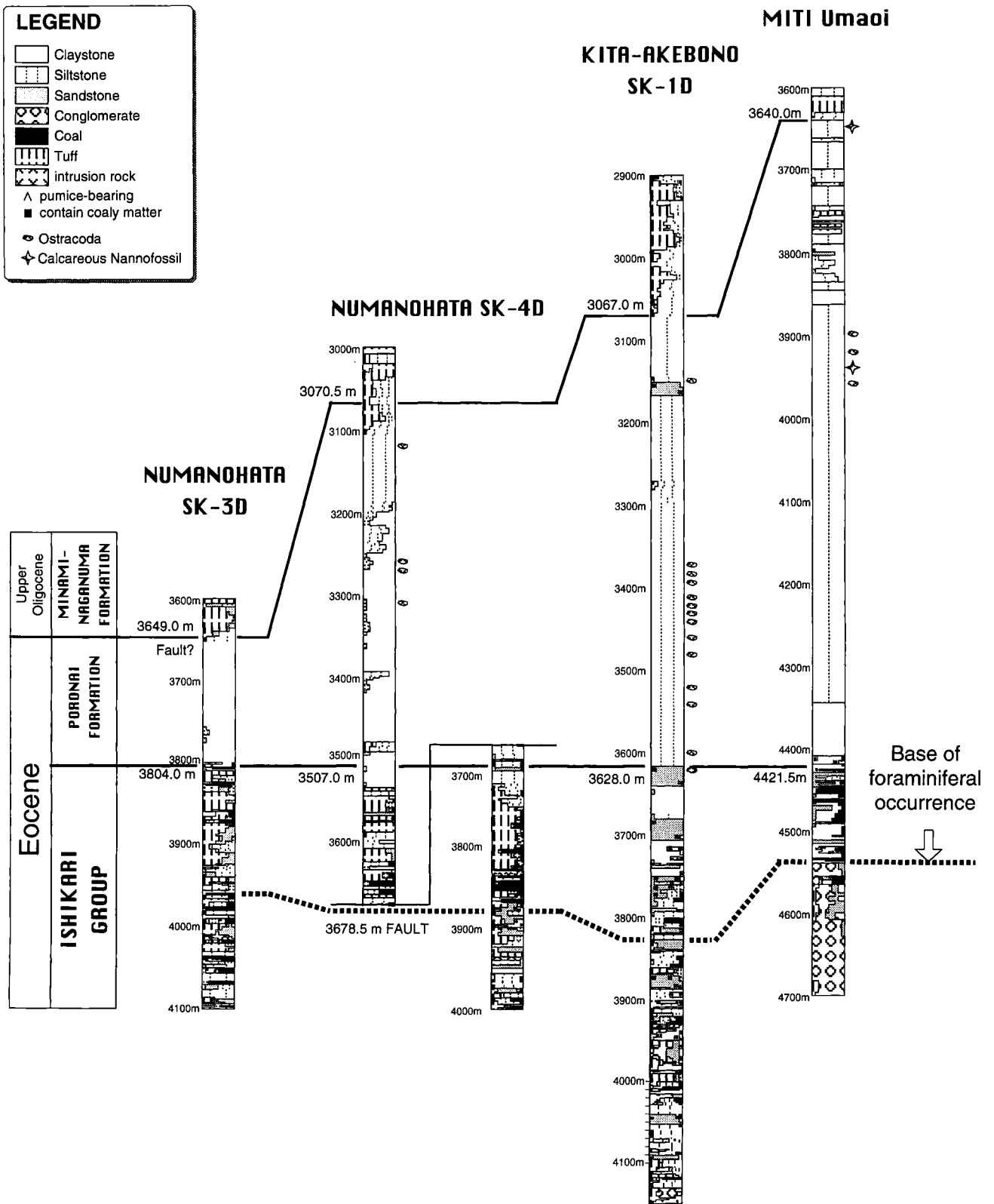
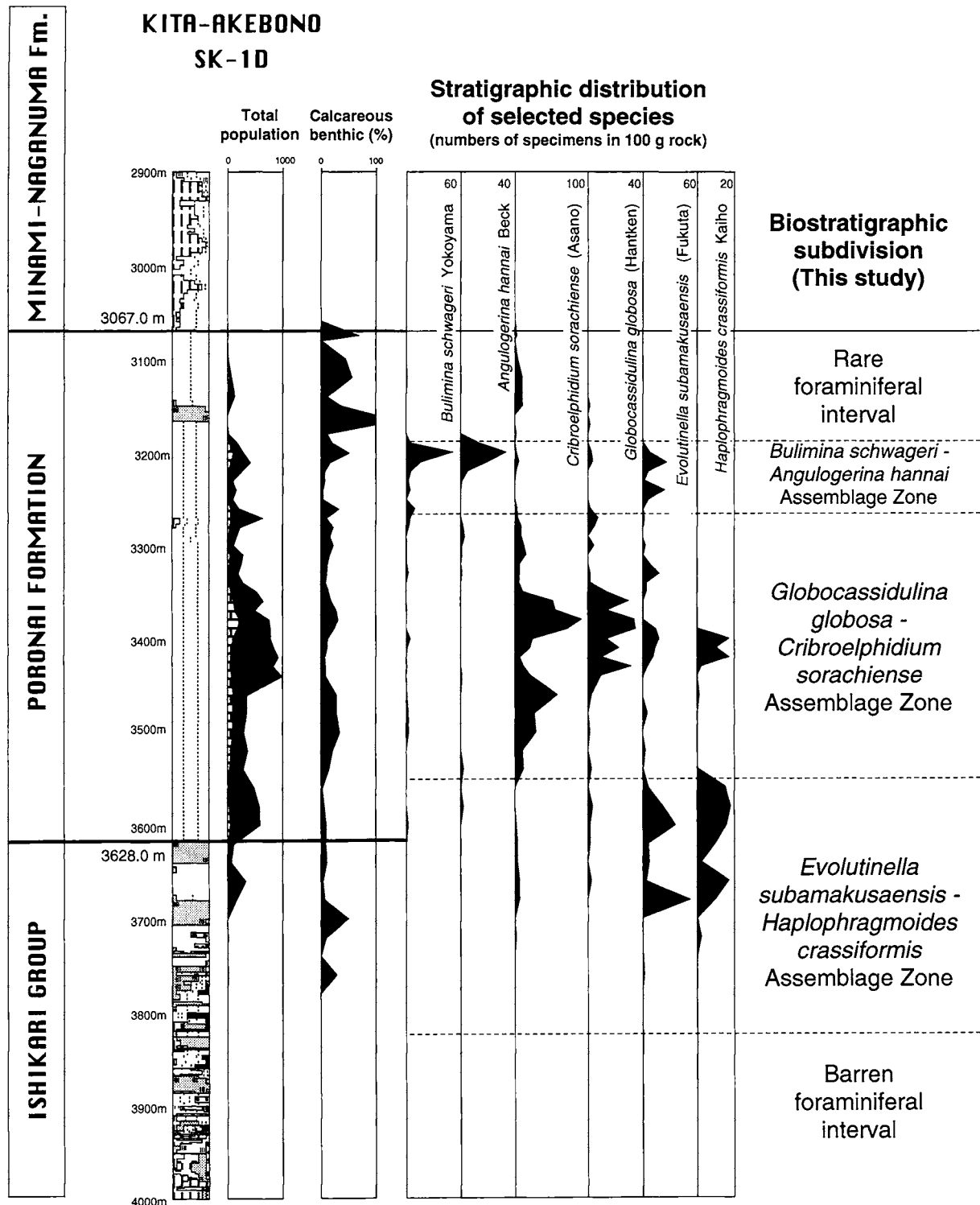


Figure 2. Stratigraphic correlation based on lithostratigraphy and wireline geophysical loggings of the study wells. Well sections are arranged at the base of the Poronai Formation.









For Legend, see Figure 2.

Figure 3. Stratigraphic occurrences of the selected species in Kita-Akebono SK-1D.

South

LEGEND

-  Total population of Calcareous Benthic foraminifera
-  Total population of Porcellaneous foraminifera
-  Total population of Agglutinated foraminifera
-  Percentage of *Evolutinella subamakusaensis* + *Haplophragmoides crassiformis*
-  Percentage of *Globocassidulina globosa* + *Criboelphidium yabei*
-  Percentage of *Bulimina schwageri* + *Angulogerina hannai*

For lithology, see Figure 2.

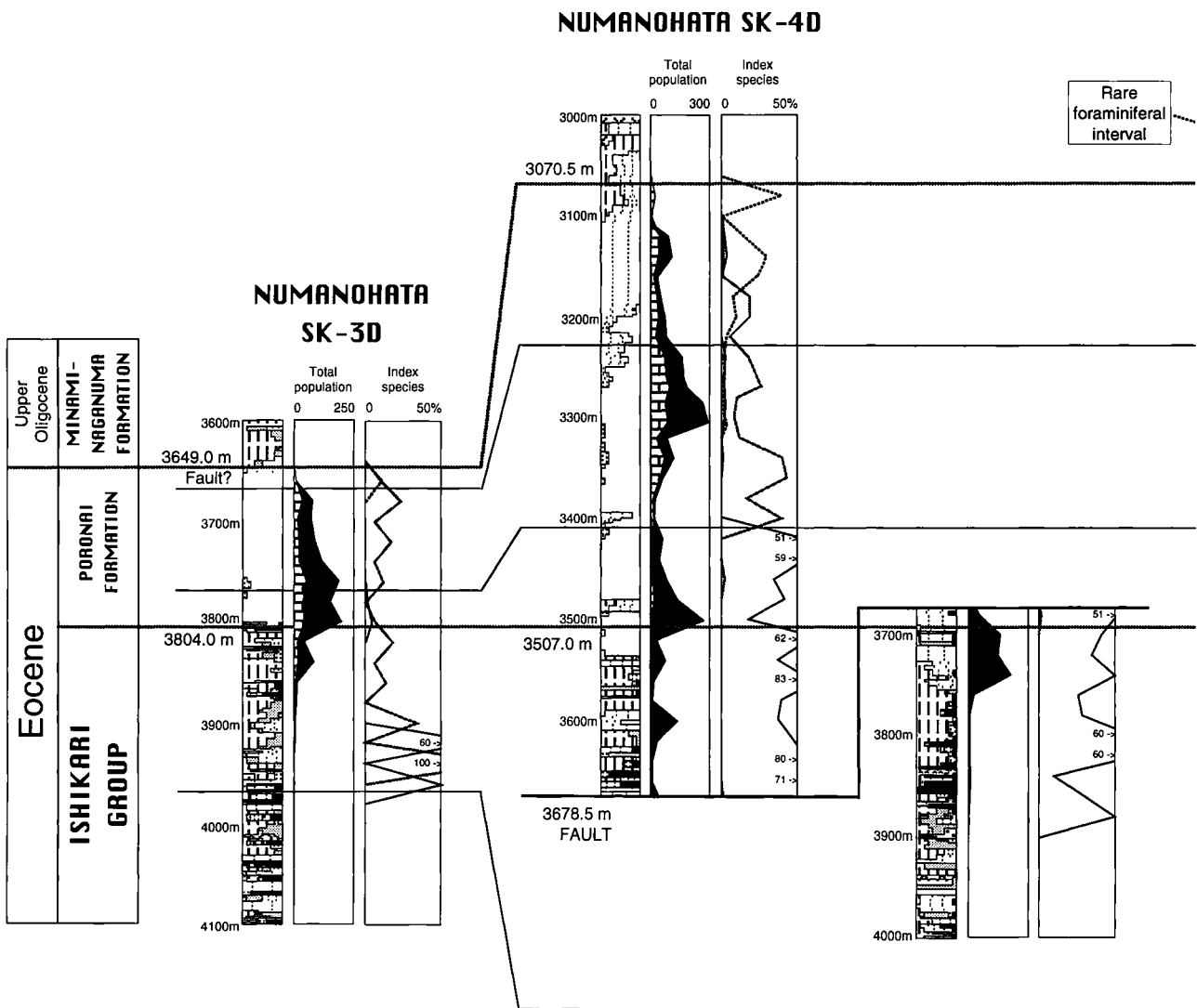
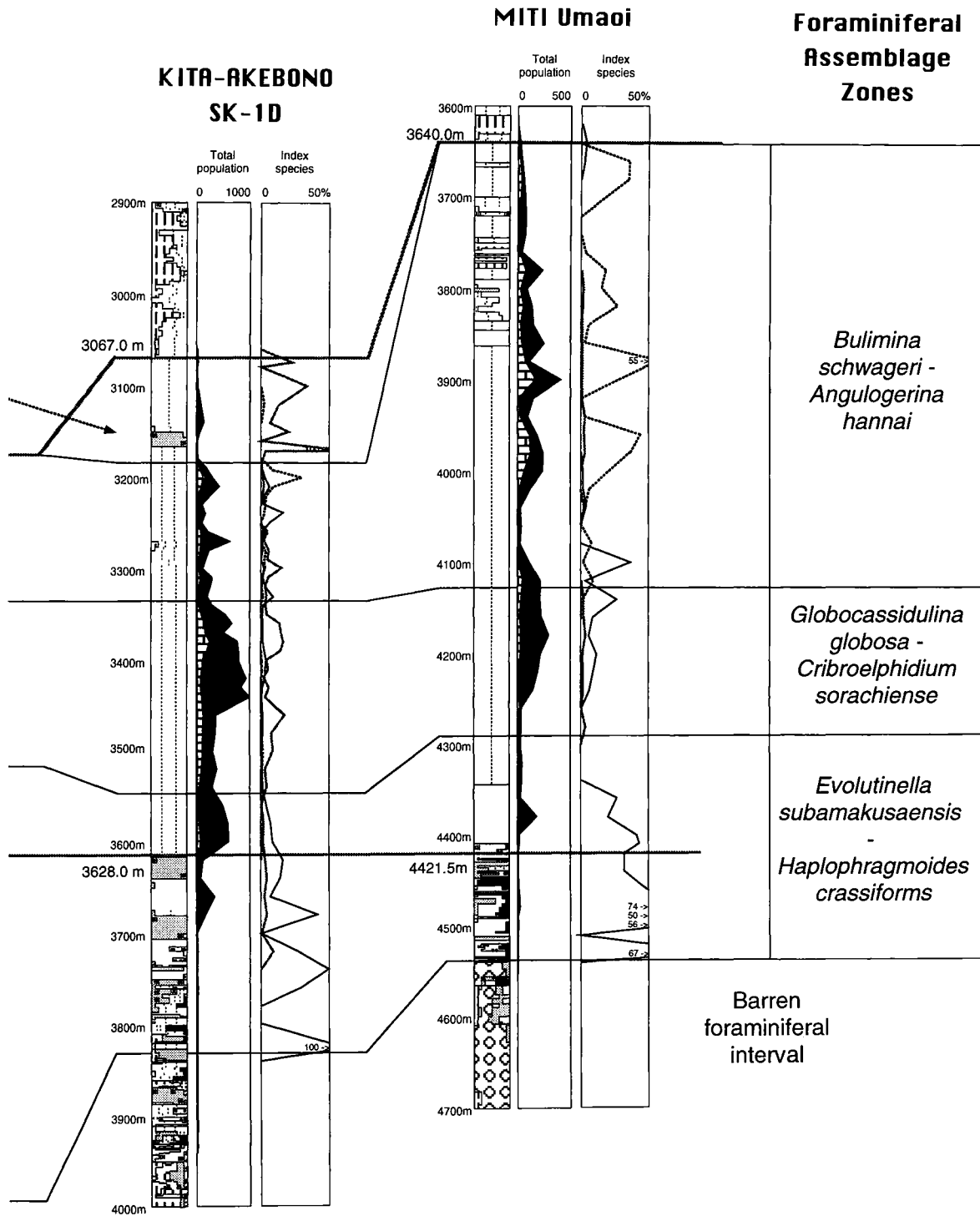


Figure 4. Stratigraphic correlation of the study wells based on the assemblage zones of foraminifera. Left columns of each well section are cumulative (agglutinated, porcellaneous and calcareous foraminifera) total populations in 100 g rock samples. Curves in right column indicate percentage of index species against total population.

North



assemblages.

Only populations of specimens identified at species rank were used to calculate diversity; species identified as "spp.", "sp. indet.", and "miscellaneous" were excluded.

Biostratigraphy

As a result of analysis, 47 species belonging to 34 genera were identified from 162 samples (Appendix 1–3). Preservation of most specimens was poor.

The present study established assemblage zones based on associations of index species based on the foraminiferal distribution. Index species are species that are abundant and have similar stratigraphic distribution among all borehole sections.

Occurrences of selected species are plotted against depth for Kita-Akebono SK-1D (Figure 3). This plot reveals that some of the species have distinct similarities in stratigraphic occurrences. On the basis of this, the following three associations are recognized.

- 1) *Evolutinella subamakusaensis* and *Haplophragmoides crassiformis*.
- 2) *Globocassidulina globosa* and *Criboelphidium sorachiense*.
- 3) *Bulimina schwageri* and *Angulogerina hannai*.

These three associations represent zones which occur in all the studied sections in the same stratigraphic order, and each has a unique distribution within the section (Figure 4). The upper part of the Poronai Formation above the *Bulimina schwageri*-*Angulogerina hannai* Assemblage Zone in Kita-Akebono SK-1D (depth 3200–3075 m) is referred to here as "rare foraminiferal interval" because the number of foraminifera in the interval is so small. As discussed later, boundaries between these assemblage zones are environmentally controlled and therefore may not indicate strict time horizons.

Characteristics of each assemblage zone are discussed below. Boundaries between the zones are defined by changes in the abundances of the index species.

Evolutinella subamakusaensis-*Haplophragmoides crassiformis* Assemblage Zone.—This zone is characterized by abundant occurrences of the two index species. It also characteristically includes agglutinated foraminifera such as *Reticulophragmium amakusaensis*, *Cyclammina pacifica*, and *Recurvoidella* sp. cf. *R. lamella*. The calcareous foraminifer *Criboelphidium sorachiense* occurs rarely in this zone. Assemblages of this zone are characterized by generally small populations and low diversity.

Globocassidulina globosa-*Criboelphidium sorachiense* Assemblage Zone.—In addition to the two index species, this zone includes abundant agglutinated foraminifera such as *Evolutinella subamakusaensis*, *Recurvoidella* sp. cf. *R. lamella*, and *Budashevaella symmetrica*, and more calcare-

ous species such as *Melonis pompilioides* and *Pullenia salisburyi* than in the assemblages of the underlying *E. subamakusaensis*-*H. crassiformis* Assemblage Zone.

Bulimina schwageri-*Angulogerina hannai* Assemblage Zone.—Although this zone is similar to the *G. globosa*-*C. sorachiense* Assemblage Zone, it is distinguished by larger numbers and higher frequencies of both *Bulimina schwageri* and *Angulogerina hannai*. Assemblages of this zone also contain numerous agglutinated foraminifera, but have higher calcareous foraminiferal abundances and higher species diversities compared to those of the previous two assemblage zones.

Paleoenvironment

The foraminiferal fauna seen in the present material is characterized by the occurrence of abundant agglutinated foraminifera, especially species belonging to the Lituolidae and Cyclamminidae. No similar fauna so dominated by these agglutinated foraminifera has been reported from anywhere else in the world. Therefore, paleoenvironmental implications of this peculiar fauna are considered based on the facts of modern foraminiferal distribution. In this section, the paleobathymetry of each assemblage zone and then the additional paleoenvironmental implications are discussed.

Paleobathymetry

As discussed by Ingle (1980) and McDougall (1980), paleobathymetric zonations of the Eocene Pacific Ocean are similar to the modern zonations. Paleobathymetric zonations used in the present study follow Akimoto and Hasegawa (1989)'s compilation of bathymetric distributions of Recent benthic foraminifera around the Japanese Islands.

Evolutinella subamakusaensis-*Haplophragmoides crassiformis* Assemblage Zone.—This zone is considered to have been deposited in a shallow marine environment for the following reasons. First, it overlaps the coal-bearing formation of the Ishikari Group that is of paralic origin. Second, it yields benthic foraminifera *Criboelphidium sorachiense* and *Sigmoidella pacifica*, both of which suggest shallow marine (sublittoral) deposition. Most modern *Criboelphidium* live in shallow marine (outer sublittoral zone or shallower) environments, such as *Criboelphidium bartletti* (*Elphidium bartletti* of Loeblich and Tappan, 1953), *C. clavatum* (*E. clavatum* of Buzas, 1966 and Lagoe, 1979). *Sigmoidella pacifica* also lives in modern shallow marine environments (Jones, 1994, as *S. elegantissima*). Third, assemblages of this zone lack *Globocassidulina* and *Bulimina* whose modern species live at depths greater than the inner sublittoral zone in the seas around the Japanese Islands (Akimoto and Hasegawa, 1989). Thus, the assem-

blages of the *E. subamakusaensis* — *H. crassiformis* Assemblage Zone are considered to indicate a paleobathymetric range from the littoral zone to the inner sublittoral zone.

Globocassidulina globosa-*Criboelphidium sorachiense* Assemblage Zone. —The assemblages of this zone include *Globocassidulina*, which has its upper depth limit in the middle sublittoral zone (Akimoto and Hasegawa, 1989). In addition, *C. sorachiense*, *C. wakkanabense* and *Sigmoidella pacifica*, all of which indicate shallow marine environments, occur frequently in this zone. Therefore, the assemblages of the *G. globosa* — *C. sorachiense* Assemblage Zone are thought to indicate the middle sublittoral zone.

Bulimina schwageri-*Angulogerina hannai* Assemblage Zone. —The assemblages of this zone are similar to those of the *Globocassidulina globosa*-*Criboelphidium sorachiense* Assemblage Zone except that the percentages of *Bulimina* and *Angulogerina* are higher. Since modern species of *Bulimina* and *Angulogerina* have upper depth limits in the outer sublittoral (Akimoto and Hasegawa, 1989), the *Bulimina schwageri*-*Angulogerina hannai* zone is considered to have been deposited in the outer sublittoral zone. The presence of *Criboelphidium* species suggests either *in situ* deposition or transport of shallower-water species into the outer sublittoral zone, possible by marine currents.

Kaiho (1992b) reported *B. schwageri* and *A. hannai* in his “intermediate-water” which ranges from depths of 100 to 1000 m. As the depth range of the outer sublittoral zone overlaps the range of Kaiho’s “intermediate water,” the present study agrees with Kaiho’s interpretation on *B. schwageri* and *A. hannai*.

Historical paleobathymetric change. —Paleobathymetric interpretation of the three assemblage zones shows that the sedimentary environments during the deposition of the upper part of the Ishikari Group and the Poronai Formation in the Yufutsu-Umaoi district changed from the littoral zone to the inner sublittoral zone, then to the middle sublittoral zone, and finally to the outer sublittoral zone. The successive change in paleobathymetry suggests that the stratigraphic interval from the first occurrence of foraminifera to the *B. schwageri*-*A. hannai* Assemblage Zone was deposited during a single transgressive phase. This interpretation supports the observation that the Ishikari Group and the Poronai Formation are conformable in the Yufutsu-Umaoi district.

The “rare foraminiferal interval” at the depth 3190 m and shallower in Kita-Akebono SK-1D well indicates that a regressive phase followed the transgression discussed above. Evidence of the regression is based on the successive disappearances of the species, *B. schwageri*, *A. hannai*, *G. globosa*, and *C. sorachiense*. Shoaling of water depth prevented distribution of these depth-controlled species.

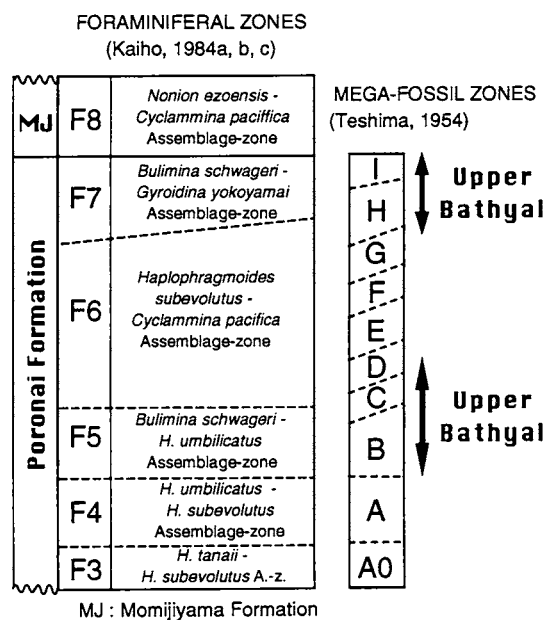


Figure 5. Stratigraphic relation between the megafossil zones and foraminiferal assemblage zones.

Consequently, the interval from the coal-bearing formation of the Ishikari Group to the Poronai Formation in the Yufutsu-Umaoi district accumulated during a single transgressive and regressive sequence. This is only observed in the Kita-Akebono SK-1D well, since the uppermost part of the Poronai Formation is missing in the other well sections.

Upper bathyal assemblages

As a result of the study discussed above, species compositions from the littoral zone to the outer sublittoral zones during the Eocene were described. Foraminiferal fauna of the upper bathyal zone (water depth approximately 180 to 550 m in northwestern Pacific coast of northern Japan), which is one rank deeper than the outer sublittoral zone, is not observed in the Yufutsu-Umaoi district. However, existence of strata which show the upper bathyal environment was reported by Teshima (1955) in the middle part of the Poronai Formation in the Yubari district. Here, I describe upper bathyal foraminiferal fauna based on the correlation between biostratigraphy of Teshima (1955) and Kaiho (1984a, b). Teshima (1955) studied megafossils and divided the Poronai Formation into the A to I megafossil zones in ascending order, stating that the megafossil assemblages of the B-C and H-I zones are similar to the molluscan association found in water depth interval of 200 to 300 m, offshore Otaru, Sea of Japan. This water depth in the Sea of Japan falls within the range of the upper bathyal zone (Akimoto and Hasegawa, 1989). According to the stratigraphic relationship between these megafossil

Species	Subittoral			Bathyal
	Inner	Middle	Outer	Upper
AGGLUTINATED				
<i>Alveolophragmium</i>	sp. A of the present study		R	
<i>Ammobaculites</i>	sp. A of Kaiho, 1984b			A
<i>Ammobaculites</i>	<i>akabiraensis</i> Asano	R	R	R
<i>Ammodiscus</i>	<i>panianus</i> Hedberg		R	C
<i>Ammodiscus</i>	<i>tenuis</i> Brady		R	C
<i>Ammomarginulina</i>	sp. A of Kaiho, 1984b			R
<i>Bathysiphon</i>	<i>eocenicus</i> Cushman and Hanna	R	R	C
<i>Bathysiphon</i>	<i>veroni</i> Hamlin	R	R	C
<i>Budashveaella</i>	sp. aff. <i>B. multicamerata</i> (Voloshinova)		R	R
<i>Budashveaella</i>	<i>symmetrica</i> (Ujiié and Watanabe)	R	C	C
<i>Cribrostomoides</i>	sp. cf. <i>C. cretacea</i> Cushman and Goudkoff	R	R	?
<i>Cyclammina</i>	<i>ezoensis</i> Asano	R	R	R
<i>Cyclammina</i>	<i>orbicularis</i> Brady		R	R
<i>Cyclammina</i>	<i>pacifica</i> Beck	R	C	A
<i>Cyclammina</i>	sp. aff. <i>C. pusilla</i> Brady	R	R	R
<i>Cyclammina</i>	<i>tani</i> Ishizaki			R
<i>Cyclammina</i>	sp. A of the present study			R
<i>Cyclammina</i>	sp. B of the present study	R	R	R
<i>Discammina</i>	sp. A of Kaiho, 1984b	R	R	R
<i>Discammina</i>	sp. B of Kaiho, 1984b		?	C
<i>Discammina</i>	sp. C of Kaiho, 1984b	R	R	R
<i>Discammina</i>	sp. A of Kaiho, 1984b	R	R	R
<i>Eggerella</i>	<i>subamakusaensis</i> (Fukuta)	A	C	R
<i>Evolutinella</i>	<i>gordialis</i> Jones and Parker		R	R
<i>Glomospira</i>	<i>crassiformis</i> Kaiho	C	C	R
<i>Haplophragmoides</i>	sp. cf. <i>H. delata</i> Sullivan		C	R
<i>Haplophragmoides</i>	<i>rugosus soyensis</i> Yasuda		C	R
<i>Haplophragmoides</i>	<i>tanii</i> Kaiho		R	R
<i>Haplophragmoides</i>	<i>yokoyamai</i> Kaiho		C	R
<i>Haplophragmoides</i>	sp. A of the present study		R	?
<i>Haplophragmoides</i>	sp. B of the present study	R	R	?
<i>Haplophragmoides</i>	sp. D of the present study	C	R	?
<i>Hyperammina</i>	<i>elongata</i> Brady		R	R
<i>Karrerulina</i>	sp. cf. <i>K. hokkaidoana</i> (Takayanagi)		C	R
<i>Martinottiella</i>	<i>crassa</i> Kaiho		R	R
<i>Martinottiella</i>	<i>rectidalicata</i> Kaiho			R
<i>Placentammina</i>	sp. A of the present study		R	?
<i>Poronaiia</i>	<i>poronaiensis</i> (Asano)	C	R	C
<i>Recurviodella</i>	sp. cf. <i>R. laemella</i> (Grzybowski)	A	C	?
<i>Recurviodes</i>	sp. A of the present study		C	?
<i>Reophax</i>	<i>minutirectus</i> Kaiho		R	C
<i>Reophax</i>	<i>multicameratus</i> Kaiho		R	C
<i>Reophax</i>	<i>tappuensis</i> Asano	C	C	C
<i>Reticulophragmium</i>	<i>amakusaensis</i> (Fukuta)	C	C	A
<i>Rhabdammina</i>	sp.		R	R
<i>Silicosigmoilina?</i>	sp.		R	R
<i>Spiroplectammina</i>	<i>nuttalii</i> Laicker			R
<i>Trochammina</i>	sp. cf. <i>T. asagaiensis</i> Asano		C	C
<i>Trochammina</i>	<i>squamata</i> Jones and Parker		C	R
<i>Vermeulinula</i>	<i>takayanagii</i> (Kaiho)		R	R
PORCELLANEUS				
<i>Quinqueloculina</i>	<i>seminula compacta</i> Serova	R	C	C
<i>Triloculina</i>	<i>gibba</i> d'Orbigny	R	R	R
CALCAREOUS HYALINE				
<i>Anomalinoidea</i>	<i>sasai</i> Kaiho			R
<i>Anomalinoidea</i>	sp. A of Kaiho, 1984b			R
<i>Bolivina</i>	<i>euplectella</i> Yokoyama		R	R
<i>Brizarina</i>	<i>saitoi</i> Kaiho		R	C
<i>Brizarina</i>	<i>serata</i> Kaiho		R	C
<i>Bulimina</i>	<i>schwageri</i> Yokoyama		A	A
<i>Bulimina</i>	<i>sculptilis</i> Cushman		R	C
<i>Bulimina</i>	sp. cf. <i>B. sculptilis</i> Cushman		R	C
<i>Bulimina</i>	<i>yabei</i> Asano and Murata		C	R
<i>Buliminella</i>	<i>robertsi</i> Howe and Ellis		C	R
<i>Cancris</i>	<i>torquatus</i> Cushman and Todd			R
<i>Cassidulina</i>	<i>lobatula</i> Kaiho		R	R
<i>Cassidulina</i>	<i>yubariensis</i> Kaiho		R	R
<i>Cassidulinoides</i>	<i>howei</i> Cushman		R	C
<i>Chilostomella</i>	sp. cf. <i>C. cylindroides</i> Reuss			R
<i>Cibicides</i>	<i>elmaensis</i> Rau		R	R
<i>Cibicides</i>	<i>complanatus</i> Kaiho		R	R
<i>Cibicides</i>	sp. A of Kaiho, 1984b		R	R
<i>Cibicides</i>	sp. B of Kaiho, 1984b			R
Species				
<i>Cribrorophidium</i>	<i>ishikariense</i> (Kaiho)	R	R	R
<i>Cribrorophidium</i>	<i>sorachiense</i> (Asano)	R	A	A
<i>Cribrorophidium</i>	<i>sorachiense</i> (Asano) var. A			R
<i>Cribrorophidium</i>	<i>wakkanabense</i> (Kaiho)	R	C	A
<i>Dentalina</i>	sp. cf. <i>D. kushiroensis</i> Yoshida			R
<i>Dentalina</i>	sp. cf. <i>D. subsoluta</i> (Cushman)			R
<i>Dentalina</i>	<i>cocaoensis</i> (Cushman)			R
<i>Dentalina</i>	<i>dusenburyi</i> Beck			R
<i>Dentalina</i>	<i>minuta</i> Kaiho			R
<i>Elphidium</i>	<i>mabutii</i> Asano*	?	?	R
<i>Elphidium</i>	sp. A of Kaiho, 1984b		R	?
<i>Epistominella</i>	<i>exigua multiloculata</i> Kaiho			R
<i>Eponides</i>	<i>lobatus</i> Kaiho		R	R
<i>Fissurina</i>	<i>marginata</i> (Montagu)		R	R
<i>Fissurina</i>	sp. A of Kaiho, 1984b		R	R
<i>Fursenkoina</i>	<i>uchioi</i> Kaiho		R	R
<i>Glandulina</i>	<i>laevigata ovata</i> Cushman and Applin		C	C
<i>Globobulimina</i>	<i>ezoensis</i> (Yokoyama)			C
<i>Globocassidulina</i>	<i>globosa</i> (Hantken)		A	C
<i>Globocassidulina</i>	sp. A of Kaiho, 1984b			R
<i>Globulina</i>	<i>gibba</i> (d'Orbigny)			R
<i>Guttulina</i>	<i>problema</i> (d'Orbigny)	C	C	C
<i>Guttulina</i>	<i>takayanagii</i> Kaiho	R	R	R
<i>Gyroidina</i>	<i>yokoyamai</i> (Ujiié and Watanabe)			R
<i>Heterolepa</i>	<i>poronaiensis</i> Kaiho	R	R	C
<i>Lagena</i>	sp. cf. <i>L. laevis</i> (Montagu)	R	R	R
<i>Lagena</i>	sp. cf. <i>L. perlucida</i> (Montagu)			R
<i>Lagena</i>	sp. cf. <i>L. sulcata</i> (Walter and Jacob)			R
<i>Lagena</i>	<i>striata</i> (d'Orbigny)		R	R
<i>Lagena</i>	sp. A of Kaiho, 1984b			R
<i>Lenticulina</i>	<i>antipoda</i> (Stache)			R
<i>Lenticulina</i>	<i>ishikariensis</i> Kaiho			R
<i>Lenticulina</i>	sp. A of Kaiho, 1984b			R
<i>Lenticulina</i>	sp. B of Kaiho, 1984b			R
<i>Melonis</i>	<i>affinis</i> (Reuss)		R	R
<i>Melonis</i>	<i>elegans</i> Kaiho			R
<i>Melonis</i>	<i>lobatus</i> Kaiho			R
<i>Melonis</i>	sp. cf. <i>M. multisuturalis</i> van Bellen			R
<i>Melonis</i>	<i>pompiolioides</i> (Fitchel and Moll)	R	C	C
<i>Melonis</i>	<i>subevolutus</i> Kaiho			R
<i>Nodogeneria</i>	sp. cf. <i>N. lepidula</i> (Schwager)			R
<i>Nodosaria</i>	<i>amchikaensis</i> (Todd)**			R
<i>Nodosaria</i>	<i>longiscata</i> d'Orbigny		R	C
<i>Nonion</i>	<i>ezoensis</i> Kaiho			R
<i>Nonion</i>	<i>subangularis</i> Kaiho			R
<i>Nonion</i>	<i>takayanagii</i> Kaiho			R
<i>Nonionella</i>	<i>japonica</i> (Yokoyama)			R
<i>Nonionella</i>	<i>mabutii</i> Asano			R
<i>Oolina</i>	<i>hexagona</i> (Williamson)			R
<i>Oolina</i>	<i>simplex</i> Reuss			R
<i>Oolina</i>	sp. cf. <i>O. globosa</i> (Montagu)			R
<i>Oolina</i>	sp. A of Kaiho, 1984b			R
<i>Planulina</i>	<i>poronaiensis</i> Asano	R		
<i>Plectofrondicularia</i>	<i>delicatula</i> Kaiho			R
<i>Plectofrondicularia</i>	<i>packardii</i> Cushman and Schencki			R
<i>Plectofrondicularia</i>	<i>smithi</i> Kaiho			R
<i>Plectofrondicularia</i>	<i>vaughani</i> Cushman			R
<i>Praeglobobulimina</i>	<i>pyrula</i> (d'Orbigny)		R	R
<i>Praeglobobulimina</i>	<i>ovata</i> (d'Orbigny)		R	R
<i>Praeglobobulimina</i>	<i>pupoides</i> (d'Orbigny)			R
<i>Procerolagena</i>	sp. cf. <i>P. gracillima</i> (Sequenza)			R
<i>Pseudonodosaria</i>	<i>conica</i> (Neugeboren)	R	R	R
<i>Pseudonodosaria</i>	<i>inflata</i> (Costa)	R	R	R
<i>Pseudopolyphorina</i>	<i>hokkaidoana</i> Kaiho	R	R	R
<i>Pullenia</i>	<i>eocenicus</i> Cushman and Siegfus	R	R	?
<i>Pullenia</i>	<i>salisburyi</i> R. E. and K. C. Stewart			C
<i>Saracenaria</i>	<i>ujiiéi</i> Kaiho			R
<i>Sigmoidella</i>	<i>pacifica</i> Cushman and Ozawa	C	C	C
<i>Sigmomorphina</i>	<i>schencki</i> Cushman and Ozawa			C
<i>Sigmomorphina</i>	sp. A of Kaiho, 1984b			R
<i>Stilostomella</i>	sp. cf. <i>S. japonica</i> (Ishiwada)			R
<i>Trifarina</i>	<i>hannai</i> (Beck)			C
<i>Uvigerina</i>	<i>ombatsuenensis</i> Kaiho			R
<i>Vaivulinaria</i>	<i>lymani</i> (Yokoyama)			R

Figure 6. Paleobathymetric distribution of benthic foraminifera. Data of Asano (1952), Ujiié and Watanabe (1960) and Kaiho (1984a, b) are also interpreted by the present study. R = Rare; C = Common; A = Abundant. Occurrences of species shown in boldface are supposed to be important for paleobathymetric interpretations. Occurrences of species with * are restricted in the Utsunai Formation (Kaiho, 1984b), and with ** to the Omagari Formation (Asano, 1952; Kaiho, 1984b).

zones (B-C and H-I) and foraminiferal assemblage zones indicated by Kaiho (1984a; Figure 5), it is obvious that foraminiferal assemblage zones F5 and F7 (Kaiho, 1984a, c) were deposited in the upper bathyal zone. The foraminiferal assemblages of these zones contain abundant

Bulimina schwageri and *Angulogerina hannai* (Kaiho, 1984a, c) as well as numerous calcareous foraminifera such as *Gyroidina yokoyamai* and *Plectofrondicularia packardii*. These latter two species were not encountered in the Yufutsu-Umaoi district and therefore must represent the

Eocene upper bathyal zone.

Paleobathymetric distributions of benthic foraminifera in the Poronai Sea are summarized in Figure 6 based on the present study and compilation of previous reports (Asano, 1952; Ujiie and Watanabe, 1960; Kaiho, 1984a, b).

Paleoenvironmental implications of abundant agglutinated foraminifera

The paleobathymetric distributions of benthic foraminifera in the study area indicate that the shallower marine assemblages include higher abundances of agglutinated foraminifera. Because similar assemblages dominated by agglutinated foraminifera have not been reported from other coastal regions of the North Pacific while various calcareous species have been reported (e.g. Ingle, 1980; McDougall, 1980), a local environmental factor is considered to have controlled the distribution.

Greiner (1970) proposed that availability of calcium carbonate for test construction is the controlling environmental factor in the distribution of calcareous foraminifera. In environments where calcium carbonate availability is insufficient for calcareous foraminifera, agglutinated foraminifera dominate. Examples of environments with insufficient calcium carbonate are found in brackish coastal areas, estuaries, and marshes (e.g., Zalesny, 1959; Bandy and Arnal, 1960; Anderson, 1963; Scott *et al.*, 1983; Zheng and Fu, 1992). Highly diverse agglutinated foraminiferal associations are also reported from the Arctic Ocean, in areas affected by the brackish surface water (Vilks, 1969; Hunt and Corliss, 1993; Schröder-Adams *et al.*, 1990).

Based on these modern examples of foraminiferal ecology, abundant occurrences of agglutinated foraminifera from the Ishikari Group and the Poronai Formation are thought to be the result of deposition in areas under the influence of brackish surface-water.

Water stratification

Previous studies on the lithostratigraphy and dinoflagellate assemblages showed that water stratification was important in the basal part of the Poronai Formation (Matsuno *et al.*, 1964; Kurita and Matsuoka, 1994). Previous studies also supposed that the Poronai Formation was deposited in an embayment called the "Poronai Sea" (Teshima, 1967; = "Paleo-Poronai Sea" of Kaiho, 1983, 1984c). This interpretation is mainly based on the geographical distribution of the Poronai Formation and its equivalents (Figure 1A). Absence or rare occurrences of planktonic foraminifera and radiolarians in the Yufutsu-Umaoi district indirectly support this interpretation. Such closed paleogeography may be an important factor for the water stratification.

According to Kaiho (1984a, b), Teshima (1955)'s megafossil zone A, found in the basal part of the Poronai

Formation, corresponds approximately to the foraminiferal zones from the *Haplophragmoides tanaii-Haplophragmoides subevolutus* Assemblage Zone to the *Haplophragmoides umbilicatus-H. subevolutus* Assemblage Zone of Kaiho (1984a, c; Figure 5). Accounting for the synonyms discussed in the taxonomic section below, species composition of Kaiho's zones is similar to the *Evolutinella subamakusaensis-Haplophragmoides crassiformis* Assemblage Zone and the *Globocassidulina globosa-Cribrorhaphidium sorachiense* Assemblage Zone of the Yufutsu-Umaoi district. This similarity shows that the stratigraphic interval from the *H. tanaii-H. subevolutus* Assemblage Zone to the *H. umbilicatus-H. subevolutus* Assemblage Zone in the Yubari district was deposited under paleobathymetric conditions within, or shallower than, the middle sublittoral zone of the Yufutsu-Umaoi district.

Matsuno *et al.* (1964) also pointed out that the megafossil zone A defined by Teshima (1955), at the basal part of the Poronai Formation in the Yubari coal field, is rich in organic carbon and presumably was deposited in an oxygen-depleted paleoenvironment.

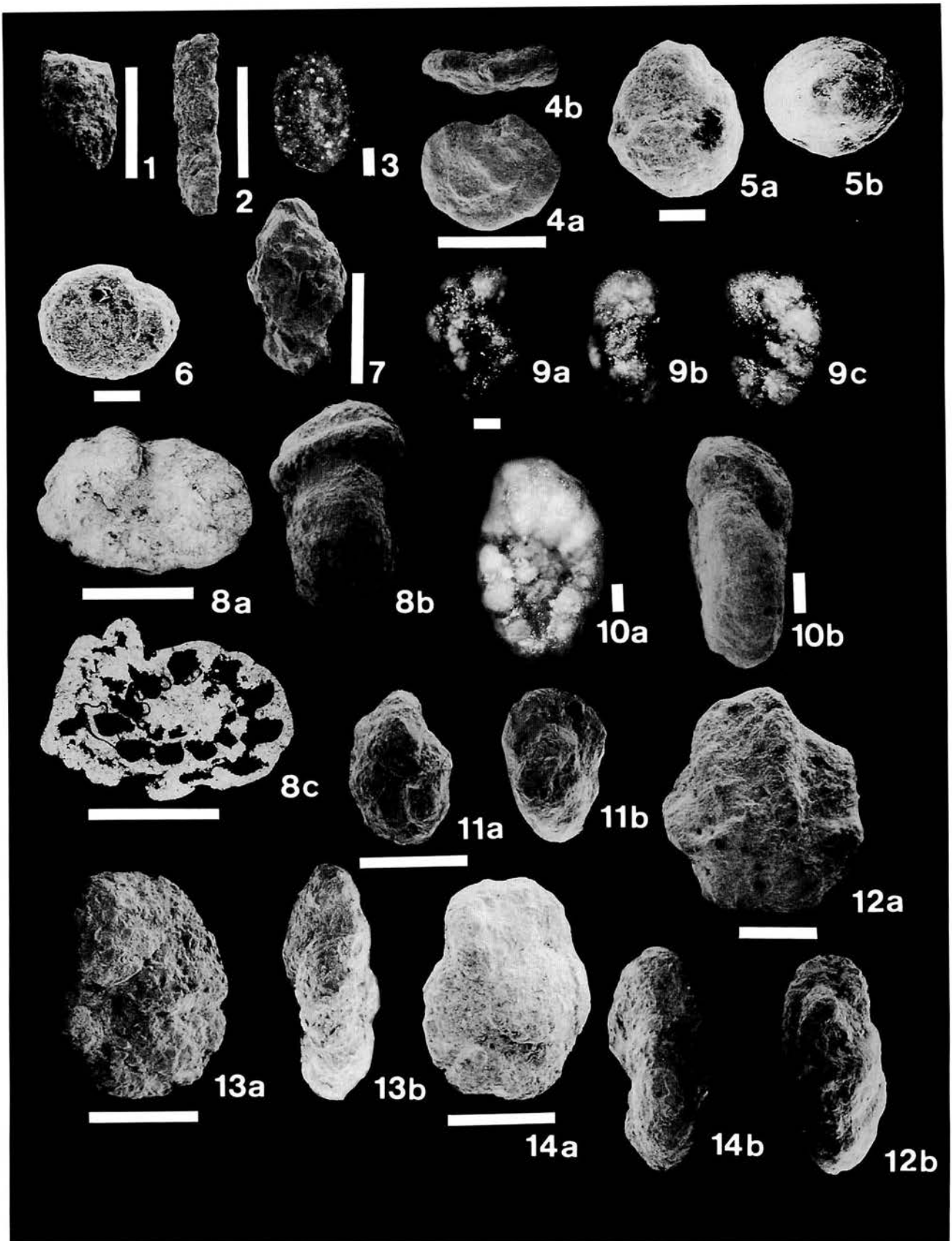
Based on these lines of evidence, sediments deposited in stratified shallow marine water masses are widely distributed in the Poronai Formation of the Yufutsu-Umaoi district and the Yubari district. These stratified water masses are believed to have formed as a result of fresh water input, as suggested by the dominant agglutinated foraminifers. In such an environment, a decreasing supply of dissolved oxygen from the sea surface may have caused oxygen depletion in substratum due to degradation of organic matter, as commonly observed in modern shallow marine areas (Tyson and Pearson, 1991).

Conclusion

Three Eocene foraminiferal assemblage zones, *Evolutinella subamakusaensis-Haplophragmoides crassiformis* Assemblage Zone, *Globocassidulina globosa-Cribrorhaphidium sorachiense* Assemblage Zone and *Bulimina schwageri-Angulogerina hannai* Assemblage Zone, in ascending order, were defined in the well sections of the Yufutsu-Umaoi district, southern central Hokkaido. Assemblages characterizing each assemblage zone indicate the littoral to inner sublittoral zone, the middle sublittoral zone and the outer sublittoral zone, respectively.

Furthermore, compositions of foraminiferal assemblages of the Eocene upper bathyal zone were described based on a reevaluation of the previous studies. The upper bathyal zone is characterized by occurrence of abundant calcareous species such as *Gyroidina yokoyamai* and *Plectofrondicularia packardii*.

Abundant occurrences of agglutinated foraminifera suggest brackish-water paleoenvironments caused by fresh-



water input. Such brackish water may cause stratification and resultant oxygen depletion.

As a result of the present study, compositions of Eocene shallow marine foraminiferal assemblages in northern Japan were revealed. These data are expected to form a basis for considering the geohistory of the Paleogene formations in Hokkaido, as well as the paleoceanography of the northwestern Pacific region during the Eocene.

Acknowledgments

Kristin McDougall (U. S. Geological Survey) kindly improved the manuscript and gave me suggestions.

I would like to thank Yokichi Takayanagi (Tohoku University) and Hiroshi Kurita (JAPEX, presently Niigata University) for critical reading of the manuscript. I also would like to express my special thanks to Michiko Miwa (JAPEX) and Tetsuro Ichinoseki (JAPEX) for fruitful suggestions, and Keiko Inaba and Yoko Kuwashima for technical assistance.

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Taxonomic notes

Species which occurred in the Yufutsu-Umaoi district are arranged in taxonomic order following Loeblich and Tappan (1987). For the present identification, topotype, ideotype and hypotype specimens collected by K. Kaiho and presently deposited in JAPEX Research Center, Chiba, Japan, were compared. Because of poor preservation of the specimens, no new species were described herein, although several synonymies are discussed. All figured specimens are deposited in the collection of JAPEX Research Center.

Bathysiphon eocenica Cushman and Hanna (Figure 7.1)

Bathysiphon eocenica Cushman and Hanna, 1927, p. 210, pl. 13, figs. 2, 3. —Asano, 1952, p. 31, pl. 3, figs. 3, 4. —Ujiié and Watanabe, 1960, p. 127, pl. 1, figs. 3, 4. —Fukuta, 1962, p. 7, pl. 1, fig. 1. —Kaiho, 1984b, p. 42, pl. 1, figs. 3a, b. —Kaiho, 1992b, p. 365, pl. 1, fig. 1, pl. 5, fig. 1, 2.

Bathysiphon vernoni Hamlin (Figure 7.2)

Bathysiphon vernoni Hamlin, 1963, p. 153, pl. 14, figs. 1a-2b. —Kaiho, 1984b, p. 42, pl. 1, fig. 4.

Placentamina sp. A (Figure 7.5, 7.6)

Description.—Test free, small, unilocular, pyriform; very finely agglutinated and almost transparent; aperture round opening at the top of pyriform shell with very short projection.

Remarks.—Almost all of the specimens were deformed secondarily.

Reophax tappuensis Asano (Figure 7.7)

Reophax tappuensis Asano, 1958, p. 71, pl. 13, figs. 8, 9. —Kaiho, 1984b, pl. 1, figs. 10a-12.

Cribrostomoides sp. cf. *C. cretacea* Cushman and Goudkoff (Figure 7.11, 7.12)

Cf. *Cribrostomoides cretacea* Cushman and Goudkoff, 1944, p. 54, pl. 9, figs. 4a, b.

Remarks.—All specimens are so distorted that accurate identification is difficult. Coiling planes are always tilted to show very weak streptospiral involute coiling, therefore this form must be assigned to genus *Cribrostomoides* following Jones *et al.* (1993). It is distinguishable from allied species in its involute coiling, six to eight inflated chambers in final whorl, finely agglutinated and slightly transparent wall.

Evolutinella subamakusaensis (Fukuta) (Figure 8.10-8.12)

Cribrostomoides cf. *cretacea* Cushman and Goudkoff. —Ujiié and Watanabe, 1960, p. 127, pl. 1, figs. 3-5.

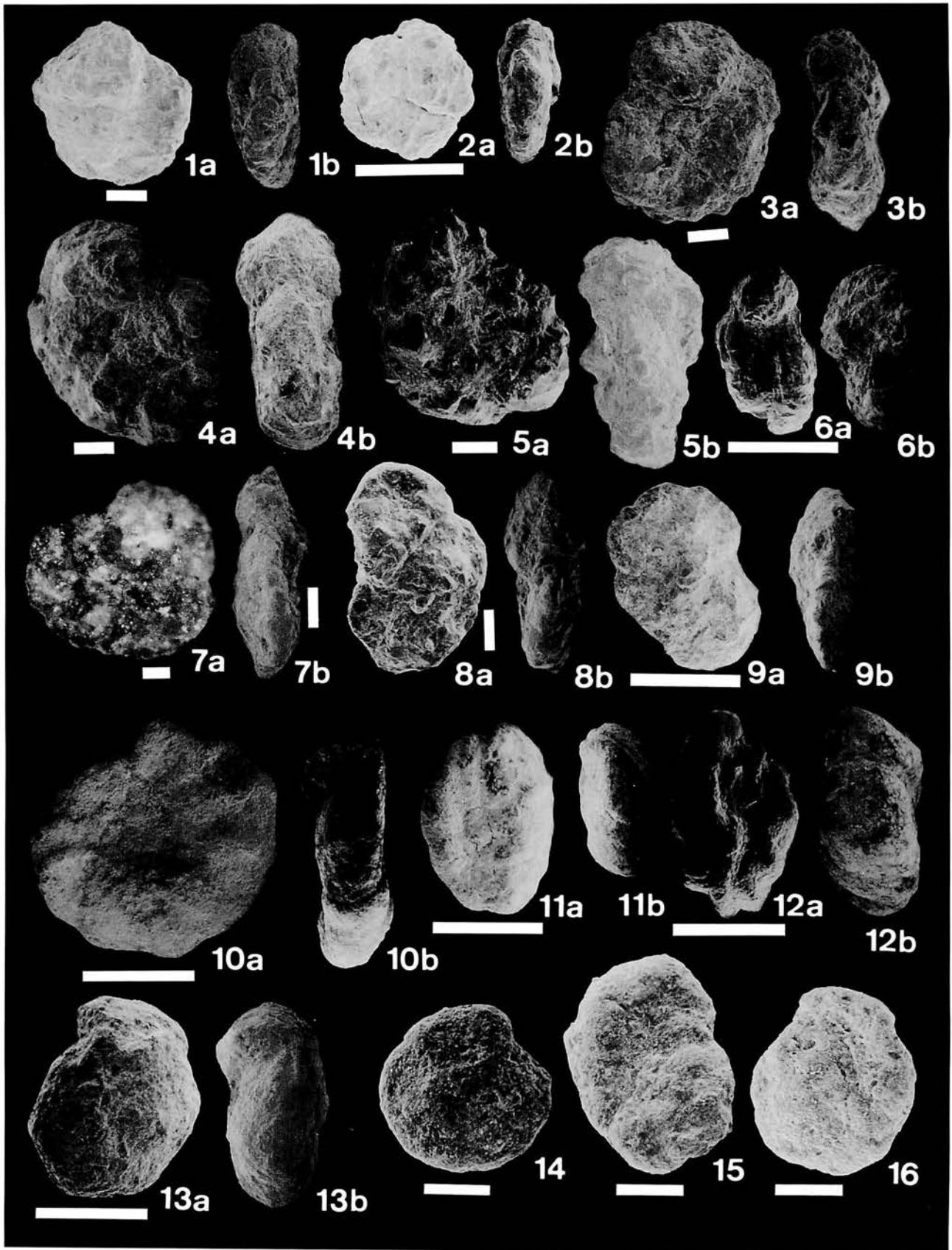
Haplophragmoides subamakusaensis Fukuta, 1962, p. 9, fig. 2, pl. 1, figs. 6-10.

Haplophragmoides subevolutus Kaiho, 1984a, p. 114, pl. 7, figs. 7a, b. —Kaiho, 1992c, pl. 1, figs. 8a, b.

Cribrostomoides sp. A. Yasuda, 1986, p. 51, pl. 3, figs. 9a, b.

Description.—Test free, planispirally enrolled, frequently coiling plane is unstable and sometimes show streptospiral appearance, slightly to completely evolute;

← **Figure 7.** Foraminifera from the Poronai Formation and Ishikari Group appearing in the wells studied. Scale bars equal 100 μ m except figs. 1, 2, 4, 7, 8, 11, 12, 13, and 14, where bars equal 500 μ m. 1. *Bathysiphon eocenica* Cushman and Hanna, from MITI Umaoi, 3840 m. 2. *Bathysiphon vernoni* Hamlin, from Kita-Akebono SK-1D, 3580 m. 3. *Ammodiscus* sp., from Numanohata SK-4D, 3600 m. 4a, b. *Glomospira* sp., from Numanohata SK-4D, 3305 m. 5a, b. *Placentamina* sp. A, from Kita-Akebono SK-1D, 3330 m. 6. *Placentamina* sp. A, from Kita-Akebono SK-1D, 3310 m. 7. *Reophax tappuensis* Asano, from Kita-Akebono SK-1D, 3320 m. 8a-c. *Budashevaella* sp. aff. *B. multicamerata* (Voloshinova), from MITI Umaoi, 4000 m. 9a-c. *Budashevaella symmetrica* (Ujiié and Watanabe), from Numanohata SK-4D, 3240 m. 10a, b. *Budashevaella symmetrica* (Ujiié and Watanabe), from MITI Umaoi, 3720 m. 11a, b. *Cribrostomoides* sp. cf. *C. cretacea* Cushman and Goudkoff, from Numanohata SK-4D, 3340 m. 12a, b. *Cribrostomoides* sp. cf. *C. cretacea* Cushman and Goudkoff, from Kita-Akebono SK-1D, 3250 m. 13a, b. *Haplophragmoides crassiformis* Kaiho, from Numanohata SK-4D, 3660 m. Specimen bilaterally compressed by secondary deformation. 14a, b. *Haplophragmoides crassiformis* Kaiho, from Kita-Akebono SK-1D, 3640 m.



biumbilicate; chambers inflated, 7–12 in final whorl; wall thin, finely agglutinated, exterior smoothly finished; aperture interiomarginal.

Remarks.—This species is assigned to the genus *Evolutinella* because of its evolute planispiral coiling. It is also characterized by numerous chambers and finely agglutinated wall. Ujiié and Watanabe (1960) first reported this species from the Poronai Formation as *Cribrostomoides cf. cretacea* Cushman and Goudkoff. Subsequently, Fukuta (1962) included the form in the synonymy of his *Haplophragmoides subamakusaensis* described from the Kyoragi Formation of the Amakusa Islands, Kyushu, and noted that this species was found also from the Poronai, Akabira and Wakkanabe Formations of the Ishikari Coal field. Later, Kaiho (1984a) described *H. subevolutus* from the Poronai Formation and synonymized *C. cf. cretacea* of Ujiié and Watanabe (1960) without reference to the study of Fukuta (1962). *H. subamakusaensis* and *H. subevolutus* have quite similar morphology and are regarded here as synonyms. Kaiho and Nishi (1989) reported *H. subevolutus* from the Middle Eocene to Early Oligocene Hyuga Group in southern Kyushu without any figures. Thus it is obvious that *E. subamakusaensis* has a broad geographic distribution from Hokkaido to Kyushu, and a long stratigraphic range from the Maastrichtian to lower Oligocene. Kaiho (1984a) included the specimens having numerous chambers, up to 14, in the final whorl in *H. subevolutus*. However, I did not find specimens having more than 13 chambers in the present study. In Figures 8–12, specimens collected from the Kyoragi Formation (not topotypes but collected from near the type locality) are shown for comparison.

Haplophragmoides crassiformis Kaiho (Figure 7.13, 7.14)

Haplophragmoides cf. emaciata (Brady). —Ujiié and Watanabe, 1960, p. 127, pl. 1, figs. 6a, b.

Haplophragmoides crassiformis Kaiho, 1984a, p. 114, pl. 7, figs. 3a, b.

Haplophragmoides rugosus soyaensis Yasuda (Figure 8.3, 8.4)

Haplophragmoides rugosus soyaensis Yasuda, 1986, p. 50, pl. 5, figs. 5a–7c.

Haplophragmoides umbilicatus Kaiho, 1984a, p. 115, pl. 7, figs. 6a, b. (non *Haplophragmoides umbilicatus* Pearcey).

Haplophragmoides apertiumbilicatus Kaiho, 1986, nom. nov.

Remarks.—This species is characterized by its deeply depressed umbilicus, seven inflated chambers in the final whorl, and compact arrangement of chambers. Distinguished from *H. amakusaensis* Asano in possessing curved sutures.

Haplophragmoides tanaii Kaiho (Figure 8.5)

Haplophragmoides tanaii Kaiho, 1984a, p. 115, pl. 7, figs. 5a, b.

Remarks.—This species is characterized by its small test size, coarsely agglutinated wall, and subacute periphery.

H. kushiroensis Asano (1962) described from the Paleogene of eastern Hokkaido has similar morphology in its test size, number of chambers, acute periphery and coarsely agglutinated wall but is supposed to be distinguished by possessing curved sutures.

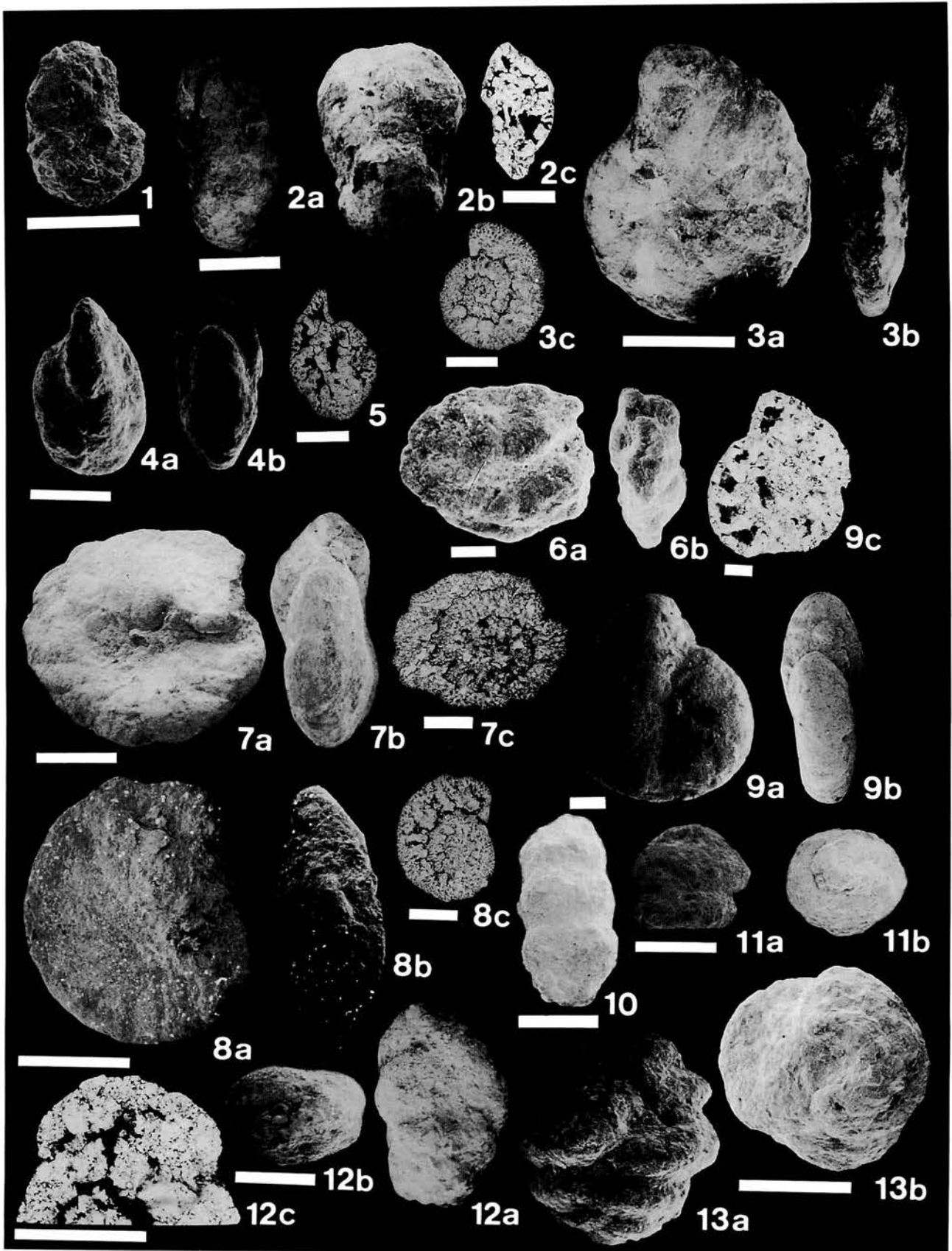
Haplophragmoides yokoyamai Kaiho (Figure 8.1, 8.2)

Haplophragmoides kirki Wickenden; Mallory, 1959, p. 112, pl. 2, figs. 8a, b. —Takayanagi, 1960, p. 72, pl. 2, figs. 3a, b.

Haplophragmoides yokoyamai Kaiho, 1984a, p. 116, pl. 7, figs. 4a, b.

Remarks.—Mallory (1959) first reported this species as *H. kirki* from the Eocene of California. Takayanagi (1960) also reported this species from the Albian to Campanian of Hokkaido as *H. kirki*. Later Kaiho (1984a) described *H. yokoyamai* from the Poronai Formation as new. The holotype of *H. kirki* from the Cretaceous of North America (Wickenden, 1932, p. 85, pl. 1, fig. 1) shows a smaller test, broadly rounded periphery and more finely agglutinated wall compared to *H. yokoyamai*. Furthermore, specimens of Mallory (1959) and Takayanagi (1960) have a compressed test, larger test size and a coarser wall than typical *H. kirki*. Moreover, *H. kirki* is synonymized to *H. excavata* Cushman and Walters by Mello (1971), who added that *H. excavatus* shows such a wide range of morphological variation that *H. kirki* falls within the range of variation of the

← **Figure 8.** Foraminifera from the Poronai Formation and Ishikari Group appearing in the wells studied. Specimens shown for comparison in Figure 12a, b were collected from the Kyoragi Formation. Scale bars equal 100 μ m except figs. 2, 6, 9, 10, 11, 12, and 13, where bars equal 500 μ m. **1a, b.** *Haplophragmoides yokoyamai* Kaiho, from MITI Umaoi, 3840m. Medium-sized specimen. **2a, b.** *Haplophragmoides yokoyamai* Kaiho, from MITI Umaoi, 3840 m. Largest-size specimen. **3a, b.** *Haplophragmoides rugosus soyaensis* Yasuda, from MITI Umaoi, 4160 m. **4a, b.** *Haplophragmoides rugosus soyaensis* Yasuda, from MITI Umaoi, 4160 m. **5a, b.** *Haplophragmoides tanaii* Kaiho, from MITI Umaoi, 4000 m. **6a, b.** *Haplophragmoides* sp. A, from Numanohata SK-4D, 3110 m. **7a, b.** *Haplophragmoides* sp. B, from MITI Umaoi, 4060 m. **8a, b.** *Haplophragmoides* sp. B, from Kita-Akebono SK-1D, 3350 m. **9a, b.** *Haplophragmoides* sp. D, from MITI Umaoi, 3820 m. **10a, b.** *Evolutinella subamakusaensis* (Fukuta), from Numanohata SK-4D, 3600 m. Specimen bilaterally compressed by secondary deformation. **11a, b.** *Evolutinella subamakusaensis* (Fukuta), from Numanohata SK-4D, 3600 m. Specimen vertically compressed by secondary deformation. **12a, b.** *Evolutinella subamakusaensis* (Fukuta), from the Kyoragi Formation. Specimen vertically compressed by secondary deformation. **13a, b.** *Recurvoides* sp. A, from MITI Umaoi, 3920 m. **14–16.** *Recurvoidella* sp. cf. *R. lamella* (Grzybowski), all specimens from Numanohata SK-4D, 3500 m.



former species.

Recurvoidella sp. cf. *R. lamella* (Grzybowski) (Figure 8.14–8.16)
Cf. *Trochammina lamella* Grzybowski, 1898, p. 290, pl. 11, fig. 25.

Cf. *Recurvoidella lamella* (Grzybowski). —Charnock and Jones, 1990, p. 173, pl. 6, figs. 11, 12, pl. 17, fig. 7; Kaminski and Geroch, 1993, p. 263–264, pl. 10, figs. 8, 9.

Remarks.—Most specimens are depressed almost completely.

Budashevaella symmetrica (Ujiie and Watanabe) (Figure 7.9, 7.10)

Trochammina symmetrica Ujiie and Watanabe, 1960, p. 134, pl. 1, figs. 10, 11.

Description.—Test free, medium, early stage compactly streptospiral; the angle between one coiling plane and subsequent one increases as growth proceeds, up to 90° in an adult form, the last whorl and half of the penultimate whorl are visible on the surface in a juvenile form, but the penultimate one becomes almost invisible in the adult, few chambers of penultimate whorl exposed in umbilical area; slightly evolute; chambers not inflated in earlier coil, become slightly inflated, seven to eight in final whorl, increasing slowly in size as added; sutures radial, slightly depressed, limbate; wall finely agglutinated, thick; aperture interiomarginal.

Remarks.—The streptospiral coiling of this species confirms the assignment to the genus *Budashevaella*. This species is similar to *Haplophragmoides subamakusaensis* Fukuta in general appearance but is distinguished by its less inflated chambers, less depressed sutures and streptospiral coiling. It is also distinguished from *Budashevaella* sp. aff. *B. multicamerata* of the present study in having fewer number of chambers in the final whorl.

Budashevaella sp. aff. *B. multicamerata* (Voloshinova) (Figure 7.8)

Aff. *Circus multicameratus* Voloshinova, in Voloshinova and Budasheva, 1961, p. 201, pl. 7, fig. 6, pl. 8, fig. 1.

Budashevaella multicamerata (Voloshinova). — McDougall,

1980, p. 34, pl.3, figs. 4–6.

Diagnosis.—Numerous chambers up to 14 in final whorl. Coiling plane of the last coil lies at about a right angle to that of the penultimate one in the umbilical area.

Remarks.—This form is distinguished from *B. multicamerata* (Voloshinova), originally described as *Circus multicameratus* from the Neogene of Sakhalin, in its broadly rounded periphery.

Reticulophragmium amakusaensis (Fukuta) (Figure 9.9)

Cyclammina amakusaensis Fukuta, 1962, p.12, text-figs. 3a–b, pl. 3, figs. 8–10.

Description.—Test free, medium, planispirally coiled and involute to very slightly evolute, 10–13 chambers in final whorl, whorls increasing rapidly in height; wall finely agglutinated; sutures depressed, straight and radial; slightly biumbilicate; aperture an interiomarginal equatorial slit.

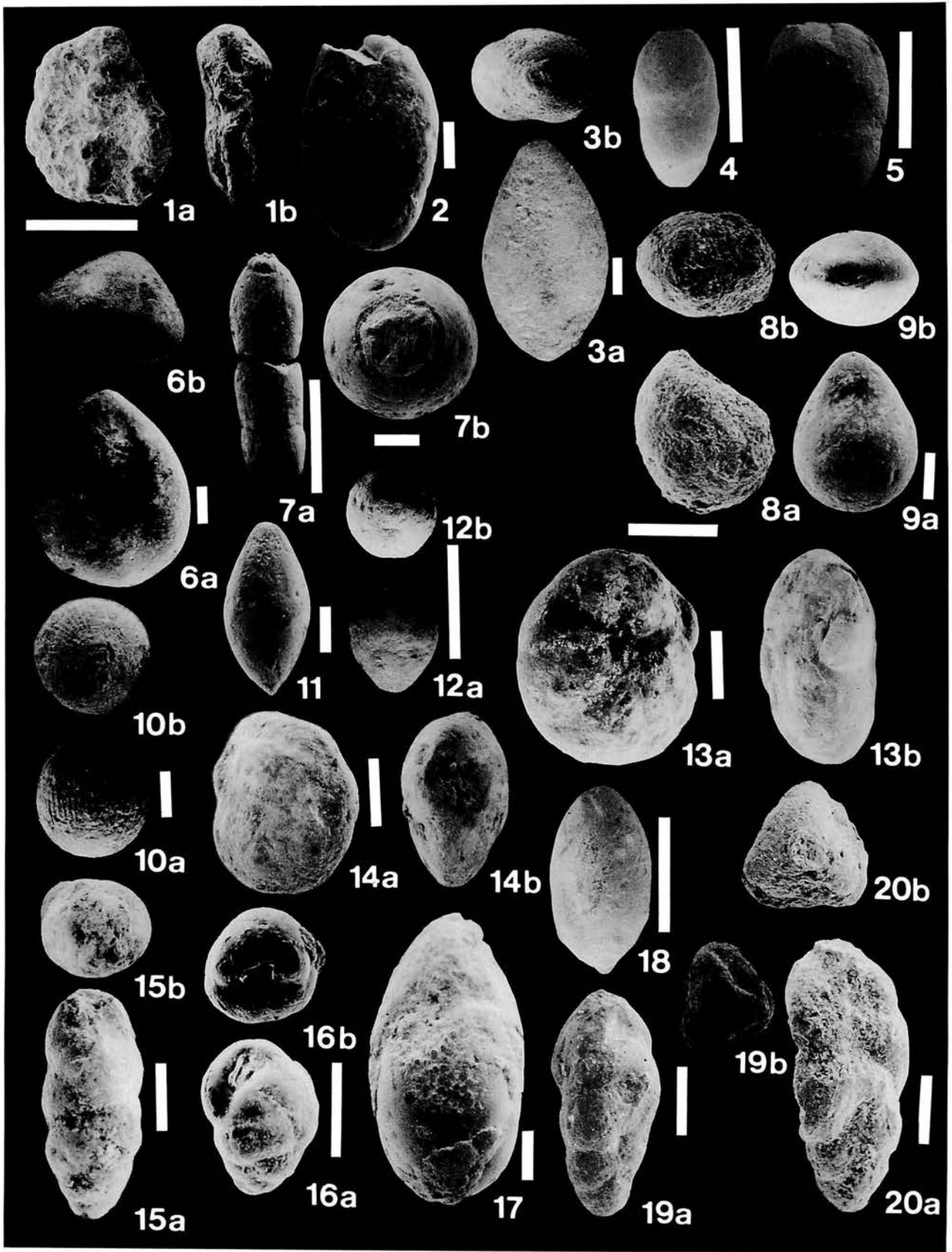
Remarks. This species was originally described from the Kyoragi Formation of the Amakusa Islands, Kyushu, as a species of *Cyclammina*. Because of the position of the aperture and reticulate wall, it is newly assigned to the current genus. Thin section showing a wide cavity in each chamber indicates that development of alveolar structure is quite weak (Figure 9.9c). It commonly occurred in the study sections, although it has never been recorded from the Poronai Formation in surface sections. It is highly possible that the present species has been assigned to other *Cyclammina* species by previous workers.

Cyclammina ezoensis Asano (Figure 9.3)

Cyclammina ezoensis Asano, 1951a, pl. 1, figs. 1a, b. —Asano, 1951b, p. 20, pl. 3, figs. 2a, b. —Ujiie and Watanabe, 1960, pl. 1, fig. 7. —Kaiho, 1984b, p. 45, 46, pl. 1, figs. 21a, b. —Kaiho, 1992b, p. 367, 368, pl. 1, figs. 5a, b.

Remarks.—This species is characterized by a compressed test with thin periphery. It was originally described from the Miocene Masuporo Formation in Hokkaido, and was commonly recovered from the Paleogene as well as Neogene formations of Japan. Neogene specimens sometimes attain much larger diame-

← **Figure 9.** Foraminifera from the Poronai Formation and the Ishikari Group appearing in the wells studied. Scale bars equal 100 µm except figs. 1, 3, 4, 5, 7, 8, 10, 11, 12, and 13, where bars equal 500 µm. **1.** *Ammobaculites* sp., from Kita-Akebono SK-1D, 3430 m. **2a–c.** *Alveolophragmium* sp. A, from MITI Umaoi, 3860 m. **3a–c.** *Cyclammina ezoensis* Asano, from MITI Umaoi, 4410 m. **4a, b.** *Cyclammina pacifica* Beck, from Kita-Akebono SK-1D, 3075 m. **5.** *Cyclammina pacifica* Beck, from Numanohata SK-4D, 3220 m. **6a, b.** *Cyclammina* sp. aff. *C. pusilla* Brady, from Kita-Akebono SK-1D, 3260 m. **7a–c.** *Cyclammina* sp., from Numanohata SK-4D, 3240 m. Note that this specimen has 15 chambers in the final whorl. **8a–c.** *Cyclammina* sp., from Numanohata SK-4D, 3760 m. Note that this specimen has 15 chambers and a bilaterally compressed test. **9a–c.** *Reticulophragmium amakusaensis* (Fukuta), from MITI Umaoi, 3740 m. **10.** “*Clavulina*” sp. from MITI Umaoi, 4060 m. **11a, b.** Fragment of last chamber of “*Clavulina*”-like species, from MITI Umaoi, 4060 m. Note the characteristic large cone-shaped last chamber. **12a–c.** *Poronaiia poronaiensis* (Asano), from Numanohata SK-4D, 3240 m. **13a, b.** *Poronaiia poronaiensis* (Asano), from Kita-Akebono SK-1D, 3210 m.



ters, as much as 4 mm, but commonly have fewer chambers in comparison with the Paleogene specimens.

Cyclammina pacifica Beck (Figure 9.4, 9.5)

Cyclammina pacifica Beck, 1943, pl. 98, figs. 2, 3. —Asano, 1952, p. 33, pl. 3, figs. 1a, b, 2, pl. 5, figs. 11a, b. —Asano, 1958, pl. 13, fig. 3. —Kaiho, 1992b, p. 368, pl. 1, figs. 6a, b.

Cyclammina cf. *pacifica* Beck. —Asano, 1951a, p. 7, figs. 24, 25. —Asano, 1951b, p. 20–21, pl. 3, figs. 5a, b. —Fukuta, 1962, p. 11, pl. 3, figs. 1–3. —Kaiho, 1984b, p. 46, pl. 2, figs. 1a, b.

Remarks.—This species has been commonly recorded from various Neogene and Paleogene formations throughout Japan. It shows compact arrangement of chambers. Although alveolar structure is rather poorly developed in the figured specimen (Figure 9.5), degree of development of alveolar structure varies among specimens.

Cyclammina sp. aff. *C. pusilla* Brady (Figure 9.6)

Aff. *Cyclammina pusilla* Brady, 1881, p. 53; Type figures: Brady, 1884, pl. 37, figs. 20–23.

Cyclammina pusilla Brady. —Kaiho, 1984b, p. 46, pl. 2, figs. 2a, b.

Remarks.—Specimens from the Poronai Formation have a smaller test size and subacute periphery, and are therefore distinguished from *C. pusilla*.

Poronai poronaiensis (Asano) (Figure 9.12, 9.13)

Plectina poronaiensis Asano, 1952, p. 33, 34, pl. 4, figs. 12, 13. —Asano, 1958, pl. 13, figs. 5–7. —Fukuta, 1962, p. 16, pl. 5, figs. 4, 5.

Poronai poronaiensis (Asano). —Ujiié and Watanabe, 1960, p. 133, 134, pl. 2, figs. 1–8.

Plectotrochammina poronaiensis (Asano). —Loeblich and Tappan, 1964, p. 279. —Kaiho, 1984b, p. 48, pl. 2, figs. 10a–d.

Description.—Test free, short and broadly cylindrical, lower trochospiral in the early stage with four chambers,

later biserial, each chambers imbricating to penultimate chambers; chambers inflated; wall finely agglutinated but occasionally includes coarse grains, internally imperfect alveolar structure developed; aperture, interiomarginal opening.

Remarks.—Specimens were occasionally deformed considerably. Loeblich and Tappan (1964) regarded the genus *Poronai* as a junior synonym of *Plectotrochammina*, and later assigned both genera to their list of “Genera of Uncertain Status” (Loeblich and Tappan, 1987). However, *Poronai* should be included in the family Textulariellidae because of possessing alveoli-like labyrinthic structure inside the test, while both *Plectina* and *Plectotrochammina* have a simple wall.

Trochammina sp. cf. *T. asagaiensis* Asano (Figure 10.1)

Cf. *Trochammina asagaiensis* Asano, 1949, p. 475, text-figs. 2a–4b.

Trochammina asagaiensis Asano. —Kaiho, 1984b, p. 47, pl. 2, figs. 5a–6b.

Remarks.—This species is characterized by its very low trochospiral and compressed test. However, specimens examined in this study and the specimens of Kaiho (1984b) show low trochospiral, obscure earlier whorls and inflated chambers compared to *T. asagaiensis*.

Quinqueloculina seminula compacta Serova (Figure 10.2)

Quinqueloculina seminulum (Linné) var. *compacta* Serova, 1960, pl. 3, figs. 7a–c.

Quinqueloculina weaveri Rau. —McDougall, 1980, p. 37, pl. 5, figs. 5–7.

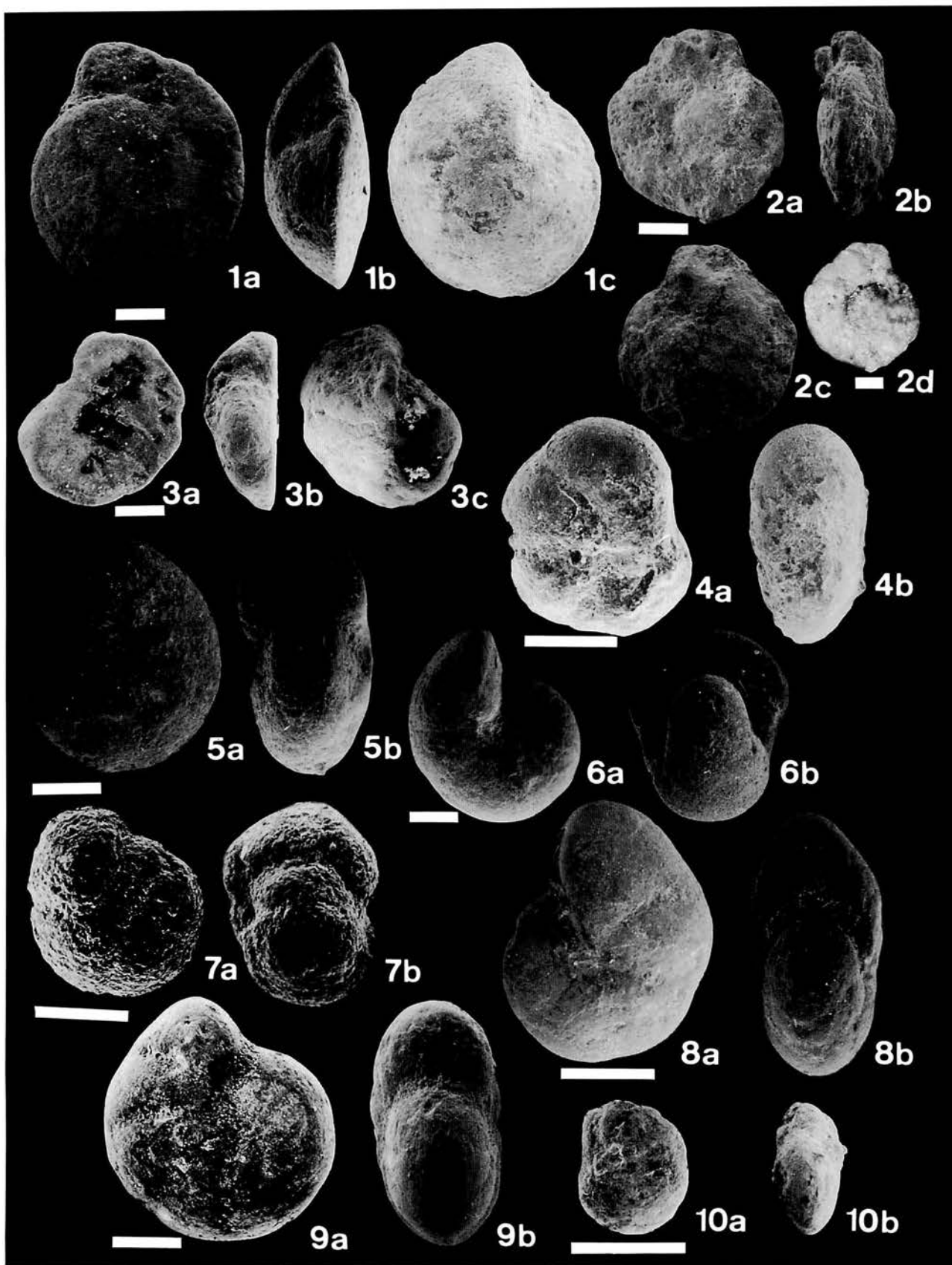
Quinqueloculina cf. *seminula compacta* Serova. —Kaiho, 1984b, p. 49, pl. 2, figs. 12a–c.

Dentalina sp. cf. *D. subsoluta* (Cushman) (Figure 10.7)

Cf. *Nodosaria subsoluta* Cushman, 1923, p. 74, pl. 13, fig. 1.

Dentalina cf. *subsoluta* (Cushman). —Kaiho, 1984b, p. 50–51, pl. 3, fig. 3. —Kaiho, 1992b, p. 373–374, pl. 1, fig. 14.

◀ **Figure 10.** Foraminifera from the Poronai Formation and Ishikari Group appearing in the wells studied. Scale bars equal 100 μ m except figs. 1, 4, 5, 7a, 12, and 18, where bars equal 500 μ m. **1a, b.** *Trochammina* sp. cf. *T. asagaiensis* Asano, from Numanohata SK-4D, 3220 m. **2.** *Quinqueloculina seminula compacta* Serova, from Numanohata SK-4D, 3260 m. **3a, b.** *Guttulina takayanagii* Kaiho, from Numanohata SK-4D, 3460 m. **4.** *Pseudopolymorphina* sp. A, from Numanohata SK-4D, 3285m. **5.** *Pseudonodosaria* sp. cf. *P. conica* (Neugeboren), from Numanohata SK-4D, 3305 m. **6a, b.** *Sigmoidella pacifica* (Cushman and Ozawa), from Numanohata SK-4D, 3400 m. **7a, b.** *Dentalina* sp. cf. *D. subsoluta* (Cushman), from Kita-Akebono SK-1D, 3360 m. **8a, b.** *Lenticulina* sp., from Kita-Akebono SK-1D, 3600 m. **9a, b.** *Fissurina* sp. cf. *F. marginata* (Montagu), from Kita-Akebono SK-1D, 3420 m. **10a, b.** *Lagena striata* (d’Orbigny), from MITI Umaoi, 3940 m. **11.** *Procerolagena* sp. cf. *P. gracilima* (Seguenza), from Kita-Akebono SK-1D, 3190 m. **12a, b.** *Glandulina laevigata ovata* Cushman and Applin, from Numanohata SK-4D, 3120 m. **13a, b.** *Globocassidulina globosa* (Hantken), from Numanohata SK-4D, 3240 m. **14a, b.** *Globocassidulina globosa* (Hantken), from Numanohata SK-4D, 3120 m. **15a, b.** *Bulimina schwageri* Yokoyama, from Numanohata SK-4D, 3120 m. **16a, b.** *Bulimina schwageri* Yokoyama (juvenile form), from Kita-Akebono SK-1D, 3120 m. **17.** *Globobulimina* sp., from MITI Umaoi, 4120 m. **18.** *Praeglobobulimina pyrula* (d’Orbigny), from Numanohata SK-3D, 3720 m. **19a, b.** *Angulogerina hannai* Beck, from MITI Umaoi, 3700 m. **20a, b.** *Angulogerina hannai* Beck, from MITI Umaoi, 3700 m.



- Pseudonodosaria* sp. cf. *P. conica* (Neugeboren) (Figure 10.5)
 Cf. *Pseudonodosaria conica* (Neugeboren). —McDougall, 1980, p. 36, pl. 9, figs. 7, 8. —Kaiho, 1992b, p. 374, figs. 17a, b.
 Cf. *Pseudoglandulina obtusissima* (Reuss). —Yoshida, 1957, p. 64, text-figs. 3–9.
 Cf. *Pseudonodosaria shitakaraensis* Kaiho, 1984a, p. 118, pl. 8, figs. 1a, b.
- Lagena striata* (d'Orbigny) (Figure 10.10)
Oolina striata d'Orbigny, 1839, p.21, pl. 5, fig.12.
Lagena becki Sullivan. —McDougall, 1980, p. 35, pl. 7, figs. 1, 4.
Lagena striata (d'Orbigny). —Kaiho, 1984b, p. 51, 52, pl. 3, figs. 13a, b. —Kaiho, 1992b, p. 377, pl. 2, fig. 7.
- Lagena* sp. cf. *L. laevis* (Montagu)
 Cf. *Vermiculum laeve* Montagu, 1803, p. 524; Type figure: Walker and Boys, 1784, pl. 1, fig. 9, as *Serpula* (*Lagena*) *laevis ovalis*.
Lagena laevis (Montagu). —Kaiho, 1984b, p. 51, pl. 3, figs. 11–13.
- Remarks.*—Specimens of this study have similar features to those of Kaiho (1984b), but are distinguished from the Recent *L. laevis* in its shorter test.
- Procerolagena* sp. cf. *P. gracillima* (Seguenza) (Figure 10.11)
 Cf. *Amphorina gracillima* Seguenza, 1862, p. 51, pl. 1, fig. 37.
Lagena gracillima (Seguenza). —Kaiho, 1984b, p. 51, pl. 3, figs. 10a, b.
 Cf. *Procerolagena gracillima* (Seguenza). —Jones, 1994, p. 62, figs. 19–22, 24–29.
- Remarks.*—This species is quite similar to *L. gracillima* of Kaiho (1984b), but different from the Recent *P. gracillima* in its shorter test.
- Guttulina takayanagii* Kaiho (Figure 10.3)
Guttulina takayanagii Kaiho, 1984a, p. 120, pl. 8, figs. 5a–d.
- Pseudopolymorphina hokkaidoana* Kaiho
Pseudopolymorphina hokkaidoana Kaiho, 1984a, p. 120, figs. 8a–c.
- Sigmoidella pacifica* (Cushman and Ozawa) (Figure 10.6)
Guttulina (*Sigmoidina*) *pacifica* Cushman and Ozawa, 1928, p. 19, pl. 2, fig. 13.
Guttulina cf. *pacifica* Cushman and Ozawa. —Fukuta, 1962, p. 23, pl. 7, figs. 9–10.
Sigmoidella pacifica Cushman and Ozawa. —Kaiho, 1984b, p. 58, fig. 53, pl. 4, figs. 12a–d.
- Remarks.*—This species is known from the Eocene formations from Kyushu to Hokkaido. It is common in the shallow marine facies in the lower part of the Poronai Formation, as discussed earlier. Since *S. pacifica* is also known from Recent shallow marine environments, it appears not to have changed habitat from the Eocene until the Recent. Although Jones (1994) regarded this species as a junior synonym of *Polymorphina elegantissima* Parker and Jones, I think these two species are distinguishable in the aspect of number of chambers visible from the the outside of the test.
- Fissurina* sp. cf. *F. marginata* (Montagu) (Figure 10.9)
 Cf. *Vermiculum marginatum* Montagu, 1803, p. 524; Type figure: Walker and Boys, 1784, pl. 1, fig. 7.
 Cf. *Fissurina marginata* (Montagu). —Loeblich and Tappan, 1953, p. 77, pl. 14, figs. 6–9.
- Glandulina laevigata ovata* Cushman and Applin (Figure 10.12)
Nodosaria (*Glandulina*) *laevigata* d'Orbigny var. *ovata* Cushman and Applin, 1926, p. 443, pl. 7, figs. 12, 13.
Glandulina laevigata ovata Cushman and Applin. —Ujiié and Watanabe, 1960, p. 129, 130, pl. 2, figs. 11, 12. —Kaiho, 1984b, pl.4, figs. 15a–c.
- Globocassidulina globosa* (Hantken) (Figure 10.13, 10.14)
Cassidulina globosa Hantken, 1875, p. 64, pl. 16, fig. 2.
Globocassidulina globosa (Hantken). —Kaiho, 1992b, p. 378, pl. 2, figs. 11a, b, pl. 5, figs. 17a, b.
- Bulimina schwageri* Yokoyama (Figure 10.15, 10.16)
Bulimina schwageri Yokoyama, 1890, p. 190, pl. 24, figs. 6–8. —Ujiié and Watanabe, 1960, pl. 2, figs. 16, 17, 18. —Kaiho, 1984b, p. 62–63, pl. 5, figs. 11–15. —Kaiho, 1992b, p. 379, pl. 3, figs. 2a, b.
Caucasina schwageri (Yokoyama). —Serova, 1976, p. 324, 325, pl. 1, figs. 6a–c.

◀ **Figure 11.** Foraminifera from the Poronai Formation and Ishikari Group appearing in the wells studied. Scale bars equal 100 μ m except fig. 10 where bar equals 500 μ m. **1a–c.** *Heterolepa poronaiensis* Kaiho, from Kita-Akebono SK-1D, 3340 m. **2a–d.** *Cibicides elmaensis* Rau, from Numanohata SK-3D, 3720 m. **3a–c.** *Cibicides* sp. A, from Kita-Akebono SK-1D, 3540 m. **4a, b.** *Nonionella japonica* (Yokoyama), from MITI Umaoi, 4000 m. **5a, b.** *Melonis affinis* (Reuss), from Numanohata SK-4D, 3340 m. **6a, b.** *Melonis pompilioides* (Fichtel and Moll), from Numanohata SK-4D, 3260 m. **7a, b.** *Pullenia eocenica* Cushman and Siegfus, from MITI Umaoi, 3980 m. **8a, b.** *Pullenia salisburyi* R. E. and K. C. Stewart, from Numanohata SK-4D, 3240 m. **9a, b.** *Criboelphidium sorachiense* (Asano), from Numanohata SK-3D, 3720 m. **10a, b.** *Criboelphidium ishikariense* (Kaiho), from Numanohata SK-3D, 3800 m.

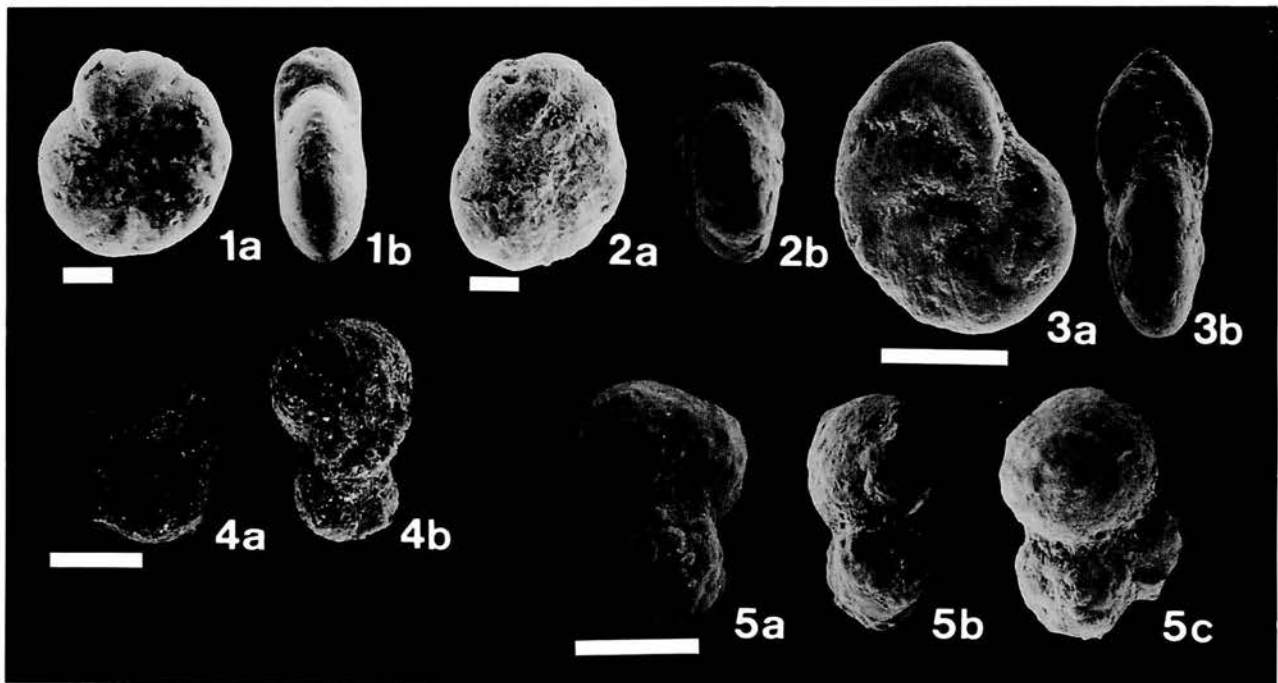


Figure 12. Foraminifera from the Poronai Formation and Ishikari Group appearing in the wells studied. Scale bars equal 100 μm . **1a, b.** *Criboelphidium wakkanabense* (Kaiho), from Numanohata SK-4D, 3240 m. **2a, b.** *Criboelphidium wakkanabense* (Kaiho), from Numanohata SK-3D, 3700 m. **3a, b.** *Criboelphidium* sp. from Kita-Akebono SK-1D, 3410 m. Note that this specimen shows subacute periphery. **4a, b.** Planktonic foraminifera genus and species indeterminate, from MITI Umaoi, 4120 m. **5a-c.** *Subbotina* sp., from Kita-Akebono SK-1D, 3440 m.

Remarks. — This species has been recorded from Hokkaido to Kamchatka. As discussed by Kaiho (1984b), *B. schwageri* has three to four chambers in the first whorl, and is distinguished from the species of *Caucasina* which always have four chambers in the final whorl. Even if there is a phylogenetic relationship between *B. schwageri* and *Caucasina* species as pointed out by Serova (1976), emendation by reexamination of the type species of the genus *Caucasina* is necessary.

Praeglobobulimina pyrula (d'Orbigny) (Figure 10.18)

Bulimina pyrula d'Orbigny, 1846, p. 184, pl. 11, figs. 9, 10.
—Asano, 1952, p. 41, figs. 10a, b. —Kaiho, 1984b, p. 62, pl. 5, figs. 10a-c.

Praeglobobulimina* sp. cf. *P. ovata (d'Orbigny)

Cf. *Bulimina ovata* d'Orbigny, 1846, p. 185, pl. 11, figs. 13, 14.
Praeglobobulimina ovata (d'Orbigny). —Kaiho, 1984b, pl. 6, fig. 2. —Kaiho, 1992b, pl. 3, fig. 5.

Angulogerina hannai Beck (Figure 10.19, 10.20)

Angulogerina hannai Beck, 1943, p. 607, pl. 108, figs. 26, 28.
Trifarina cushmani Todd and Knifer, 1952, p. 23, pl. 4, figs. 6a, b.
Trifarina maiyai Kaiho, 1984a, p. 122, 123, pl. 9, figs. 7a, b.

Trifarina hannai (Beck). —Kaiho, 1992b, p. 380, pl. 3, figs. 7a, b.

Remarks. — Relationship between *T. maiyai* and *T. hannai* follows the study of Kaiho (1992b). *T. cushmani* was originally reported from the Eocene in Chile and also reported from the Poronai Formation by Maiya (1979). Although Maiya (1979) did not figure any specimens, observation of his specimens by the present author revealed that they are conspecific with *A. hannai*. I regard *T. cushmani* as a junior synonym of *A. hannai* because of their similarity in morphology, such as test size and subacute periphery, on the basis of the original illustration by Todd and Knifer (1952).

Cibicides elmaensis Rau (Figure 11.2)

Cibicides elmaensis Rau, 1948, p. 173, pl. 31, figs. 18-26.
—Fukuta, 1962, p. 25, pl. 8, figs. 3a, b, 7a, b.
Cibicides biconbexus Kaiho, 1984a, p. 124, pl. 9, figs. 7a-c.
? *Cibicides yabei* Asano, 1952, p. 43, pl. 4, figs. 1a-c.

Remarks. — *Cibicides yabei* Asano (1952) was described from the basal part of the Poronai Formation, but was not recorded by Kaiho (1984a, b) who studied the same formation in the same area. As discussed by Asano (1952), *C.*

yabei is distinguished from *C. elmaensis* in lacking shell material filling the umbilical area, but I think that this is insufficient to separate *C. yabei* as a different species.

Nonionella japonica (Yokoyama) (Figure 11.4)

Pilvulineria japonica Yokoyama, 1890, p. 192, pl. 24, figs. 15 a-c.

Nonionella japonica (Yokoyama). —Ujiié and Watanabe, 1960, p. 131, pl. 3, figs. 4a-c. —Kaiho, 1984b, p. 72, pl. 7, figs. 4a-c.

Melonis affinis (Reuss) (Figure 11.5)

Nonionina affinis Reuss, 1851, p. 72, pl. 5, figs. 32a, b.

Nonion aimonoi Matsunaga, 1963, p. 109, pl. 37, figs. 2a, b.

Melonis crassus Kaiho, 1984a, p., pl. 2, figs. 6a, b, 129. —Kaiho, 1992b, p. 383, pl. 4, figs. 6a, b.

Melonis pompilioides (Fichtel and Moll) (Figure 11.6)

Nautilus pompilioides Fichtel and Moll, 1798, p. 31, pl. 2, figs. a-c.

Nonion pompilioides shimokinense Asano, 1958, p. 71, pl. 13, figs. 14a, b.

Melonis pompilioides (Fichtel and Moll). —Kaiho, 1984b, p. 74, figs. 12a, b. —Kaiho, 1992b, p. 383, pl. 4, figs. 7a, b, pl. 6, figs. 5a, b.

Remarks.—Recent *Melonis pompilioides* lives in water deeper than the middle bathyal zone around Japan (Akimoto and Hasegawa, 1989). However, in the Poronai Formation, this species occurred in shallow marine fossil assemblages. The Paleogene *M. pompilioides* has a larger test than the Neogene specimens but in other biometrical aspects it fits the Recent *M. pompilioides* studied by Hasegawa (1983).

Pullenia eocenica Cushman and Siegfus (Figure 11.7)

Pullenia eocenica Cushman and Siegfus, 1939, p. 31, pl. 7, figs. 1a, b. —Asano, 1958, pl.11, figs. 13a, b.

Pullenia cf. *quinqueloba angusta* Cushman and Todd. —Fukuta, 1962, p. 25, pl. 8, figs. 4a, b.

Pullenia compressiuscula Reuss. —Ujiié and Watanabe, 1960, p. 131, pl. 3, Fig. 5.

Remarks.—This species is distinguished from *P. compressiuscula* and *P. quinqueloba angusta* in having a broadly rounded periphery and fewer chambers in the final whorl. All specimens examined in this study are replaced with pyrite.

Pullenia salisburyi R. E. and K. C. Stewart (Figure 11.8)

Pullenia salisburyi R. E. and K. C. Stewart, 1930, p. 72, pl. 8, figs. 2a, b. —Asano, 1958, pl. 8, fig. 17. —Ujiié and Watanabe, 1960, p. 15, pl. 3, fig. 5. —Kaiho, 1984b, p. 72, pl. 7, figs. 7a,

b.

Remarks.—There are many records of this species around the North Pacific region, ranging in age from the Eocene to Recent. There has, however, been confusion among researchers on the relationship between *P. salisburyi* and *P. subcarinata* (d'Orbigny), which was originally described as *Nonionina subcarinata*. This study follows the views of the previous workers of the Japanese Paleogene.

Heterolepa poronaiensis Kaiho (Figure 11.1)

Heterolepa poronaiensis Kaiho, 1984a, p. 128, pl. 11, figs. 5a-c, 7a-c.

Criboelphidium ishikariense (Kaiho) (Figure 11.10)

Elphidium ishikariense Kaiho, 1984a, p. 125, pl. 10, figs. 2a, b.

Remarks.—This is the first record of this species from the Poronai Formation.

Criboelphidium sorachiense (Asano) (Figure 11.9)

Nonion sorachiense Asano, 1954, p. 48, figs. 4a-5c.

Elphidium sorachiense (Asano). —Ujiié and Watanabe, 1960, p. 132, pl.3, figs. 11, 12. —Kaiho, 1984b, p. 70, 71, pl. 6, figs. 12a, b.

Criboelphidium wakkanabense (Kaiho) (Figure 12.1, 12.2)

Elphidium asanoi Kaiho, 1984a, p. 124, 125, pl. 10, figs. 1a, b. (non *E. asanoi* Matsunaga, 1963)

Elphidium wakkanabense Kaiho, 1992a, nom. nov. p.143.

Remarks.—This species was originally described from the Wakkanabe Formation, Ishikari Group as *Elphidium asanoi*, and was first recorded from the Poronai Formation in the present study. *Elphidium wakkanabense* was proposed as a new name replacing *E. asanoi* Kaiho. The homonymic relationship with *E. asanoi* Matsunaga (1963) is still a primary one even though Matsunaga's species has features which cause me to remove it to the genus *Criboelphidium* based on my observation of Neogene specimens.

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Appendix 1. Distributions of foraminifera in the

		*1 : Barren Foraminifera ; *2 : <i>Bulimina schwageri</i> - <i>Angulogerina hannai</i> ; *3 : Minaminaganuma Formation																															
well name		Numanohata SK-3D																	Numanohata														
Depth of Formation boundary (wireline depth in meter)		3649.0m								3804m									3070.5m														
Formation		*3 Poronai Formation								Ishikari Group									*3														
Assemblage Zone		*1 *2 <i>G. subgl.-C. sorachi.</i> <i>E. subamakusaensis</i> - <i>H. crassiformis</i> *1																	*1 <i>Bulimina schwageri</i> -A														
Sample Depth (drilling depth in meter)		3640	3660	3680	3700	3720	3740	3760	3780	3800	3820	3840	3860	3880	3900	3920	3940	3960	3980	3060	3080	3100	3110	3120	3140								
Ostracoda																																	
AGGLUTINATED																																	
<i>Bathysiphon</i>	<i>eocenica</i> Cushman and Hanna																		1														
? <i>Ammodiscus</i>	sp. indet.																											1					
<i>Glomospira</i>	sp.																																
<i>Cribrostomoides</i>	sp. cf. <i>C. cretacea</i> Cushman and Goudkoff																											1					
<i>Evolutinella</i>	<i>subamakusaensis</i> (Fukuta)																		6									2					
<i>Evolutinella</i>	sp. cf. <i>E. subamakusaensis</i> (Fukuta)																		1														
<i>Haplophragmoides</i>	<i>crassiformis</i> Kaiho																		2									3					
<i>Haplophragmoides</i>	<i>rugosus soyaensis</i> Yasuda																		1									1					
<i>Haplophragmoides</i>	sp. cf. <i>H. rugosus soyaensis</i> Yasuda																		1														
<i>Haplophragmoides</i>	<i>tanaii</i> Kaiho	2																															
<i>Haplophragmoides</i>	sp. cf. <i>H. tanaii</i> Kaiho																											1					
<i>Haplophragmoides</i>	sp. A																																
<i>Haplophragmoides</i>	sp. B	4																	1														
<i>Haplophragmoides</i>	sp. D																											2					
<i>Haplophragmoides</i> *	spp.	18																	9									10					
<i>Budashaevella</i>	sp. aff. <i>B. multicaemata</i> (Voloshinova)																																
<i>Budashaevella</i>	<i>symmetrica</i> (Ujije and Watanabe)																											3					
<i>Budashaevella</i>	sp. cf. <i>B. symmetrica</i> (Ujije and Watanabe)																											3					
<i>Budashaevella</i>	sp. indet.																																
<i>Recurvoidella</i>	sp. cf. <i>R. lamella</i> (Grzybowski)																		1									13					
<i>Reticulophragmium</i>	<i>amakusaensis</i> (Fukuta)																		2									2					
<i>Reticulophragmium</i>	sp. cf. <i>R. amakusaensis</i> (Fukuta)																																
<i>Cyclammina</i>	<i>ezoensis</i> Asano																		3														
<i>Cyclammina</i>	sp. cf. <i>C. ezoensis</i> Asano																		2									1					
<i>Cyclammina</i>	<i>pacifica</i> Beck	1																	1														
Cyclaminidae genus et sp. indet.																			3									9					
<i>Poronaiia</i>	<i>poronaiensis</i> (Asano)																		1														
<i>Poronaiia</i>	sp. cf. <i>P. poronaiensis</i> (Asano)																		1														
<i>Trochammina</i>	sp. cf. <i>T. asagaiensis</i> Asano	4																	1									11					
Trochaminidae genus et sp. indet.		4																	10									5					
Agglutinated miscellaneous		36																	24									52					
PORCELLANEOUS																																	
<i>Quinqueloculina</i>	<i>seminula compacta</i> Serova																																
<i>Quinqueloculina</i>	sp. indet.																											1					
CALCAREOUS HYALINE																																	
? <i>Dentalina</i>	spp.																		1														
<i>Pseudonodosaria</i>	sp. cf. <i>P. conica</i> (Neugeboren)																																
<i>Pseudonodosaria</i>	sp. indet.																																
<i>Lagena</i>	sp. cf. <i>L. laevis</i> (Montagu)	1																															
<i>Procerolagena</i>	sp. cf. <i>P. gracilima</i> (Seguenza)																																
<i>Guttulina</i>	<i>takayanagii</i> Kaiho																																
<i>Guttulina</i>	sp. cf. <i>G. takayanagii</i> Kaiho																																
<i>Pseudopolymorphina</i>	sp. A																																
<i>Sigmoidella</i>	<i>pacifica</i> Cushman and Oazwa																																
Polymorphinidae genus et sp. indet.																			1									2					
<i>Fissurina</i>	sp. cf. <i>F. marginata</i> (Montagu)																											1					
<i>Glandulina</i>	<i>laevigata ovata</i> Cushman and Applin																		1														
<i>Glandulina</i>	sp. indet.																		2									1					
<i>Globocassidulina</i>	<i>globosa</i> (Hantken)	1																	1									1					
<i>Globocassidulina</i>	spp.	1																	1									1					
<i>Bulimina</i>	<i>schwageri</i> Yokoyama	1																										16					
<i>Praeglobobulimina</i>	sp. cf. <i>P. ovata</i> (d'Orbigny)																											3					
<i>Praeglobobulimina</i>	<i>pyrula</i> d'Orbigny	2																	1									1					
<i>Praeglobobulimina</i>	sp. indet.																																
Buliminidae genus et sp. indet.																												1					
<i>Angulogerina</i>	<i>hannai</i> Beck																																
<i>Cibicides</i>	<i>elmaensis</i> Rau	2																	1									1					
<i>Melonis</i>	<i>affinis</i> (Reuss)																																
<i>Melonis</i>	<i>pompilioides</i> (Fichtel and Moll)	1																	2									3					
<i>Melonis</i>	sp. indet.																											1					
<i>Pullenia</i>	<i>eocenica</i> Cushman and Siegfus																											1					
<i>Pullenia</i>	<i>salisburyi</i> R.E. and K.C. Stewart																																
<i>Cribrorophidium</i>	<i>ishikariense</i> (Kaiho)																											1					
<i>Cribrorophidium</i>	<i>sorachiense</i> (Asano)	17																	3									15					
<i>Cribrorophidium</i>	sp. cf. <i>C. sorachiense</i> (Asano)	6																	20									13					
<i>Cribrorophidium</i>	<i>wakkanabense</i> Kaiho	1																	12									2					
<i>Cribrorophidium</i>	spp.	13																	4									3					
Calcareous miscellaneous		4																	2									1					
Percentage of Agglutinated Foraminifera		10	56	80	78	82	73	76	79	71	79	67	70	50	80	0	100																
Percentage of Porcellaneous Foraminifera		0	0	0	0	0	0	0	0	0	1.2	0	0	0	0	0	0	0															
Percentage of Calcareous Foraminifera		90	44	20	22	18	27	24	21	29	20	33	30	50	20	100	0																
Total population of Foraminifera		10	79	74	89	117	187	153	201	451	86	15	10	6	5	1	2																
Diversity (Species Richness)		4	4	10	5	5	5	3	7	3	4	3	0	2	2	1	1																
Diversity (Simpson's Index for Diversity)		3.6	1.7	7.4	1.6	2.7	2.5	3	3.5	1.9	3.6	2.8	1.8	1.8	1	1	1																

		*1 Barren foraminifera; *2 Minaminaganuma Formation																							
well name		KITA-AKEBONO SK-1D																							
Depth of Formation boundary (wireline depth in meter)		3067.0m																							
Formation		*2 Poronai Formation																							
Assemblage Zone		*1 Rare foraminifera										Bulimina schwageri - Angulogerina hanna													
Sample Depth (drilling depth in meter)		3060	3075	3080	3100	3120	3140	3150	3160	3170	3180	3190	3200	3210	3220	3230	3240	3250	3260	3270	3280	3290	3300	3310	3320
Ostracoda								1																	
Subbolina		PLANKTONIC																							
?PLANKTONIC miscellaneous		sp. indet.																							
		AGGLUTINATED																							
Bathysiphon		eocenica Cushman and Hanna																							
Bathysiphon		veroni Hamlin																							
?Bathysiphon		sp.																							
Placentalmina		sp. A																							
Ammodiscus		spp.																							
Glomospira		spp.																							
Reophax		tappuensis Asano																							
Reophax		sp. cf. R. tappuensis Asano																							
Reophax		sp.																							
Cnbrostomoides		sp. cf. C. cretacea Cushman and Walters																							
Evolutilinella		subarnakusensis (Fukuta)																							
Evolutilinella		sp. cf. E. subarnakusensis (Fukuta)																							
Haplophragmoides		crassiformis Kaiho																							
Haplophragmoides		sp. cf. H. crassiformis Kaiho																							
Haplophragmoides		rugosus soyaensis Yasuda																							
Haplophragmoides		sp. cf. H. tanaii Kaiho																							
Haplophragmoides		yokoyamai Kaiho																							
Haplophragmoides		sp. A																							
Haplophragmoides		sp. B																							
Haplophragmoides		sp. D																							
Haplophragmoides		spp.																							
Discammina		sp. indet.																							
Gudashvevella		sp. aff. B. multicameratus (Voloshinova)																							
Gudashvevella		symmetrica (Ujia and Watanabe)																							
Recurvoides		sp. A																							
Recurvoides		spp.																							
Recurvoidella		sp. cf. R. lamella (Grzybowski)																							
?Ammobaculites		spp.																							
*Clavulina *		sp. indet.																							
Alveolophragmium		spp.																							
Reticulophragmoides		amakusaensis (Fukuta)																							
Cyclamina		ezoensis Asano																							
Cyclamina		pacific Beck																							
Cyclamina		sp. aff. C. pusilla Brady																							
Cyclaminidae genus et sp. indet.																									
?Dorothyia		sp. indet.																							
Poronaiia		poronaiensis (Asano)																							
Trochammina		sp. cf. T. asegaensis Asano																							
Trochammina		spp.																							
Fragment Clavulina like species's aperture end																									
Agglutinated miscellaneous																									
		PORCELLANEOUS																							
Quinqueloculina		seminula compacta Serova																							
Quinqueloculina		spp.																							
Miliolidae miscellaneous																									
		CALCAREOUS HYALINE																							
Dentalina		sp. cf. D. subsoluta (Cushman) of Kaiho, 1984																							
*Dentalina *		spp. (fragments)																							
Pseudonodosaria		conica (Neugeboren)																							
?Astacolus		sp.																							
Lenticulina		sp.																							
Marginulina		sp.																							
Lagena		sp. cf. L. laevis (Montagu)																							
*Lagena *		spp.																							
Procerolagena		sp. cf. P. gracilima (Seguenza)																							
Guttulina		problema (d'Orbigny)																							
Guttulina		takayanagii Kaiho																							
Guttulina		sp. cf. G. takayanagii Kaiho																							
*Guttulina *		spp.																							
Pseudopolymorphina		hokkaidoana Kaiho																							
Sigmoidella		pacific Cushman and Ozawa																							
Fissurina		sp. cf. F. marginata (Montagu)																							
Glanulina		laevigata ovata Cushman and Applin																							
Globocassidulina		globosa (Hantken)																							
Globocassidulina		spp.																							
Bulimina		schwageri Yokoyama																							
Praeglobobulimina		syrula (d'Orbigny)																							
Globobulimina & Praeglobobulimina spp.																									
Angulogerina		hanna Back																							
Cibicides		sp. A																							
Cibicides		spp.																							
Nonionella		japonica (Yokoyama)																							
Melonis		affinis (Reuss)																							
Melonis		pompilioides (Fichtel and Moll)																							
Pullenia		eocenica Cushman and Sieglus																							
Pullenia		salsburyi R.E. and K.C. Stewart																							
Halteriopa		poronaiensis Kaiho																							
Cribroepikidium		ishikawense Kaiho																							
Cribroepikidium		sorachiense (Asano)																							
Cribroepikidium		wakkanabense Kaiho																							
Cribroepikidium		spp.																							
Calcareus miscellaneous																									
Percentage of Planktonic species		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Percentage of Agglutinated species		0	33.3	100	55.6	43.3	89.5	63.6	0	0	88.9	79.7	49.5	83.3	93.4	92.8	96	96.7	68	90.7	77.9	83.2	77.6	84.8	88.7
Percentage of Calcareous benthic species		0	66.7	0	44.4	56.2	10.5	36.4	100	100	11.1	20.3	50.5	16.7	6.64	7.22	4.03	3.3	32	9.27	22.1	16.8	22.4	15.2	11.3
Total population		0	9	2	9	67	124	55	1	1	27	172	277	408	241	97	149	91	197	626	217	161	107	282	247
Diversity (Species Richness)		3	1	2	7	4	7	0	1	5	11	17	16	13	11	8	7	12	13	13	8	12	15	13	
Diversity (Simpson's Index for Diversity)		2.33	1	1.6	3.57	2.04	4.31		1	3	5.21	5.78	9.58	7.26	6.02	5.02	6.02	2.92	2.61	8.28	4.54	5.59	3.48	3.26	

Casing shoe depth: 3096m

		*1 : Barren Foraminifera ; *2 : Minaminaganuma Formation																										
well name		MITI Umaoi																										
Depth of Formation boundary (wireline depth in meter)		3640.0m																										
Formation		*2 Poronai Formation																										
Assemblage Zone		*1 <i>Bulimina schwageri</i> - <i>Angulogerina hannai</i>																										
Sample Depth (drilling depth in meter)		3620	3640	3660	3680	3700	3720	3740	3760	3780	3800	3820	3840	3860	3880	3900	3920	3940	3960	3980	4000	4020	4040	4060	4080	4100	4120	
Ostracoda																76	72											
PLANKTONIC																												
Planktonic foraminifera genus et sp. indet.																												
AGGLUTINATED																												
<i>Bathysiphon</i> <i>ecenica</i> Cushman and Hanna																												
? <i>Ammodiscus</i> sp. indet.																												
<i>Glomospira</i> sp.																												
<i>Reophax</i> sp.																												
<i>Cribrostomoides</i> sp. cf. <i>C. cretacea</i> Cushman and Goudkoff																												
<i>Evolutinella</i> <i>subamakusaensis</i> (Fukuta)																												
<i>Evolutinella</i> sp. cf. <i>E. subamakusaensis</i> (Fukuta)																												
<i>Haplophragmoides</i> <i>rugosus soyaensis</i> Yasuda																												
<i>Haplophragmoides</i> sp. cf. <i>H. rugosus soyaensis</i> Yasuda																												
<i>Haplophragmoides</i> <i>crassiformis</i> Kaiho																												
<i>Haplophragmoides</i> sp. cf. <i>H. crassiformis</i> Kaiho																												
<i>Haplophragmoides</i> <i>tanaii</i> Kaiho																												
<i>Haplophragmoides</i> <i>yokoyamai</i> Kaiho																												
<i>Haplophragmoides</i> sp. B																												
<i>Haplophragmoides</i> sp. D																												
* <i>Haplophragmoides</i> spp.																												
<i>Ammobaculites</i> sp. indet.																												
<i>Budashevaella</i> sp. aff. <i>B. multicamerata</i> (Voloshinova)																												
<i>Budashevaella</i> <i>symmetrica</i> (Ujije and Watanabe)																												
<i>Budashevaella</i> sp. indet.																												
<i>Recurvoides</i> sp. A																												
<i>Recurvoidella</i> sp. cf. <i>R. lamella</i> (Grzybowski)																												
<i>Alveolophragmium</i> sp. A																												
<i>Reticulophragmium</i> <i>amakusaensis</i> (Fukuta)																												
<i>Cyclammina</i> <i>ezoensis</i> Asano																												
<i>Cyclammina</i> <i>pacifica</i> Beck																												
Cyclamminidae genus et sp. indet.																												
<i>Poronia</i> <i>poroniaensis</i> (Asano)																												
<i>Trochammina</i> sp. cf. <i>T. asagaiensis</i> Asano																												
Trochamminidae genus et sp. indet.																												
? <i>Clavulina</i> sp. A																												
<i>Clavulina</i> sp. indet.																												
fragment of <i>Clavulina</i> * like apertural end																												
Agglutinated miscellaneous																												
PORCELLANEOUS																												
<i>Quinqueloculina</i> sp. indet.																												
CALCAREOUS HYALINE																												
? <i>Dentalina</i> spp.																												
<i>Lagena</i> <i>striata</i> (d'Orbigny)																												
<i>Lagena</i> sp. cf. <i>L. laevis</i> (Montagu)																												
<i>Guttulina</i> <i>takayanagii</i> Kaiho																												
<i>Guttulina</i> sp. cf. <i>G. problema</i> (d'Orbigny)																												
<i>Pseudopolymorphina</i> sp. indet.																												
<i>Sigmoidella</i> <i>pacifica</i> Cushman and Oazwa																												
Polymorphinidae genus et sp. indet.																												
<i>Glandulina</i> <i>laevigata ovata</i> Cushman and Applin																												
<i>Glandulina</i> sp. indet.																												
? <i>Cassidulinoides</i> sp.																												
<i>Globocassidulina</i> <i>globosa</i> (Hantken)																												
<i>Globocassidulina</i> spp.																												
<i>Bulimina</i> <i>schwageri</i> Yokoyama																												
<i>Globobulimina</i> sp. indet.																												
Buliminidae genus et sp. indet.																												
<i>Angulogerina</i> <i>hannai</i> Beck																												
<i>Nodogeneria</i> sp. cf. <i>N. lepidula</i> (Schwager)																												
* <i>Nonion</i> sp. indet.																												
<i>Nonionella</i> <i>japonica</i> Yokoyama																												
<i>Melonis</i> sp. cf. <i>M. affinis</i> (Reuss)																												
<i>Melonis</i> <i>pomplioides</i> (Fichtel and Moll)																												
<i>Melonis</i> sp. indet.																												
<i>Pullenia</i> <i>ecenica</i> Cushman and Siegfus																												
<i>Pullenia</i> <i>salisburyi</i> R.E. and K.C. Stewart																												
<i>Cibicides</i> <i>sorachiense</i> (Asano)																												
<i>Cibicides</i> spp.																												
Calcareous miscellaneous																												
Percentage of Agglutinated Foraminifera		100	54	53	72	100	94	81	69	73	66	86	87	40	60	99	81	42	52	75	92	89	97	79	95	83		
Percentage of Porcellaneous Foraminifera		0	0	0	0	0	0	0	0.4	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	
Percentage of Calcareous Foraminifera		0	46	47	28	0	5.9	19	30	27	34	14	13	60	40	0.7	19	58	48	25	7.6	11	2.9	21	4.6	17		
Total population of Foraminifera		23	39	55	67	75	68	36	232	85	131	147	242	111	407	145	90	181	241	233	118	28	34	24	109	209		
Diversity (Species Richness)		2	6	6	6	4	6	4	12	8	11	10	14	10	13	9	10	11	12	14	11	7	4	7	7	12		
Diversity (Simpson's Index for Diversity)		1	1.8	2.1	1.9	2.3	3.6	2.7	3.9	3.5	2.9	6.8	5.7	1.7	2.7	5.5	5.2	2.9	3.6	5.6	4.8	5.3	2.1	5.3	1.4	4.3		

foraminifera in the well MITI Umaoi.

4421.5m																								
Ishikari Group																								
<i>Globo. globosa-Cri. sorachiense</i>										<i>Evolutinella subamakusaensis-H. crassiformis</i>										*1				
4140	4160	4180	4200	4220	4240	4260	4280	4300	4320	4340	4360	4380	4400	4410	4420	4440	4480	4490	4500	4510	4520	4530	4540	4560
				1																				
55	20	12	25	17	8						1	32	7	4	1	1	14	1	4			1		
	13	7			5																			
		3	1								6	4		2					1		1	1		
	7	3	2																					
15	45	80	19	20	20				7	1	5	10	4	1		1	1	1		1	1	1	3	
1		1																						
1	2	9			7																			
		3	2																					
18	2	47	106	52	32	9	11	17	24	11		108												
6	2		2				2		1													1		
3	1												2											
14	5	8	6	3	3	2	3			11		6		3	2		1	1				2		
1																								
64	107	99	30	76	66	5	8	4	3	15	15	19	3	2			2			1				
			1	2			1																	
2																								
3								1																
								2																
4	1	9	1	1	2																			
			1		1																			
4																								
11	1	6	2	2					1					1										
6	14	7	13	4	2	10	1	1	3															
86	92	93	91	94	94	52	77	81	88	97	100	100	94	93	100	100	100	100	100	100	100	100	100	
0	0	0	0.5	1.1	0	0	3.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
14	8.1	7.5	8.9	5.3	5.6	48	19	19	13	2.6	0	0	5.9	7.1	0	0	0	0	0	0	0	0	0	
208	222	294	213	188	142	31	31	26	40	39	27	179	17	14	3	3	19	2	9	1	2	3	3	
12	10	9	8	9	7	2	6	4	4	2	3	4	4	4	2	3	3	2	4	1	2	3	1	
3.3	3.8	3.5	1.6	2.3	2.2	1	2.2	1.4	1.2	1	1.3	1.6	1.9	2.3	1	2	1.1	1	2		1	2		

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Feeding strategy of an Early Miocene cetothere from the Toyama and Akeyo Formations, central Japan

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Received March 21, 2001; Revised manuscript accepted January 31, 2002

Abstract. The feeding strategy of cetothere from the Toyama and Akeyo Formations is discussed based on the mandibles of two individuals. Three synapomorphic characters in the mandible that are shared with balaenopterid whales (a laterally projecting coronoid process, a marked inward elevation at the dorsal edge of the ramus posterior to the coronoid process, and a sharply edged ventral margin on the middle part of the mandible) suggest that some cetotheres had already acquired an engulfment feeding mechanism by the late Early Miocene. Two other apomorphic characters (a quite high and elongated dorsal mandibular ridge and a ventrally well-projected mandibular angle) suggest robust development of the musculature of the mandible during the feeding process in the studied specimens in contrast to the weak development of the musculature in the balaenopterids. This may represent a primitive transitional stage of the engulfment feeding mechanism which could be related to the lack or poor development of highly elastic elements in the ventral pouch.

Key words: Cetotheriidae, Early Miocene, engulfment feeding, feeding mechanism, mandible, Mysticeti

Introduction

Mysticetes have acquired baleen plates and developed a unique filter feeding mechanism during the process of their evolution. The feeding strategy of the extant Mysticeti is generally divided into three types: skim feeding for plankton (Balaenidae), mud scooping (Eschrichtiidae), and engulfment feeding for fast-swimming krill and fish (Balaenopteridae) (Brodie, 1977; Pivorunas, 1979; Berta and Sumich, 1999). The evolution of filter feeding was a primary factor for the origin of mysticetes (Fordyce, 1980, 1989). Since the Cetotheriidae are the earliest true baleen-bearing, toothless mysticete family (Barnes, 1984; McLeod *et al.*, 1993; Fordyce and Barnes, 1994), the study of their feeding mechanism is important for considering the evolution of filter feeding in mysticetes. McLeod *et al.* (1993) pointed out that cetotheres have the following three morphological characteristics as compared with balaenopterids—(1) more posteriorly directed mandibular condyle; (2) larger coronoid process of mandible; and (3) longer zygomatic process of squamosal. Based on these characters, these authors briefly mentioned that cetotheres were probably engulfment feeders displaying a less specialized mandible and skull morphology and with a weaker throat groove than balaenopterids. However, there is no other detailed discussion in the literature about cetothere feeding

strategy.

Two cetothere mandibles were found from the Lower Miocene Toyama and Akeyo Formations, Gifu Prefecture, Japan. The mandible has a primary functional role for feeding, and its morphology may reflect to a high degree the feeding strategy. The purpose of this paper is to examine the feeding strategy of the cetotheres based on the two mandibles and to discuss the evolution of the engulfment feeding mechanism.

Materials

Two cetothere specimens were examined in this study. Both specimens are deposited in the Mizunami Fossil Museum, Mizunami, Gifu Prefecture, Japan (MFM).

MFM18124, Cetotheriidae gen. et sp. indet. (Figure 1).—Both mandibles, skull fragments, cervical and thoracic vertebrae, ribs, a sternum, a humerus, and some bone fragments. The right mandible is almost complete. This specimen was found from the Kubohara Facies of the Toyama Formation, Iwamura Group, Iwamura town, Ena County, Gifu Prefecture, Japan (Kimura *et al.*, 2000). The horizon from which this specimen was collected is correlated to the Maki Member of the Toyama Formation, Iwamura Group (Ujihara *et al.*, 1992). The Maki Member is assigned to the *Crucidentricula sawamurae* Zone (late

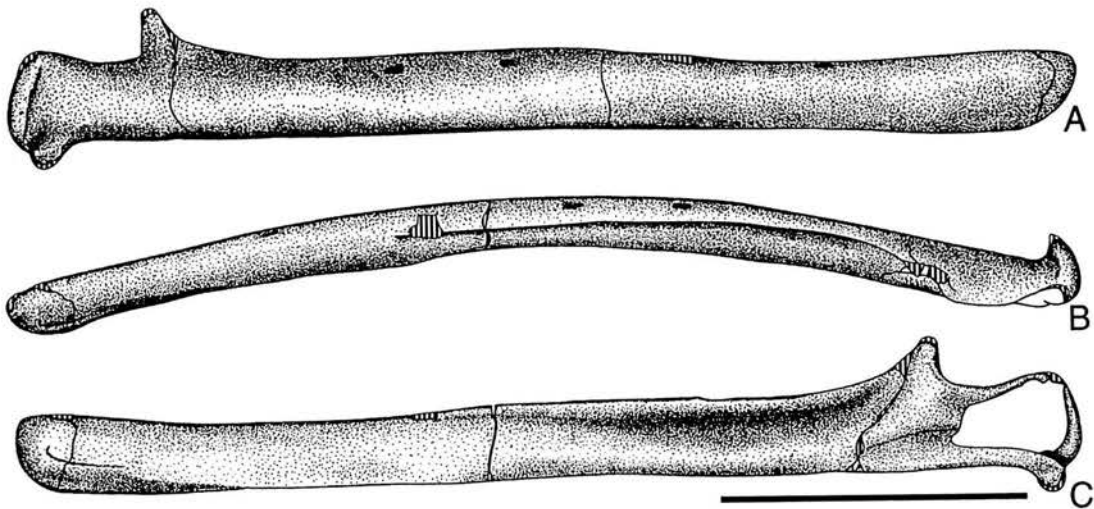


Figure 1. Cetotheriidae gen. et sp. indet. from Toyama Formation, MFM18124, right mandible. A. Lateral view. B. Dorsal view. C. Medial view. Hachures indicate areas where mandible is damaged. Scale bar equals 50 cm. After Kimura *et al.* (2000).

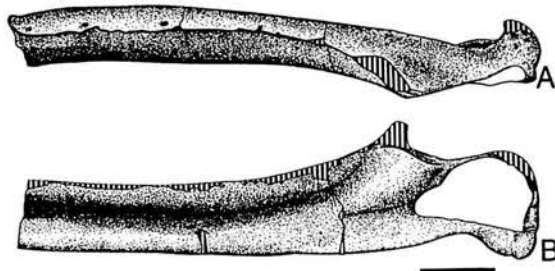


Figure 2. Cetotheriidae gen. et sp. indet. from Akeyo Formation, MFM18125, right mandible. A. Dorsal view. B. Medial view. Hachures indicate areas where mandible is damaged. Scale bar equals 10 cm.

Early Miocene: Barron and Gladenkov, 1995; Yanagisawa and Akiba, 1998) based on diatom biostratigraphy (Ito *et al.*, 1999). This specimen was originally described by Kimura *et al.* (2000).

MFM18125, *Cetotheriidae* gen. et sp. indet. (Figure 2). —Right mandible. A posterior half of the mandible including condyle and angle is preserved. This specimen was found from the Lower Miocene Yamanouchi Member, Akeyo Formation, Mizunami Group, Togari, Mizunami City, Gifu Prefecture, Japan and was once referred to *Mysticeti*, gen. and sp. indet. (Kamei and Okazaki, 1974: p. 283, pl.97, figs.6a, b). The Akeyo Formation consists of the Tsukiyoshi, Togari, Yamanouchi, and Hazama Members in ascending stratigraphic order (Itoigawa, 1974, 1980). Kobayashi (1989) estimated the age of the Akeyo Formation to be 17–17.5 Ma on the basis of fission-track dating. Itoigawa and Sibata (1992) suggested that the

Yamanouchi Member is assigned to Upper Zone N.7 to Lower Zone N.8 of Blow (1969). Kohno (2000) also suggested that the Yamanouchi Member is late Early Miocene (ca. 18–17 Ma) based on the radiolarian and diatom dating.

These two mandibles share a characteristic morphology of a quite high and elongated dorsal ridge with a concavity at its medial side. This character clearly distinguishes the present species from any other known mysticetes. These edentulous specimens are clearly distinct from primitive, toothed mysticete families. Additionally, these two mandibles are characterized by the following combination of characters: (1) a large mandibular foramen; (2) a well-developed coronoid process that projects dorsally, laterally, and posteriorly; (3) a posteriorly directed articular surface of the condyle; (4) a sharply edged ventral margin on the middle part of the mandible. This combination of characters is not found in any extant mysticete families (Balaenopteridae, Eschrichtiidae, Balaenidae, and Neobalaenidae). Therefore, these two specimens are recognized as the same species in the *Cetotheriidae*, gen. and sp. indet. as will be discussed below (Kimura *et al.*, 2000). The *Cetotheriidae* have long been considered as a paraphyletic grade lacking the diagnostic characters of more derived mysticete families (e.g., Fordyce and Barnes, 1994).

For comparison, I examined the material of the following extant *Mysticeti* housed in the National Science Museum, Tokyo (NSMT): Balaenopteridae: *B. acutorostrata* (NSMT-M15941, NSMT-M32543), *B. edeni* (NSMT-M03538, NSMT-M32599); Eschrichtiidae: *E. robustus* (NSMT-M15940); Balaenidae: *B. glacialis* (NSMT-M03538).

Table 1. Measurements of right mandible (in mm), Cetotheriidae gen. et sp. indet. from Toyama (MFM18124) and Akeyo (MFM18125) Formations.

	MFM18124	MFM18125		
Length of mandible in a straight line	1777	734+		
Length of mandible along outside curvature	1810	735+		
Distance from anterior end of ramus to level of center of coronoid process along outside curvature	1572	—		
Vertical diameter through coronoid process	214+	154+		
Vertical diameter of hinder end of ramus including condyle	187+	152+		
Transverse diameter of condyle	108+	80+		
Vertical (H) and transverse (W) diameter in 100-mm increments from the anterior end of ramus			H	W
	100	140	49	104+
	200	132	53	105
	300	123	59	113
	400	117	65	119+
	500	121	68	154+
	600	121	70	107
	700	123+	73	
	800	132	74	
	900	132	75	
	1000	135	78	
	1100	136	80	
	1200	136	80	
	1300	138	72	
	1400	147	78	
	1500	172+	85	
	1600	133	84	
	1700	145	71	

Description

The right mandible of MFM18124 is almost complete except for erosion of an angle (an), a dorsolateral edge of a coronoid process (cp), and a dorsal and lateral part of a condyle (co) (Figure 1). All of the epiphyses on the preserved vertebrae (cervical and thoracic) are firmly ankylosed to the centra, and this condition in extant mysticetes is regarded as evidence of physical maturity (Omura, 1975). MFM18125 consists of only the posterior half of a right mandible and is smaller than MFM18124 by approximately 75% (Table 1). In MFM18125, the coronoid process is broken off except for its base and the dorsal and lateral portion of the condyle was eroded away (Figure 2). Unless otherwise mentioned, the descriptions

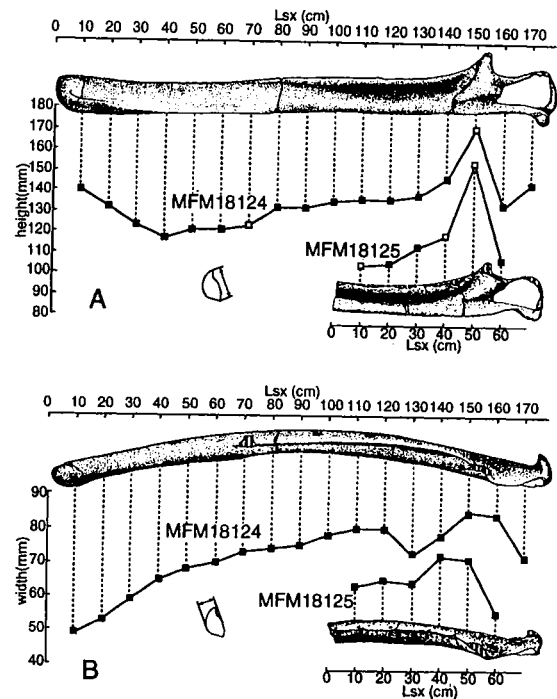


Figure 3. Change in measurements. A, B. Height (A) and width (B) of right mandible of MFM18124 and MFM18125 in 100-mm increments from anterior end, at left. Open squares represent minimum values, owing to breakage of specimen. Abbreviations: Lsx, distance between anterior end of ramus and measurement points along a straight line. Modified from Kimura *et al.* (2000).

are based on MFM18124.

A roughened area at the anterior tip of the mandible is short and does not exceed 75 mm. A longitudinal crease on the medial surface at the anterior tip of the mandible is 142 mm long. The horizontal ramus is rotated around its axis and its medial surface slopes lingually. The amount of rotation at the anterior tip of the horizontal ramus is about 30° against the medial surface at the region of the coronoid process. The horizontal ramus tapers slightly in dorsoventral diameter from the region of the coronoid process toward the anterior tip (Figure 3). However, the dorsoventral diameter increases at the anterior one-fifth of the mandible.

MFM18124 preserves three mental foramina along the dorsolateral surface of the mandible. These foramina occur at 485, 1010, and 1199 mm behind the anterior tip of the mandible and lie at 7, 31, and 43 mm below the dorsal margin of the horizontal ramus. These foramina open into an anteriorly directed groove.

Figure 4 shows the cross sections of the mandibles. There is a noticeable flattening of the anterior one-third of the medial surface of the mandible. Posterior to this, the medial surface of the ramus becomes convex medially. A concavity occurs at the medial side of the high dorsal ridge.

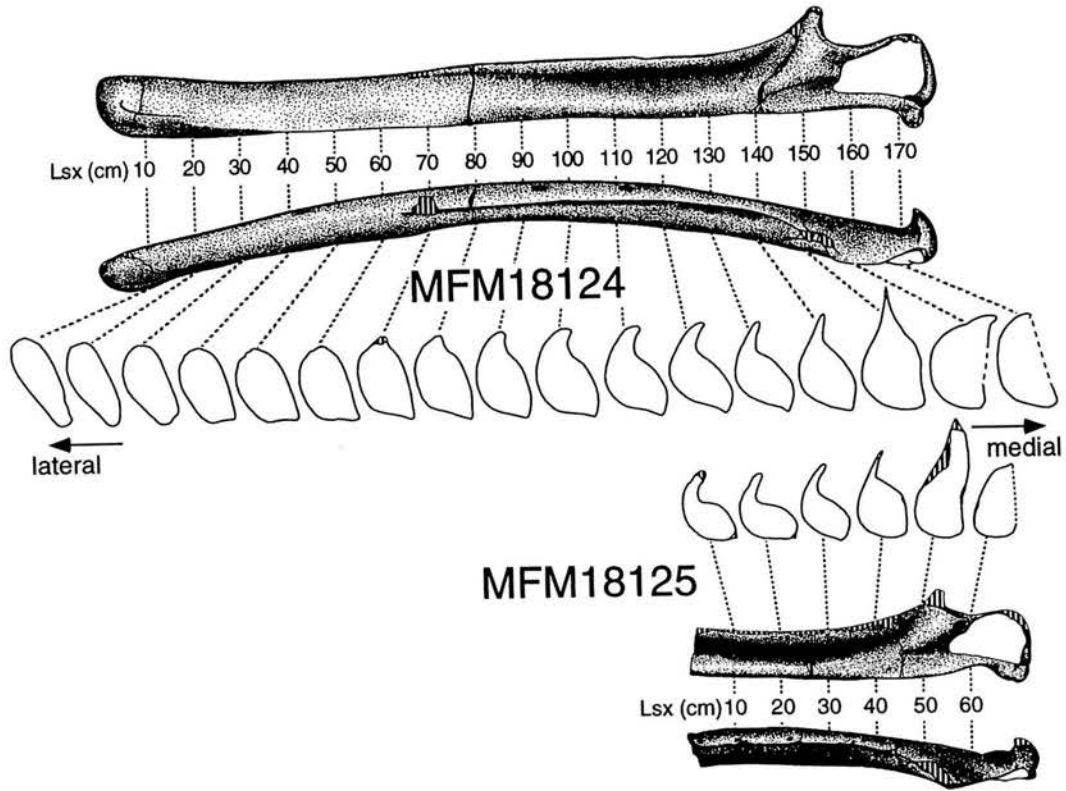


Figure 4. Cross sections of right mandible of MFM18124 (above) and MFM18125 (below). Hachures indicate areas where mandible is damaged. Dashed line in cross section represents mandibular foramen. Abbreviation: Lsx, distance between anterior end of ramus and measurement point along a straight line.

A groove is present on the medial surface of the horizontal ramus anterior to the mandibular foramen (mf). The lateral surface of the mandible becomes progressively convex dorsoventrally toward the posterior end. The greatest transverse diameter is below the midline at the middle part of the mandible. Further posteriorly, the greatest diameter shifts dorsally. Ventrally the lateral surface meets the medial surface to form a well-defined angular edge in the middle part of the mandible. This angular edge approaches the internal face anteriorly. The angular edge becomes rounded posteriorly at the region of the coronoid process.

In dorsal view, the mandible is only slightly bowed laterally (Figure 1B). The length of the mandible along the outside curvature represents only 102% of the length of the mandible in a straight line. The outward curvature is gradual and not abruptly flexed. There is no reflexion at the region of the coronoid process as in the balaenopterids. In lateral view, the ventral profile of the horizontal ramus is almost straight (Figure 1C). But in MFM18125, the ventral margin of the mandible anterior and posterior to the coronoid process is dorsally arched (Figure 2B).

The coronoid process projects dorsally, posteriorly, and laterally. The apex of the coronoid process is located at

87% of the length of the mandible along the outside curvature from the anterior extremity. The anterior margin of the coronoid process rises gradually, but its posterior margin descends abruptly. A shallow concavity occurs on the medial surface of the coronoid process along its anterior margin (Figure 5). Behind the apex, the posterior edge of the coronoid process thickens whereas the anterior edge remains thin. An inward elevation (ie) occurs on the medial surface of the upper border near the middle of the ramus behind the coronoid process (Figure 5). The inward elevation has a sharp edge and projects inward. It becomes more prominent anteriorly. This inward elevation continues anteriorly and dorsally to a ridge on the medial surface of the coronoid process. In MFM18125, because of breakage, a longitudinal groove occurs at a dorsomedial edge of the corresponding part of the ramus. But the remaining part projects slightly medially, and this suggests the development of the inward elevation in MFM18125. The inward elevation is also found in the Balaenopteridae. However, the elevation in the Balaenopteridae is more rounded than that of MFM18124 and MFM18125 (personal observation). For a distance of at least 880 mm anterior to the apex of the coronoid process, a relatively high dorsal

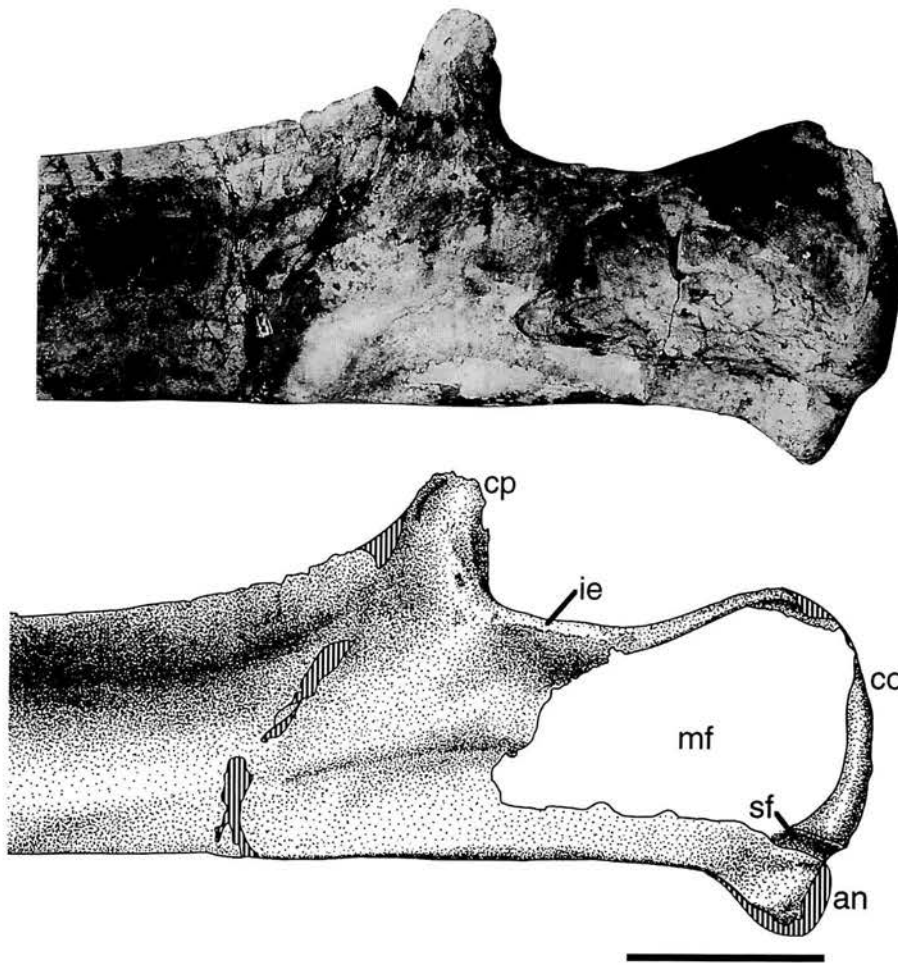


Figure 5. Cetotheriidae gen. et sp. indet. from Toyama Formation, MFM18124. **A, B.** photograph and drawing of posterior part of right mandible, medial view. Hachures indicate areas where mandible is damaged. Abbreviations: an, angle; co, condyle; cp, coronoid process; ie, inward elevation; mf, mandibular foramen; sf, subcondylar furrow. Scale bar equals 10 cm. Modified from Kimura *et al.* (2000).

ridge forms the dorsal edge of the horizontal ramus (Figures 1, 4). Anteriorly, the dorsal ridge becomes rounded and curved medially.

A mandibular foramen is large. The condyle is expanded from side to side and is more convex transversely than dorsoventrally. The forward-curving external border of the condyle projects beyond the lateral surface of the adjacent portion of the ramus. The maximum transverse expansion of the condyle (MFM18124, 108 mm+; MFM18125, 80 mm+) occurs below the midline of its vertical diameter. Ventrally, the condyle almost maintains its width. Ventrally, the condyle is bounded by a subcondylar furrow (sf) above the angle. This furrow extends across the posterior face of the condyle and decreases in depth laterally. Although the angle of MFM18124 is damaged, the preserved portion projects far ventrally. In MFM18125, the angle is almost complete, robust and projects ventrally (Figure 2).

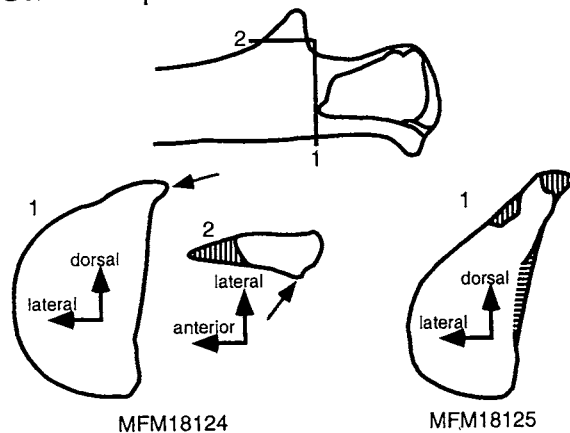
Discussion

Morphological characters of mysticetes can reflect their feeding strategy (McLeod *et al.*, 1993). Since the mandible plays an important role in feeding process, we can make inferences about the feeding strategy of fossil mysticetes from their mandibular morphology.

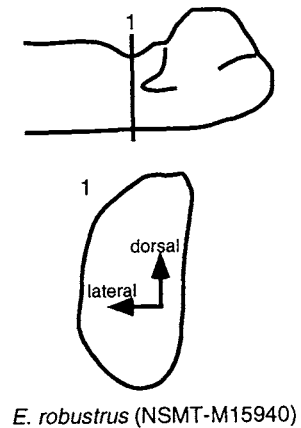
Apomorphies for engulfment feeding

Coronoid process.—The coronoid process of the mandible in the balaenopterids is large and projects both posteriorly and laterally. The coronoid process in the basal suborder Archaeoceti and the toothed mysticetes Aetiocetidae is also large, but does not project laterally (Kellogg, 1936; Barnes *et al.*, 1995; Gingerich and Uhen, 1996; Hulbert *et al.*, 1998). The laterally projected coronoid process of the balaenopterids is considered to be a derived condition. In contrast, the non-engulfment feed-

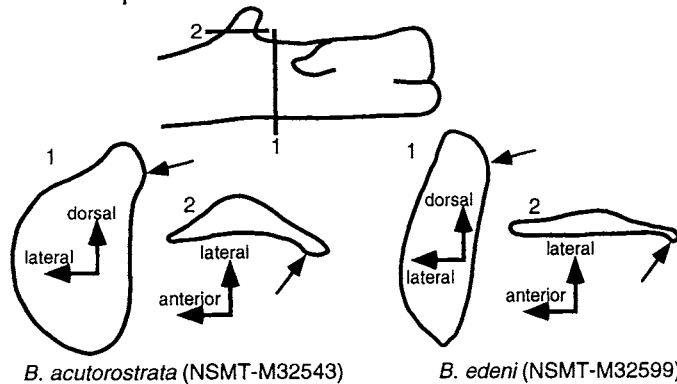
Studied Specimens



Eschrichtiidae



Balaenopteridae



Balaenidae

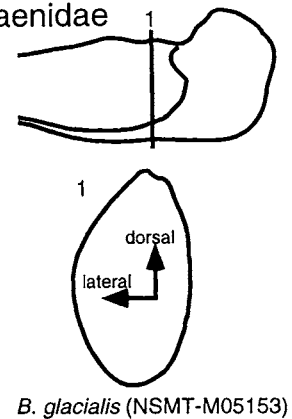


Figure 6. Cross sections of mandible just behind (1) and base (2) of coronoid process (not to scale). Arrows indicate an inward elevation. Hachures indicate areas where mandible is damaged.

ers (Balaenidae, Neobalaenidae, and Eschrichtiidae) convergently acquired a quite small coronoid process (Barnes and McLeod, 1984) unless those three families form a monophyletic group.

The coronoid process provides the insertion for the temporal muscle which generates most of the elevating force during feeding in rorquals (Carte and MacAlister, 1868; Schulte, 1916; Lambertsen, 1983; Lambertsen *et al.*, 1995). The shape of the coronoid process is functionally important for engulfment feeding because it requires a complicated motion of the mandible (Lambertsen *et al.*, 1995). MFM18124 has a large and laterally projected coronoid process similar to the balaenopterids (Figures 1, 5). Although the coronoid process of MFM18125 is missing, the base of the process also suggests that the process is curved laterally (Figure 2B).

Ventral margin of the mandible.—The cross-sectional shape of the ventral margin of the middle part of the mandible is clearly differentiated among the mysticete families (Deméré, 1986; Nagasawa, 1994). In the Balaenopteridae,

the ventral margin of the cross section in the middle part of the mandible forms a well-defined angular edge (Deméré, 1986; Kimura *et al.*, 1987; Nagasawa, 1994). The sharply edged ventral margin of the cross section in the middle part of the mandible is also developed in MFM18124 and MFM18125. The mylohyoid muscle is attached along this ventral ridge (Pivorunas, 1977; Lambertsen, 1983). In engulfment feeding, the mylohyoid muscle, together with other muscles (multiple muscle layers: Lambertsen, 1983), plays an important role in expelling the sea water through the baleen plates (Lambertsen, 1983; Orton and Brodie, 1987). The marked ridge on the ventral margin of the mandible suggests the presence of well-developed mylohyoid muscles.

Inward elevation of the mandible.—The degree of development of the elevation is variable in the Balaenopteridae, stronger in *B. acutorostrata* than in *B. edeni* (Figure 6). This inward elevation is also found in *B. musculus* (Struthers, 1889). In *Megaptera novaeangliae*, the elevation rises upward on the same part of the mandible and

is called the post-coronoid elevation (Struthers, 1889). The studied specimens have a remarkable inward elevation on the medial surface of the upper border near the middle of the ramus behind the coronoid process similar to the balaenopterids.

In contrast, the structure of the corresponding part is quite different in the Eschrichtiidae and Balaenidae. In the Eschrichtiidae, the coronoid process is quite low and projects laterally. Posterior to the coronoid process, there is a low process which projects dorsally, and this process continues posteriorly to a low ridge on the medial surface of the ramus. Below this low ridge, another longitudinal faint ridge is also present. In the Balaenidae (*B. glacialis*), the coronoid process is faint and, posterior to the coronoid process, a shallow groove is present on the dorsomedial surface of the ramus (anteroposterior length of the groove: right 46 mm/left 59 mm). This groove makes a low bump on the medial surface of the upper part of the ramus. Although there is a ridge on the dorsomedial surface of the ramus in both families, the ridge is faint and does not project medially (Figure 6). Further, there is no ridge on the medial surface of their quite low coronoid process. Therefore, these structures found in the Eschrichtiidae and Balaenidae are clearly distinguished from the prominent inward elevation present in the studied species and the Balaenopteridae.

The frontomandibular stay is a functionally and anatomically specialized tendon of the temporal muscle and is attached to the inward elevation (Struthers, 1889; Lambertsen *et al.*, 1995). This stay apparatus is common among the balaenopterids and serves to support the motion of the mandible during the feeding process, especially in initiating engulfment (Lambertsen *et al.*, 1995).

The above three characters suggest that the species had an acquired engulfment feeding mechanism. The Cetotheriidae is believed to include taxa closely related to the ancestor of the Balaenopteridae (Fordyce and Barnes, 1994). The three apomorphies are also found in the Balaenopteridae. However the phylogenetic relationship between the cetothere species in this study and the Balaenopteridae is still unclear and the analysis of the relationship is beyond the scope of this study. So, more detailed consideration is needed to ascertain whether these characters are synapomorphies between the two.

Efficiency of engulfment feeding

One aspect of engulfment feeding efficiency relates to the size of the mouth cavity. The mandible of the studied specimens is slightly curved, a primitive condition (Barnes and McLeod, 1984). Deméré (1986) suggested that the width of the rostrum is directly proportional to the extent of the lateral curvature of the mandible. This suggests that the mouth cavity of the studied specimens was relatively

small and that engulfment feeding in MFM18124 and MFM18125 was less efficient than in the extant balaenopterids.

The mandible of the balaenopterids changes continuously in its position during the engulfment feeding process by three motions—(1) alpha rotation: an inward and outward rotation around the longitudinal axis of the mandible; (2) delta rotation: depression and elevation of the mandible; and (3) omega rotation: medial and lateral movement of a condyle of the mandible (Lambertsen *et al.*, 1995). The temporomandibular articulation in extant balaenopterids is, unlike other mammals, composed of a fibrous meniscus infiltrated with oil (Hunter, 1787; Carte and MacAlister, 1868; Beaugard, 1882; Beneden, 1882; Struthers, 1889; Schulte, 1916). Since this meniscus enables the movement of articulation more effectively, like planar quadrilateral connecting system, the squamomandibular articulation of the balaenopterids can perform its complicated movements (Lambertsen *et al.*, 1995). Cetotheres are generally characterized by having a more or less flattened articular surface of the squamosal (Miller, 1923). This suggests that the temporomandibular articulation composed of a fibrous meniscus was not acquired or poorly developed in the Cetotheriidae. Neither of the studied specimens includes the squamosal, and it is unclear that they were able to perform these complicated movements of the mandible.

Lambertsen *et al.* (1995) suggested that stronger lateral curvature and elongation of the mandible would increase alpha-rotation of the mandible. If these specimens were able to perform alpha-rotation, the small amount of curvature suggests that this could not contribute greatly to the enlargements of the mouth. This suggests that cetotheres fed less efficiently than the balaenopterids.

Feeding strategy of Balaenopteridae

In the Balaenopteridae, the musculature of the mandible mainly braces the jaw during engulfment feeding and does not actively open it (Lambertsen, 1983; Orton and Brodie, 1987; Lambertsen *et al.*, 1995). This passive movement of the mandible is mainly caused by water pressure resulting from locomotion and allied action of a ventral pouch (Brodie, 1977; Orton and Brodie, 1987; Lambertsen *et al.*, 1995; Bakker *et al.*, 1997). The ventral pouch (body wall below the cavum ventrale: Lambertsen, 1983) is a highly elastic grooved structure which consists mainly of blubber and multiple muscle layers, covering the ventral surface of the whale from the anterior border of the mandible to the umbilicus or further (Pivorunas, 1979; Lambertsen, 1983; Orton and Brodie, 1987). The pouch is filled by voluntary increase of the curvature of its elastic ventral wall by contraction of multiple muscle layers. This changes the water flow between the upper and lower surface of the head and causes asymmetry of the hydraulic pressure which assists in

depressing the mandible (Bernoulli principle) (Lambertsen *et al.*, 1995). The passive movement of the mandible in filling the pouch is also suggested by the fact that the relaxation of jaw musculature makes the lower jaw drop (Lambertsen, 1983). Lambertsen *et al.* (1995) also suggested that as a result of the mode of attachment of the ventral pouch to the mandible, hydraulic pressure can rotate the mandible around its longitudinal axis (alpha rotation). Active contraction of musculature is required for water expulsion, especially in the final phase (Lambertsen, 1983; Orton and Brodie, 1987). Orton and Brodie (1987) suggested two sources for passive motion of the mandible in expulsion and these are accompanied with changes in swimming speed. They are based on a recoil of hydraulic pressure and resiliency of elastic elements of the ventral pouch. In addition, when the whale ceases propulsive action, the energy of the frontomandibular stay against the water flow is released and the stored energy of the stay assists closure of the mouth (Lambertsen *et al.*, 1995).

Therefore, we can summarize the source for the efficient feeding mechanism of the Balaenopteridae as follows: (1) the strong development of the highly elastic elements in the ventral pouch; (2) the multiple muscle layers which serve to deepen the oral cavity; (3) the frontomandibular stay.

Feeding strategy of studied specimens

The specimens studied display the aforementioned synapomorphies with the balaenopterids, but also show two apomorphic characters, which are clearly different from the Balaenopteridae. Both these characters suggest that engulfing is a more active muscular process than in the Balaenopteridae.

Dorsal ridge.—The specimens studied have a relatively high and elongated dorsal ridge with a concavity at its medial side (Figures 1, 2, 4). In MFM18124, there is a roughened area on most of the medial surface of the ridge. This area can be considered as the origin of the caudal part of the mylohyoid muscle. The mylohyoid muscle is only attached along the ventral border in the extant Mysticeti (*B. acutorostrata*: Pivorunas, 1977, Lambertsen, 1983; *B. borealis*: Schulte, 1916) and the extant Odontoceti (Reidenberg and Laitman, 1994) at the middle part of the mandible. But in ungulates, the muscle is separated into rostral and caudal parts, and the caudal part originates from the medial surface of the mandible just ventral to the alveolar border (Getty, 1975; Sisson, 1975; Nickel *et al.*, 1986). The close relationship between cetaceans and ungulates has been confirmed by much paleontological and molecular data (e.g., Van Valen, 1966; Shimamura *et al.*, 1997). It appears that cetotheres display the primitive ungulate muscle pattern; the dorsal ridge and allied concavity may indicate the area for the attachment of the mylohyoid muscle. Therefore,

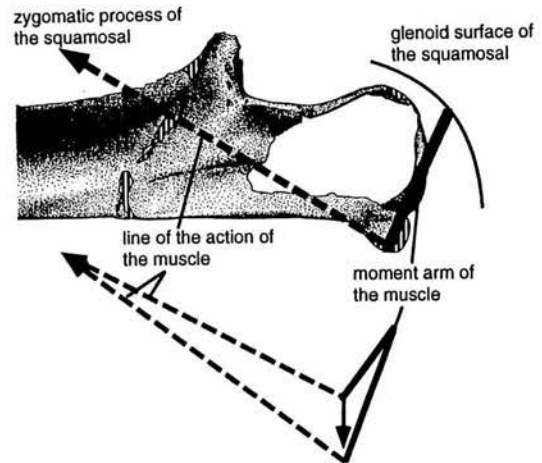


Figure 7. Schematic diagram showing moment arm of superficial portion of masseter muscle (above) and changing of moment arm caused by ventral projection of angle (below). Solid and dashed lines indicate moment arm of muscle and line of action of muscle, respectively.

the relatively high dorsal ridge with the well-developed concavity of the specimens studied suggests a highly developed mylohyoid muscle, unlike the balaenopterids.

The mylohyoid muscle is the largest muscle in the multiple muscle layers of the floor of the mouth. The multiple muscle layers of the ventral pouch are the primary contributor for active expulsion of water through the baleen (Lambertsen, 1983). In addition, at the final phase of water expulsion, the tongue is forced upwards by contraction of the mylohyoid muscle and this forcibly expels the remaining sea water through the baleen (Lambertsen, 1983). The mylohyoid muscle is primarily an elevator of the tongue (Yamaoka *et al.*, 1992). Thus, the development of the mylohyoid muscle suggests that the studied specimens required active musculature for water expulsion during feeding.

Angle.—The angle provides the insertion of the muscles for the movement of the mandibles, such as the medial pterygoid muscle, the digastricus muscle, and the superficial portion of the masseter muscle (Carte and MacAlister, 1868; Schulte, 1916; Lambertsen *et al.*, 1995). The angle of the specimens studied is large and projects ventrally (Figure 1, 2). This is clearly shown by the ratio of mandibular height through angle to mandibular length along outside curvature of the adult individual (converted to percentages): MFM18124 10.3+%; *B. acutorostrata* 8.5–9.5% (Turner, 1891–1892; Omura, 1975), *B. edeni* 7.9–9.2% (Omura *et al.*, 1981), *B. musculus* 8.3–9.3% (Struthers, 1889; Omura *et al.*, 1970), *B. borealis* 7.6–8.1% (Nishiwaki and Kasuya, 1971), *M. novaeangliae* 9.1% (Struthers, 1889). The ventrally projected angle implies that the area for the insertion of the muscle is also posi-

tioned ventrally. This would increase the moment arm of the superficial masseter and thus improve the mechanical advantage of the mandible (Herring and Herring, 1974; Vizcaíno and Bargo, 1998) (Figure 7). Therefore, the morphology of the angle suggests that the specimens studied could produce a more powerful motion of the mandible compared with the balaenopterids.

Both of these characters suggest the active contribution of the musculature of the mandible during feeding. This is in marked contrast to the passive contribution of the musculature of the mandible in the Balaenopteridae. The sources for the efficient feeding mechanism in the Balaenopteridae have been summarized above. In the specimens studied, the sharply edged ventral margin at the middle part of the mandible and the well-developed inward elevation indicates the development of the mylohyoid muscle and therefore the multiple muscle layers and frontomandibular stay, respectively. Therefore the robust contribution of the musculature of the specimens studied can be explained by the lack or poor development of the highly elastic elements in the ventral pouch.

Conclusion

I propose the following scenario of evolution of the engulfment feeding mechanism in baleen whales. Early mysticetes (aetiocetids) used filter feeding with teeth, and later cetotheres used baleen. Engulfment feeding was present in Cetotheriidae by the late Early Miocene. However, the feeding mechanism in the Early Miocene cetotheres required more active musculature than in the balaenopterids because of poor development or lack of the highly elastic elements in the ventral pouch. The well developed elastic elements in the skin are highly characteristic and are one of the key structures enabling passive movement of the mandible in the Balaenopteridae. The elastic elements evolved in the Balaenopteridae and enhanced efficiency of the mandible. In addition, balaenopterids have lost the apomorphic characters unrelated to the active musculature of the mandible during engulfment feeding. The feeding strategy suggested by the studied specimens may represent a primitive transitional stage of the evolution of the engulfment feeding mechanism.

The skull morphology may also exert an influence on the feeding mechanism (McLeod *et al.*, 1993). However, no skull was preserved in both specimens studied, except for a few fragments of the skull in MFM18124. Generally, cetotheres are characterized by primitive skull morphology. The apomorphic characters of the specimens studied which suggests more active contribution of the musculature of the mandible during the feeding process might not only be due to its feeding mechanism, but also to its primitive skull morphology. An additional specimen with a well-

preserved skull is needed to address the feeding strategy of the studied specimens in more detail.

Acknowledgments

This study is a part of my doctoral thesis submitted to the Department of Earth and Planetary Sciences, Graduate School of Science, Nagoya University. I am most grateful to T. Ozawa (Nagoya University) for valuable comments. I gratefully acknowledge the constructive reviews of the manuscript and valuable comments by John E. Heyning (Natural History Museum of Los Angeles County) and J. G. M. Thewissen (Northeastern Ohio Universities). Thanks are extended to anonymous reviewers for their constructive comments and suggestions. I am indebted to T. K. Yamada (National Science Museum) for valuable comments which improved the manuscript and for allowing access to specimens in his care, to Y. Okumura and H. Karasawa (both Mizunami Fossil Museum) for allowing access to specimens and their assistance, and to T. Kuramochi (National Science Museum) for assistance in observing extant mysticete specimens. This study was supported in part by Grant-in-Aid for JSPS Fellows from the Ministry of Education, Science, Sports and Culture of Japan.

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Ostracodes from the Inter-trappean beds (Early Paleocene) of the east coast of India

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Received October 26, 2000; Revised manuscript accepted March 15, 2002

Abstract. Twenty-seven ostracode species from the Inter-trappean beds (Paleocene) of Duddukuru, West Godavari District, Andhra Pradesh, east coast of India are recorded and/or described. Nine species—*Cytheromorpha godavariensis*, *Cytherura duddukuruensis*, *Hapsicytheridea undulata*, *Krithe bhandarii*, *Paracandona andhraensis*, *Munseyella indica*, *Neomonoceratina paraoertlii*, *Semicytherura diluta*, and *Uroleberis rasilis*—are new. The identification of 6 species, previously described from the east coast of India, and also recorded in this work, are revised. The stratigraphic distribution, age and affinity and paleoecology of the ostracode fauna are also discussed.

Key words: Duddukuru, East Coast of India, Inter-trappean beds, Ostracodes, Paleocene

Introduction

The Inter-trappean beds of the east coast of India are a key marker horizon in the stratigraphy of the country. They are of great significance in fixing the age limits of the Deccan Traps, at least those of this part of the peninsula, with which these beds are closely associated. This is because of their unique stratigraphic position (Table 1) and the prolific marine microfauna they contain. There are, however, varied opinions about the age of the Inter-trappean beds and vis à vis of the associated Deccan Traps. Most of the earlier workers until the nineteen seventies considered the Inter-trappean beds as Tertiary in age, ranging from Paleocene to Eocene (Hislop in Hislop *et al.*, 1860; Sahni, 1934; Rao and Rao, 1935, 1937a, 1937b; Rao *et al.*, 1936; Rao, 1956; Sastri, 1961; Bhalla, 1967). However, these views changed markedly in the nineteen eighties during which the Deccan volcanism was demonstrated to be a major Cretaceous-Tertiary boundary (KTB) event (Courtilot *et al.*, 1986, 1988, 1990; Baksi, 1987; Duncan and Pyle, 1988; Hallam, 1988; Sahni and Bajpai, 1988). Govindan (1981) using foraminifera from the Inter-trappean sediments from Narsapur-1 well section from Krishna-Godavari (KG) Basin (of which the present area of Duddukuru under study is a part) assigned the Deccan Traps of this well to late Maastrichtian, emplaced between 70–67 Ma. Subsequently, Raju *et al.* (1991, 1994, 1995), Jaiprakash *et al.* (1993), Saxena and Mishra (1994), and Mishra *et al.* (1994) studied foraminifera, calcareous nannoplankton and dinoflagellate cysts from more

well sections from the K-G Basin. The data suggest that the volcanism began during 65.5 to 65 Ma (considering KTB at 65 Ma, Sharpton *et al.*, 1992) in the terminal Cretaceous and continued across the KTB into the early Paleocene.

The microfauna of the Inter-trappean beds of the east coast of India comprises mainly foraminifers and ostracodes. A survey of the literatures reveals that important contributions on these foraminifers have been made by Rao and Rao (1937a), Sastri (1961), Bhalla (1967), Govindan (1981), Raju and Dave (1993), and Jaiprakash *et al.* (1993), while on ostracodes by Jain (1978) and Bhandari (1995).

With the intention of working on the ostracode fauna of the Inter-trappean beds of the east coast of India the authors collected samples of these beds from two sections. The location of the sections is given below and also in Figure 1.

Section I is from a limestone quarry, belonging to M/S Facor Ltd., about 1 km south of the village of Duddukuru (17° 2' 15'' N; 81° 35' 30'' E) on the Eluru-Kovvur Road, West Godavari District, Andhra Pradesh, east coast of India. Section II is from an abandoned quarry about 2 km southeast of Duddukuru. Both sections yielded a prolific, well preserved ostracode fauna much richer than those reported by Jain (1978) and Bhandari (1995). The assemblage comprises a total of 27 species including 9 new ones and a number of species being reported for the first time from the region. This has necessitated revising the ostracode fauna of the Inter-trappean beds of the east coast of India. A new genus *Costabuntonia* has recently been

proposed for the species previously described as *Protobuntonia hartmanni* Jain (Khosla, 1999).

Previous work

Among the earlier works on the ostracode fauna from the Inter-trappean beds of the east coast of India, an important contribution was made by Sastri (1961 and 1963) who reported the occurrence of nine species from these beds at Kuntamuru village near Rajahmundry. These species are *Cytherella* sp., *Cytheropteron* sp., *?Eucythere* sp., *Loxococoncha* sp., *Bairdia subdeltoidea* (Münster), *Cythere* (*?Xestoleberis*) *ranikotiana* Latham, *Cythereis bowerbanki* Jones, *Cythereis* cf. *mersondaviesi* Latham, and *Cytherelloidea* sp. Of these only the last five species were described and illustrated in his 1963 paper while the specific name *Cythere* (*?Xestoleberis*) *ranikotiana* was modified as *Cythere ranikotiana*. Bhalla (1965) recognised 16 ostracode species from Pangadi, Andhra Pradesh. These are: *Brachycythere* sp., *Bythocypris* sp., *Costa* sp., *Cytherella* sp., *Cytheretta* [possibly *C. laticostata* (Reuss)], *Hermanites* sp. A, *H.* sp. B, *Krithe* [provisionally identified as *K. bartonensis* (Jones)], *Leguminocythereis* sp. A, *L.* sp. B, *Neocyprideis* sp., *Occultocythereis* sp., *Quadracythere* sp., *?Schizocythere* sp., *Semicytherura* [provisionally identified as *S. forestensis* (Keij)], and *Xestoleberis* [provisionally identified as *X. subglobosa* (Bosquet)]. Their stratigraphic distribution and paleoecologic significance were given in his subsequent paper (Bhalla, 1967). Bhalla (1979a-c, 1980) described and illustrated the following new species from the Pangadi area: *Hermanites sastryi*, *Loxococoncha singhi*, *Occultocythereis elongatum*, and *Quadracythere tewarii*.

Guha (1970) recorded *Cythereis* cf. *tamulicus*, *Hermanites* cf. *pondicheriensis*, *Paracypris* sp., *Protobuntonia* sp., *Xestoleberis* sp., and the genus *Ovocytheridea*.

Jain (1978) described and illustrated twelve ostracode species from Kateru, Rajahmundry. Of these two species, *Ovocytheridea raoi* and *Protobuntonia hartmanni* are new, the other species represented being "*Bairdia*" sp. indet., *?Bythocypris* sp. indet., *Cytherella* sp. cf. *münsteri* (Roemer), *Cytherelloidea* sp. cf. *C. keiji* McKenzie, *?Cytheridea* sp. indet., *Hermanites* sp. cf. *H. cracens* Siddiqui, *Limnocythere* sp. indet., *Loxococoncha* sp. indet., *Quadracythere* (*Hornibrookella*) *subquadrata* Siddiqui, and *?Xestoleberis* sp. indet.

Bhandari (1995) recorded 15 species from the Inter-trappean beds near Duddukuru, Andhra Pradesh. Of these four species—*Cushmanidea bhatai*, *Cytherella mohani*, *Cytheridella rajahmundryensis* and *Palmoconcha rajui* are new. The other species reported are *Bythocypris?* sp., *Cytherelloidea* sp. cf. *C. keiji* McKenzie, *Cytheridella* sp., *Gyrocythere* sp. cf. *G. parvicarinata* Siddiqui, *Hermanites*

sastryi Bhalla, *Hermanites* sp., *Hornibrookella tewarii* (Bhalla), *Nucleolina diluta* Al-Furaih, *Ovocytheridea raoi* Jain, *Protobuntonia hartmanni* Jain, and *Xestoleberis* sp.

Stratigraphy

The geology of the region, along with a detailed map, has been adequately described by Bhalla (1967) and this has been followed in this work. The Inter-trappean beds are set of sedimentary strata composed mainly of limestone with shale/claystone intercalations lying in between the Deccan trap. The generalised stratigraphy of the coastal tract of the Krishna-Godavari districts, Andhra Pradesh is summarised in Table 1 (for details see references in Ramam and Murty, 1997).

The Intra-trappean beds have a gentle dip of 4 to 6 degrees towards the southeast and thickness varying from less than a meter to a little over 9 meters. The samples from which the present ostracode fauna was obtained come from the two sections. The sequence of these sections is given in Tables 2 and 3.

Materials and methods

The samples were broken into small pieces and boiled for 3–4 hours in water to which one or two tablespoons of soda ash were added. The disintegrated material was wet screened through set of sieves of 30, 80, and 150 mesh size. The dried, washed residue was uniformly spread on a picking tray and scanned under a stereozoom microscope. The ostracodes present were hand picked with a fine sable-hair brush and arranged in assemblage slides. The type specimens were photographed on Jeol SEM using ORWO 120, black and white 100 ASA film. A total of 4,040 ostracodes were picked up, counting both complete carapaces and open valves as individual specimens. Their distribution is given in Table 4 and all the species recognized in this work are illustrated in Figures 2–5.

Composition, age and affinity of ostracode fauna

The ostracode fauna of the Inter-trappean beds of Duddukuru comprises 27 species (Table 1). These belong to 13 families, 4 species each to the families Cytherellidae, Cytheridae, and Cytheruridae, 3 species each to the families Hemicytheridae and Trachyleberididae, two species to the family Xestoleberididae, and one species each to the families Bairdiidae, Candonidae, Cushmanidae, Cytherideidae, Krithidae, Limnocythereidae and Loxoconchidae. An analysis of these is given below.

1. Three species are left under open nomenclature and nine species are considered new. These are of little use in age interpretation at present.

Table 1. Generalized stratigraphy of the coastal tract of the Krishna-Godavari districts, Andhra Pradesh.

Age	Formation
Quaternary	Alluvium
Mio-Pliocene	Rajahmundry Formation
Late Maastrichtian-Early Paleocene	Deccan Trap with Inter-trappean beds
Late Maastrichtian	Infra-trappean Limestone
Late Cretaceous	Tirupati Formation
Early Cretaceous	Raghavapuram Formation
Triassic-Jurassic	Kota Formation (Upper Gondwana)
Permian	Kamthi Formation (Lower Gondwana)
Archean	Khondalite

Table 2. Stratigraphic succession of Section I.

Sample No.	Lithology	Thickness in meters
	Black colored basalt	1.2
	Grey shale	0.45
	Red shale	0.45
I/10-11	Light yellow limestone	2
I/9	Yellowish grey clay	0.15
I/8	Light yellow limestone	0.76
I/6-7	Yellowish grey clay	0.25
I/4-5	Brownish yellow marl	0.3
I/3	Grey clay	0.3
I/2	Greyish white clay	0.25
I/1	Light yellow limestone	2.44
	Black colored basalt	Base not exposed

Table 3. Stratigraphic succession of Section II.

Sample No.	Lithology	Thickness in meters
II/6-8	Greyish white limestone	0.81
II/5	Grey clay	0.38
II/1-4	Light yellow limestone	1.22
		Base not exposed

2. Eight species, *Costabuntonia hartmanni* (Jain), *Cushmanidea bhatiai* Bhandari, *Cytherella mohani* Bhandari, *Falsocythere elongata* (Bhalla), *Hermanites sastryi* Bhalla, *Hornibrookella tewarii* (Bhalla), *Neocyprideis raoi* (Jain), and *Palmococoncha rajui* Bhandari, have so far been known only from Duddukuru (Jain, 1978; Bhalla, 1979b, c, 1980; Bhandari, 1995).

3. One species, *Xestoleberis subglobosa* (Bosquet), has been recorded widely from the Eocene beds of France, Belgium, Netherlands (Keij, 1957) and also from the Middle Eocene of Kachchh, western India (Guha, 1968; Khosla and Pant, 1988), Himachel Pradesh, northern India (Mathur, 1969) and the Lower Eocene of Rajasthan, western India (Khosla, 1972).

4. One species, *Bairdia beraguaensis* Singh and Tewari, has previously been recorded from the Early Eocene beds

of Jammu and Kashmir (Tewari and Singh, 1966), Pakistan (Sohn, 1970), Rajasthan (Khosla, 1972), Meghalaya (Singh, 1984) and from the Middle Eocene beds of Assam (Neale and Singh, 1985).

5. Three species, *Cytherelloidea bhatiai* Guha and Shukla, *Paijenborchellina indica* (Khosla) and *Paracypris khuialaensis* Bhandari, have been described from the Early Eocene beds, the first from Vridhachalam, Tamilnadu, southern India (Guha and Shukla, 1974), the other two from Rajasthan (Khosla, 1972; and Bhandari, 1996). *P. indica* has also been reported from Kachchh (Khosla and Pant, 1988).

6. Two species, *Holcopocythere bassiporosa* Al-Furaih and *Nucleolina diluta* Al-Furaih, have been recorded from the latest Cretaceous and Early Paleocene beds of Saudi Arabia (Al-Furaih, 1980).

From the analyses given above it is apparent that the majority of the ostracodes are either new or have so far been known from the Inter-trappean beds of the east coast of India. One species, *X. subglobosa*, occurs widely in the Eocene beds. Four species, *B. beraguaensis*, *C. bhatiai*, *P. indica*, and *P. khuialaensis*, were originally reported from the lower Eocene beds, and two species, *H. bassiporosa* and *N. diluta*, are characteristic of Early Paleocene age. So far as the Early Eocene species are concerned, it is feared that the stratigraphic horizons from where the occurrences of these species were reported; i.e. Fuller's Earth at Palana, Bikaner District, Rajasthan (Khosla, 1972), Kakdi Stage, Kachchh District (Khosla and Pant, 1988), and sub-surface samples from Vridhachalam District (Guha and Shukla, 1974), have not been precisely dated on the basis of planktonic foraminifers and might be of Paleocene age. The presence of *H. bassiporosa* and *N. diluta* in the Inter-trappean beds of the east coast of India is suggestive of an Early Paleocene age for the beds.

This is in conformity with the views of Bhandari (1995), who has proposed an Early Paleocene age for these beds on the basis of similarity of their ostracode fauna with the ostracodes of the Karimpur Member of the Ghatal Formation of Dhananjapur Well No. 1, West Bengal Basin. In the Karimpur Member ostracodes are associated with a few planktonic foraminifers like *Morozovella pseudobulloidis* and smaller benthics like *Protelphidium adamsi*, *Discorbis midwayensis* var. *soldadoensis* etc., suggesting an Early Paleocene (Danian) age (= 1PB on Planktic scale).

Paleoenvironments

The Inter-trappean beds of the Rajahmundry area (as is true of other coastal formations in India) are the result of a marine transgression, which took place in Early Paleocene times. The paleoenvironment of the beds is discussed on the basis of evidence furnished by ostracodes.

Table 4. Distribution of ostracodes in the Inter-trappean beds of the east coast of India.

Horizon	Sample number																Total				
	Section I											Section II									
	1	2	3	4	5	6	7	8	9	10	11	1	2	3	4	5		6	7	8	
<i>Bairdia beraguaensis</i> Singh & Tewari																			1	1	
<i>Costabuntonia hartmanni</i> (Jain)						3	4	2	42	4	2			3					16	6	82
<i>Cushmanidea bhatiai</i> Bhandari												2	1	1	10				4		18
<i>Cytherella mohani</i> Bhandari														3					11	6	20
<i>Cytherella</i> sp. A																			4		4
<i>Cytherella</i> sp. B																			1		1
<i>Cytherelloidea bhatiai</i> Guha & Shukla									1										5	1	7
<i>Cytheromorpha godavariensis</i> sp. nov.						2					1	14	75	35							127
<i>Cytherura duddukuruensis</i> sp. nov.									3	29	9	8	106	136					18		309
<i>Falsocythere elongata</i> (Bhalla)								4					1						35		40
<i>Paijenborchellini</i> gen. et sp. indet. A					2	1															3
<i>Hapsicytheridea undulata</i> sp. nov.						1			2	34	6	37	164	105	4					11	364
<i>Hermanites sastryi</i> Bhalla					6	10			31	3		4	7						38	3	102
<i>Holcopocythere bassiporosa</i> Al-Furaih						18			2				4								24
<i>Hornibrookella tewarii</i> (Bhalla)									16	24				2				4	69	33	148
<i>Krithe bhandarii</i> sp. nov.									4	2	2	25	76	138					17		264
<i>Munseyella indica</i> sp. nov.									1										6		7
<i>Neocyprideis raoi</i> (Jain)				85	203	304	418	38	53	12	10	211	360	130			41	69			1934
<i>Neomonoceratina paraoertlii</i> sp. nov.							1					39	143	92							275
<i>Nucleolina diluta</i> Al-Furaih																			8	10	18
<i>Paijenborchellina indica</i> (Khosla)																			24		24
<i>Palmoconcha rajui</i> Bhandari						5	3		2	51	8	2	6	4						38	119
<i>Paracandona andhraensis</i> sp. nov.			10																		10
<i>Paracypris khuialaensis</i> Bhandari													8	4					4		16
<i>Semicytherura diluta</i> sp. nov.													33	63	14						110
<i>Uroleberis rasilis</i> sp. nov.																			3		3
<i>Xestoleberis subglobosa</i> (Bosquet)										3									7		10
TOTAL	0	0	10	85	211	344	430	40	157	162	40	383	1017	664	4	0	45	339	109		4040

Section I

In Section I ostracodes make their first appearance in grey clay (Sample No. 3) where they are represented by a solitary species of *Paracandona*. The underlying beds, in ascending order, light yellow limestone (Sample No. 1) and greyish-white clay (Sample No. 2) are devoid of ostracode fauna. *Paracandona* is a characteristic freshwater genus. Its occurrence in the grey clay suggests that the bed might have accumulated in a similar environment.

In the succeeding brownish-yellow marl (lower part, Sample No. 4) appears a species of *Neocyprideis*, which occurs commonly in it. Soon, however, the species becomes enormously abundant in the overlying beds. In brownish-yellow marl (upper part, Sample No. 5) it constitutes 97% of the entire ostracode assemblage, while in yellowish-grey clay, sample Nos. 6 and 7, it forms 84% and 98% respectively. The other ostracodes present in their order of predominance are *Hermanites*, *Costabuntonia*, *Holcopocythere*, Genus A, *Palmoconcha*, *Cytheromorpha*, *Hapsicytheridea* and *Neomonoceratina*.

Of these ostracodes, little is known about the ecology of

the genera *Costabuntonia*, Genus A, *Holcopocythere* and *Hapsicytheridea* as they do not occur in the present day. The genera *Hermanites* and *Neomonoceratina* are epineritic and the genus *Cytheromorpha* is characteristic of mesohaline to littoral environments (Morkhoven, 1963). A Recent species of *Palmoconcha* has been described by Swain and Gilby (1974) from Station I, Bahia Sebastian Vizcaino, Baja California at a depth of 59 m. The genus *Neocyprideis* is closely related to the living genus *Cyprideis*, which probably evolved from it (Morkhoven, 1963). The latter genus inhabits freshwater to hypersaline conditions, but is most abundant in mesohaline salinities and hence is regarded as the most typical brackish-water ostracode. According to Keij (1957), Morkhoven (1963), Oertli (1967), Keen (1977) and Neale (1988), *Neocyprideis* also occurs predominantly in brackish-water environments. Keen (1977) records the genus from three brackish-water assemblages, maximum predominance being in assemblage IV of the Upper Eocene beds of the Hampshire Basin, U. K. Assemblage IV is taken to represent salinities of 9.0 to 16.5‰. Neale (1988) has observed that minimum di-

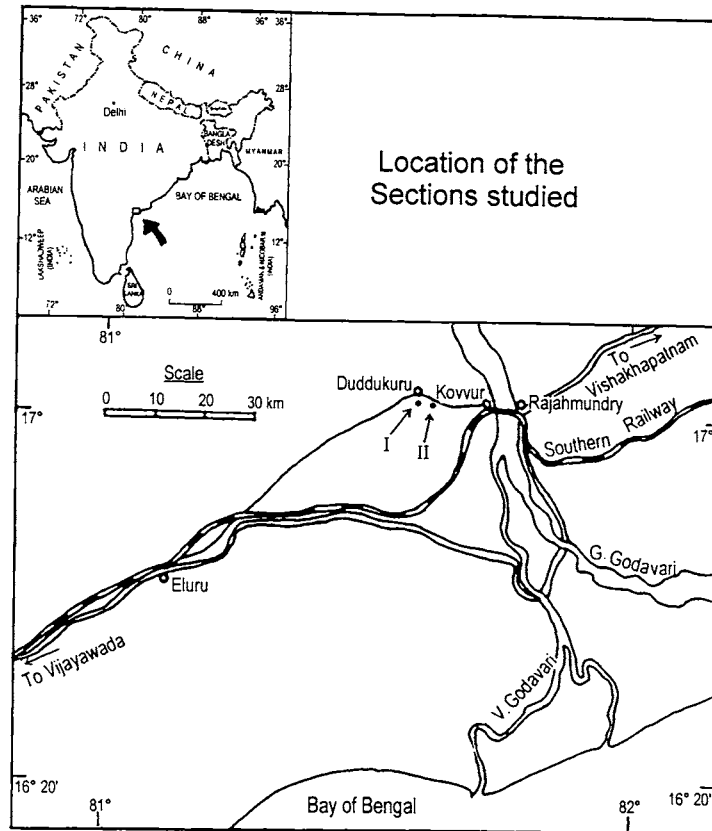


Figure 1. Index map of part of Andhra Pradesh showing locations of the sections studied.

versity of species and abundance of individuals and reached in low brackish-water environments. In the present Sample Nos. 4-7 of Section I *Neocyprideis* constitute a very high proportion of the ostracode assemblages (84 to 100%) and other ostracodes together form small fractions, suggesting that the brownish yellow marl and yellowish-grey clay were deposited in a mesohaline (9 to 16.5‰), outer bay environment.

There is a sharp decline both in diversity as well as frequency of ostracode fauna in the overlying light yellow limestone (Sample No. 8). Only two species of *Neocyprideis* and *Costabuntonia* are encountered in this bed suggesting a temporary shallowing of the basin, and the bed might have been deposited in the marginal estuarine environments. This view is further corroborated by disappearance of foraminifers except for some *Nonion*. Megafossils are represented by *Ostrea*, characteristic of near-shore environments.

There was again an influx of a large number of ostracode species in the succeeding yellowish-grey clay (Sample No. 9) and light yellow limestone (Sample Nos. 10 and 11). The ostracodes in order of predominance are: *Neocyprideis*, *Palmoconcha*, *Cytherura*, *Costabuntonia*, *Hermani-*

tes, *Hapsicytheridea*, *Hornibrookella*, *Krithe*, *Cushmanidea*, *Cytherelloidea*, *Cytheromorpha*, *Falsocythere*, *Holcopocythere*, *Munseyella* and *Xestoleberis*. Of these, eight genera appear for the first time. Their ecological significance is as follows. The genus *Hornibrookella* is extinct and therefore little is known about its ecology. The genus *Cytherelloidea* inhabits shallow, warm marine waters; occasionally it is also found in brackish-water (mesohaline) environments (Morkhoven, 1963). According to Sohn (1964), the genus is a good paleotemperature indicator and in the present-day seas it does not survive in temperatures less than 10 °C. The genus *Cytherura* inhabits mesohaline to littoral environments (Morkhoven, 1963). The genus *Falsocythere* is a shallow marine form. A living species of the genus has been described from the coastal waters of the Adriatic Seas by Bonaduce *et al.* (1975) and the Gulf of Aquaba (Red Sea) by Bonaduce *et al.* (1980). There is some difference of opinion about the ecology of the genus *Krithe*. According to van den Bold (1960), it occurs in a near-shore as well as an open-shore facies, while Morkhoven (1963) is of the view that the genus is strictly marine and most commonly occurs in infraneritic to bathyal environments. The genus *Munseyella* thrives well in an

epineritic environment predominantly in warmer waters (Morkhoven, 1963). Studies of living species of *Cushmanidea* by Ascoli (1964) and McKenzie and Swain (1967) suggest that the genus inhabits lagoonal to shallow-water environments. Keen (1977) records it from the assemblage V (polyhaline, 16.5 to 33‰) of the Upper Eocene beds of Hampshire, U.K.

Ecological significance of the genera *Neocyprideis*, *Palmoconcha*, *Hermanites* and *Cytheromorpha* has already been discussed. In the present beds under discussion the frequency of *Neocyprideis* declines considerably as compared to underlying beds (Sample Nos. 4 to 7) and the appearance of a number of marine genera suggests that the yellowish-grey clay and light yellow limestone might have been deposited in a polyhaline bay (16.5 to 33 ‰).

Section II

The section II is only 2.41 meters thick and comprises, in ascending order, light yellow limestone (Sample Nos. 1 to 4), grey clay (Sample No. 5) and greyish-white limestone (Sample Nos. 6–8). The ostracode fauna in the section is much varied and of high frequency in the lower and upper limestone beds, but absent in the middle grey clay. This succession corresponds with the upper part of the succession in Section I (i.e. yellowish-grey clay and light yellow limestone). The paleoecology of the ostracodes in Section II is discussed below.

The ostracodes in the light yellow limestone (Sample Nos. 1–4) in their order of predominance are *Neocyprideis*, *Hapsicytheridea*, *Neomonoceratina*, *Cytherura*, *Krihe*, *Cytheromorpha*, *Semicytherura*, *Costabuntonia*, *Cushmanidea*, *Palmoconcha*, *Hermanites*, *Paracypris*, *Cytherella*, *Falsocythere*, *Holcopocythere* and *Hornibrookella*.

The genera *Cytherella*, *Paracypris* and *Semicytherura* appear for the first time in this bed. These are essentially marine genera (Morkhoven, 1963). The genus *Cytherella* occurs at all depths and rarely is also found in brackish-water (mesohaline) environments. The genus *Paracypris* mainly occurs in deeper water but is very rare in occurrence, and hence may not be of much significance. The genus *Semicytherura* is epineritic, predominantly littoral. The high diversity of shallow marine genera and presence of *Neocyprideis* in large numbers suggest that the limestone bed might have accumulated in a polyhaline-bay, brackish-water environment similar to the top two beds of Section I.

The overlying grey clay (Sample No. 5) is devoid of ostracodes. Possibly there was a temporary shallowing of the basin and the bed was deposited in marginal estuarine environments similar to the light yellow limestone (Sample no. 8) of Section I.

The succeeding greyish white limestone is again rich in ostracode fauna. It is represented in order of dominance

by *Hornibrookella*, *Neocyprideis*, *Costabuntonia*, *Hermanites*, *Falsocythere*, *Palmoconcha*, *Cytherella*, *Cytherura*, *Hapsicytheridea*, *Krihe*, *Xestoleberis*, *Paijenborchellina*, *Cytherelloidea*, *Nucleolina*, *Bairdia*, *Cushmanidea*, *Munseyella*, *Paracypris* and *Uroleberis*.

The genera *Paijenborchellina*, *Nucleolina*, *Bairdia* and *Uroleberis* appear for the first time in this bed. The genus *Nucleolina* does not extend in the present day. Therefore little is known about its ecological significance. Studies of certain living species of the genus *Paijenborchellina* from the Abu Dhabi lagoon, Persian Gulf (Bate, 1971) show that it occurs from littoral to near-shore shelf environments. The genus *Bairdia* is a characteristic marine form occurring both in very shallow as well as very deep waters (Morkhoven, 1963). In the present day the genus *Uroleberis* occurs in epineritic environments (Morkhoven, 1963). The ecological significance of other genera has already been discussed.

Like the light yellow limestone (Sample Nos. 1–4) of Section II and the upper two beds of Section I, the present bed is characterised by varied shallow marine ostracodes, suggesting that it was also deposited in a polyhaline bay.

The paleoenvironmental inferences drawn above are more or less similar to those of Bhalla (1967) and Bhandari (1995) who also worked on the Inter-trappean beds of this region. According to Bhalla (1967), the foraminiferal and ostracode assemblages reflect rhythmic facies changes with alternate brackish-water and normal marine environments of deposition. He also recorded two marine incursions in the area. Bhandari (1995) inferred that the Inter-trappean beds of Duddukuru were deposited in brackish-water to shallow inner neritic conditions around 0–10 m deep with intermittent freshwater conditions.

Systematic paleontology

The classification of ostracodes in this paper follows that of Hartmann and Puri (1974). Descriptions of already known and well established species are omitted for the sake of brevity. The illustrated specimens are deposited in the museum of the Department of Geology, Mohan Lal Sukhadia University, Udaipur and catalogued with the prefix SUGDMF.

Order Podocopida
Suborder Platycopina
Family Cytherellidae
Genus *Cytherella* Jones, 1849

Type species.—*Cytherina ovata* Roemer, 1840.

Cytherella sp. A

Figure 2.3

Cytherella sp. cf. *muensteri* (Roemer). Jain, 1978, p. 52, pl. 1, fig. 1.

Material.—Four carapaces.

Remarks.—The species was recorded as *Cytherella* sp. cf. *muensteri* by Jain (1978) from the Inter-trappean beds of Kateru, Rajahmundry. It, however, differs from *Cytherella muensteri* (Roemer) in having an angulated dorsal margin, the greatest height located near the middle, and a smooth surface. *C. muensteri*, in contrast, has the greatest height located at the posterior 1/3 of the length, has a pitted surface, and lacks the dorsal angulation. The species is left under open nomenclature.

Dimensions.—A carapace, SUGDMF no. 565, length 0.69 mm, height 0.42 mm, width 0.27 mm.

Occurrence.—Section II.

Cytherella sp. B

Figure 2.4

Material.—One carapace.

Description.—Carapace subrectangular in lateral outline; height equal in anterior and posterior halves; right valve slightly overlaps left valve along dorsal and ventral margins; dorsal margin nearly straight; ventral margin slightly concave, anterior and posterior margins rounded; valve surface smooth.

Remarks.—This species differs from *Cytherella mohani* Bhandari, 1995 and *Cytherella* sp. A recorded herein in the lateral outline and degree of overlap. *C. mohani* is subovate in shape with a pronounced overlap, while *Cytherella* sp. A is an elongate form having an angulated dorsal margin. The present species is left under open nomenclature.

Dimensions.—A carapace, SUGDMF no. 566, length 0.74 mm, height 0.42 mm, width 0.32.

Occurrence.—Section II.

Genus *Cytherelloidea* Alexander, 1929

Type species.—*Cythere* (*Cytherella*) *williamsoniana* Jones, 1849.

Cytherelloidea bhatiai Guha and Shukla, 1974

Figure 2.5

Cytherelloidea bhatiae Guha and Shukla, 1974, p. 96, 97, pl. 2, fig. 10.

Cytherelloidea sp. cf. *C. keiji* McKenzie. Jain, 1978, p. 52, 53, pl. 1, figs. 2, 3. Bhandari, 1995, p. 94, pl. 1, fig. 3.

Material.—Seven carapaces.

Description.—Carapace subrectangular in lateral outline, with height equal in both anterior and posterior halves; valve surface ornamented by elongate punctation; two prominent, sinuate, transverse ridges extending three-fourths of length joined by a posterior vertical ridge; and marginal rim along dorsal, anterior and ventral margins.

Remarks.—The present specimens from Duddukuru are referred to *Cytherelloidea bhatiai* Guha and Shukla (1974) (species name misspelled as *bhatiae*) described from the Lower Eocene of Gopurapuram well, Vridhachalam, Tamilnadu. The form described as *Cytherelloidea* sp. cf. *C. keiji* from the Inter-trappean beds of the east coast of India by Jain (1978) and Bhandari (1995) belongs to this species. According to McKenzie *et al.* (1990) *Keijcyoidea keiji* (earlier referred to *Cytherelloidea*) is a Pleistocene-Recent species ranging in distribution from the southwestern Pacific to northwestern and southern Australia.

Dimensions.—A carapace, SUGDMF no. 567, length 0.48 mm, height 0.29 mm, width 0.21 mm.

Occurrence.—Sections I and II.

Suborder Podocopa
Superfamily Cytheracea
Family Cytheridae
Subfamily Cytherinae
Tribe Cytherini

Genus *Cytheromorpha* Hirschmann, 1909

Type species.—*Cythere fuscata* Brady, 1869.

Cytheromorpha godavariensis sp. nov.

Figure 2.7–2.9

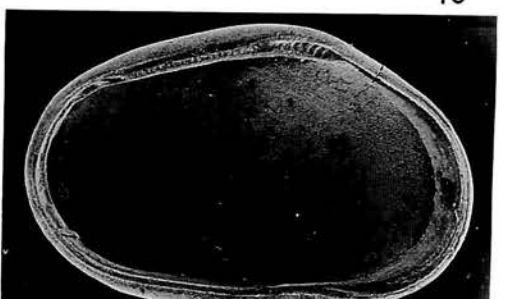
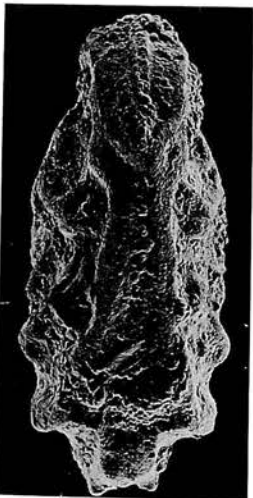
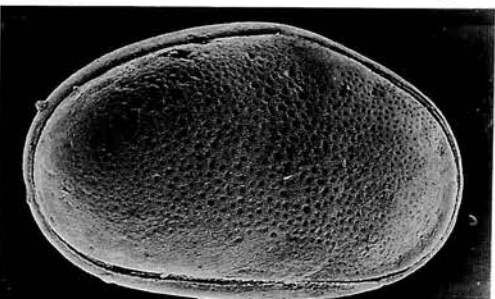
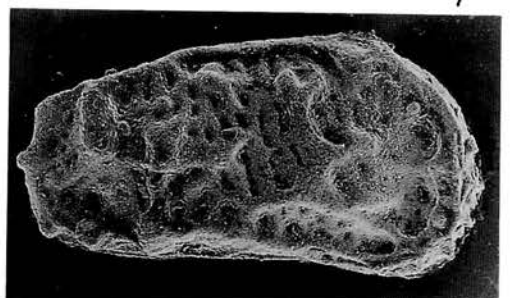
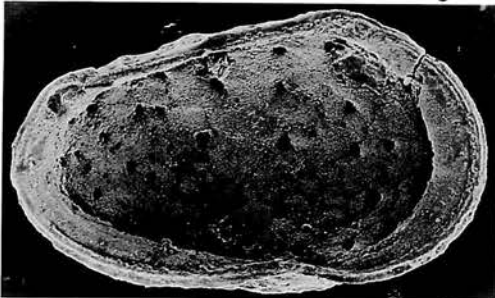
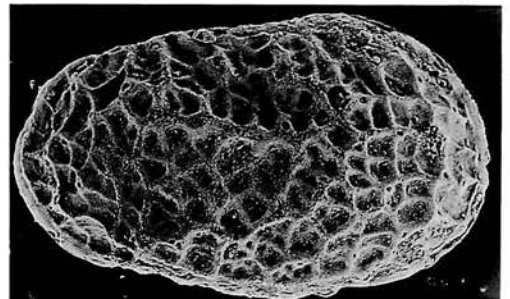
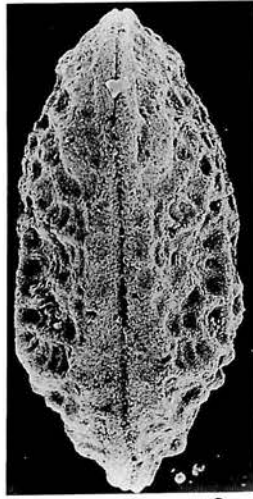
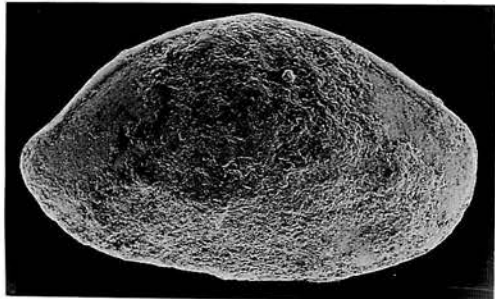
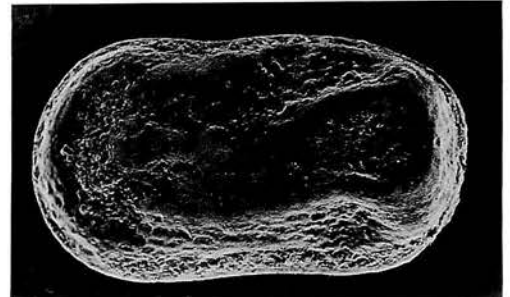
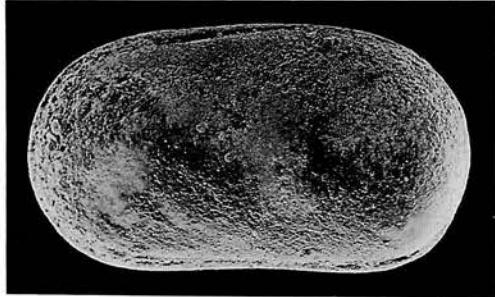
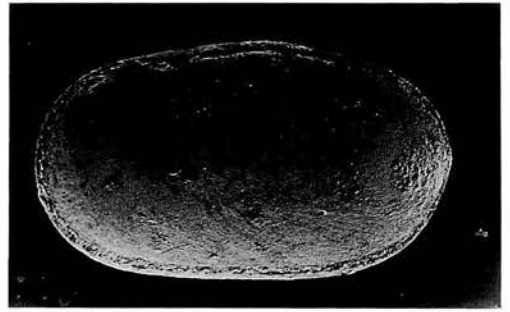
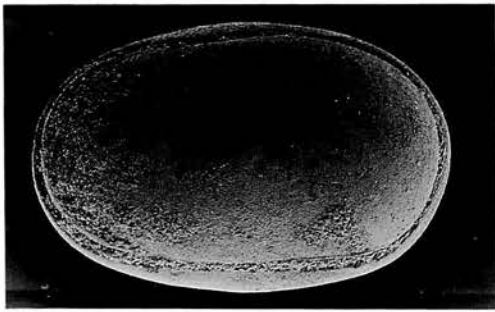
Etymology.—After the Indian River Godavari.

Material.—124 carapaces and 3 valves.

Type locality.—Light yellow limestone (Sample SUGDMF no. 3/II), Inter-trappean beds, Paleocene, Section II.

Diagnosis.—Surface strongly reticulate and with a transverse median ridge.

Description.—Carapace subquadrate in lateral outline, with greatest height at anterior cardinal angle; overlap indistinct; valve inflated ventrally; dorsal margin straight converging posteriorly; ventral margin obscured medially; anterior margin broadly rounded; posterior margin much narrower, subangulate near mid-height; in dorsal view carapace somewhat biconvex, both ends taper, more in posterior than in anterior, maximum width posterior to middle. Valve surface strongly reticulate, edges of reticulation meshes in anterior half raised in low costae; a transverse ridge in median region. Inner lamella moderately wide along anterior and posterior margins and narrows ventrally;



vestibule present; selvage near outer periphery; normal pores few, widely spaced. Hinge gongyodont; in left valve it consists of an indistinct socket surrounded by a crenulate anterior tooth, which is a continuation of the median crenulate bar and a posterior socket with a distinct tooth at its inner edge.

Dimensions.—Holotype, SUGDMF no. 569, a carapace, length 0.30 mm, height 0.19 mm, width 0.14 mm; paratype I, SUGDMF no. 570, a left valve, length 0.32 mm, height 0.19 mm; paratype II, SUGDMF no. 571, a carapace, length 0.30 mm, height 0.18 mm, width 0.16 mm.

Discussion.—*Cytheromorpha godavariensis* sp. nov. resembles *Cytheromorpha kirtharensis* Guha (1968) described from the Middle Eocene of Kachchh in general appearance. *C. kirtharensis*, however, differs from the present species in having concentrically arranged reticulation and a lack of median transverse ridge. *Cytheromorpha bulla* Haskin (1971) described from the Tertiary beds of the Isle of Wight also resembles *C. godavariensis* sp. nov. in overall lateral outline and surface ornamentation but differs in having three distinct vertical ridges in the anterior half.

Occurrence.—Sections I and II.

Tribe Pectocytherini
Genus *Munseyella* van den Bold, 1957

Type species.—*Toulminia hyalokystis* Munsey, 1953.

Munseyella indica sp. nov.

Figure 2.10, 2.11

Etymology.—After the country of India.

Material.—Six carapaces and one valve.

Type locality.—Greyish-white limestone (Sample SUGDMF no. 7/II), Inter-trappean beds, Paleocene, Section II.

Diagnosis.—Surface ornamented by ridges and vertically arranged pits.

Description.—Carapace subquadrate in lateral outline, with greatest height about half of length at anterior cardinal angle; posterior cardinal angle well marked; valves almost equal; dorsal margin nearly straight, sloping down posteriorly; ventral margin concave; anterior margin broadly rounded; posterior straight, nearly perpendicular to

ventral margin; anterior margin fringed with 6 or 7 spines and posterior margin with two spines, one at mid-posterior and the other at posteroventral region; in dorsal view carapace rather compressed. Valve surface ornamented by anterior marginal ridge which also continues ventrally slightly above margin; a dorsal ridge extending from anterior cardinal angle backward overhanging margin, in posterodorsal region it turns downward forming a thick knob; two short furcating transverse ridges, one in posteromedian-median region and the other in ventromedian-anterioventral region; a vertical ridge extending downward from anterodorsal region; vertically arranged deep elongate pits over rest of area.

Dimensions.—Holotype, SUGDMF no. 572, a right valve, length 0.38 mm, height 0.21 mm; paratype, SUGDMF no. 573, a carapace, length 0.42 mm, height 0.22 mm, width 0.19 mm.

Discussion.—The species closely resembles *Munseyella japonica* (Hanai, 1957), a Recent species from Kanagawa Prefecture, Japan in overall shape but differs in surface ridge pattern and having vertically arranged, elongate pits.

Occurrence.—Sections I and II.

Tribe Paijenborchellini
Genus *Neomonoceratina* Kingma, 1948

Type species.—*Neomonoceratina columbiformis* Kingma, 1948.

Neomonoceratina paraoertlii sp. nov.

Figure 3.1, 3.2

Etymology.—From Greek *para*, meaning “beside,” with reference to its resemblance with *Neomonoceratina oertlii* Guha, 1967.

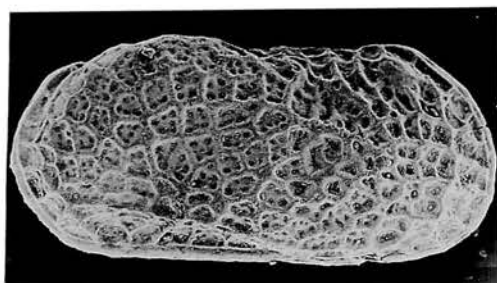
Material.—275 carapaces.

Type locality.—Light yellow limestone (Sample SUGDMF no. 3/II), Inter-trappean beds, Paleocene, Section II.

Diagnosis.—Surface distinctly reticulate, meshes with 5 or 6 pores, and a depression between ventral ridge and margin.

Description.—Carapace elongate, subrectangular in lateral outline, height almost equal in anterior and posterior halves; overlap indistinct; dorsal margin nearly straight

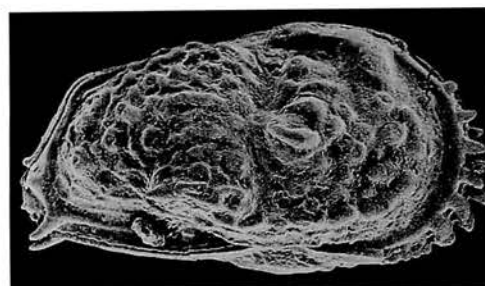
← **Figure 2.** 1, 2. *Cytherella mohani* Bhandari. 1, carapace, SUGDMF no. 563, left valve view, $\times 78$; 2, carapace, SUGDMF no. 564, dorsal view, $\times 80$. 3. *Cytherella* sp. A, carapace, SUGDMF no. 565, left valve view, $\times 83$. 4. *Cytherella* sp. B, carapace, SUGDMF no. 566, left valve view, $\times 81$. 5. *Cytherelloidea bhatiai* Guha and Shukla, carapace, SUGDMF no. 567, left valve view, $\times 123$. 6. *Bairdia beraguaensis* Singh and Tewari, carapace, SUGDMF no. 568, right valve view, $\times 76$. 7–9. *Cytheromorpha godavariensis* sp. nov. 7, holotype, SUGDMF no. 569, carapace, right valve view, $\times 210$; 8, paratype I, SUGDMF no. 570, left valve, internal view, $\times 200$; 9, paratype II, SUGDMF no. 571, carapace, dorsal view, $\times 213$. 10, 11. *Munseyella indica* sp. nov. 10, holotype, SUGDMF no. 572, right valve, lateral view, $\times 166$; 11, paratype, SUGDMF no. 573, carapace, dorsal view, $\times 152$. 12, 13. *Neocyprideis raoi* (Jain). 12, carapace, SUGDMF no. 579, right valve view, $\times 80$; 13, left valve, SUGDMF no. 580, internal view, $\times 81$.



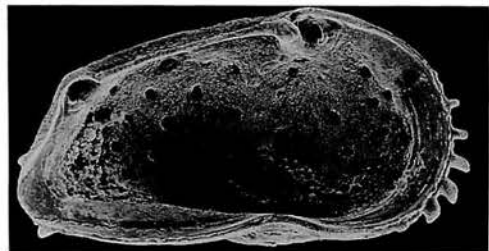
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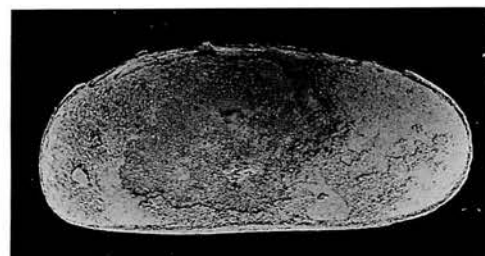
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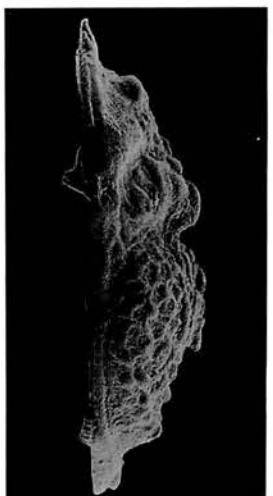
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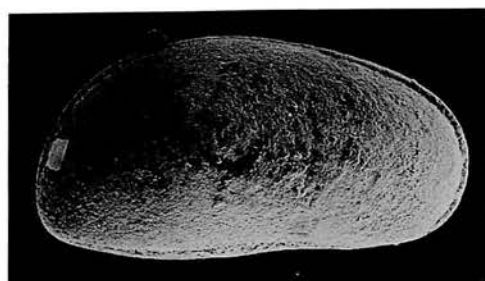
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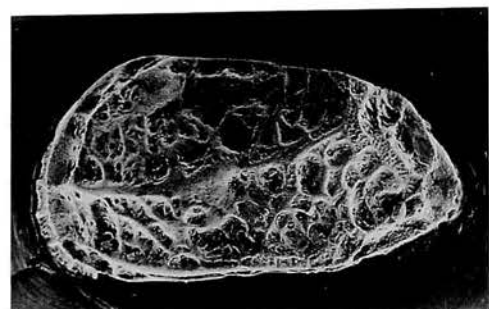
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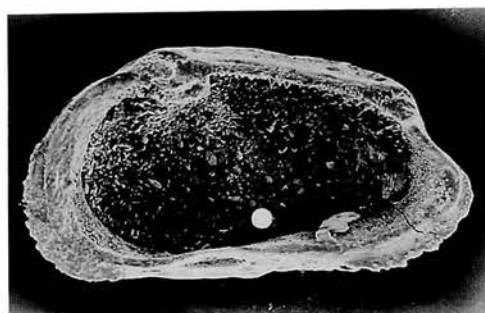
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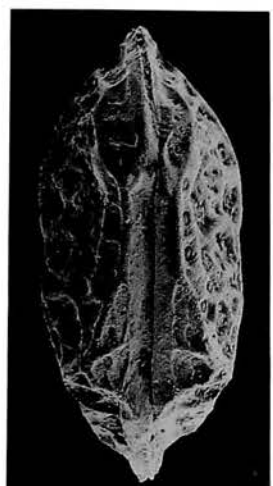
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anteriorly and with a distinct hump posteriorly, obscuring margin; ventral margin straight; anterior margin broadly rounded; posterior margin less so; in dorsal view ends compressed, sides more or less parallel. Eye tubercle present. Valve surface marked by a shallow depression in mid-dorsal and dorsomedian regions; distinct reticulation, meshes mostly quadrangular in shape and with 5 or 6 pores; three feeble longitudinal ridges, median ridge extending from mid-anterior region to posteromedian region, ventral ridges nearly parallel, sloping up and back from mid-ventral region; and a prominent depression between ventral ridge and margin. Internal characters not known.

Dimensions.—Holotype, SUGDMF no. 574, a carapace, length 0.42 mm, height 0.19 mm, width 0.18 mm; paratype, SUGDMF no. 575, a carapace, length 0.40 mm, height 0.19 mm, width 0.19 mm.

Discussion.—The species very closely resembles *Neomonoceratina oertlii* Guha (1967) from the Miocene of Saurashtra, Gujarat in lateral outline and overall surface ornamentation. The latter species, however, differs in being much larger in size and having a distinct vertical sulcus.

Occurrence.—Sections I and II.

Paijenborchellini gen. et sp. indet. A

Figure 3.3–3.5

Material.—One carapace and two valves.

Description.—Carapace elongate, subtrapezoidal in lateral outline, with greatest height about half of length at anterior cardinal angle; left valve slightly overlaps right valve along anterodorsal and posteroventral margins; valves somewhat inflated ventrally, overhanging margin in median and anteroventral region; dorsal margin straight, converging backward; posterior cardinal angle well marked; anterior margin broad, obliquely rounded and fringed with 5 large, downwardly curved spines; posterior margin drawn out ventrally and fringed with two spines; in dorsal view carapace sagittate, distinctly compressed near anterior and posterior ends. Valve surface strongly tuberculate, superimposed by punctation, and marked by a row of about 10 tubercles extending from mid-anterior to mid-ventral region, with a subcentral swelling and a vertical sulcus posterior to it. Inner lamella moderately wide; line of concrescence and inner margin coincide; selvage periph-

eral; normal pore widely scattered; central muscle scars comprise a vertical row of four scars, lowest being largest, frontal scar not known. Hinge schizodont; in left valve it consists of an anterior socket with two loculi, a postadjacent bilobate anteromedian tooth, a long crenulate posteromedian bar and a large posterior socket, open interiorly; hinge complementary in right valve, anterior tooth bilobate, posterior tooth indistinctly crenulate.

Remarks.—The species probably belongs to a new genus but no name is proposed because of insufficient material.

Dimensions.—A carapace, SUGDMF no. 576, length 0.62 mm, height 0.32 mm, width 0.27 mm; a left valve, SUGDMF no. 577, length 0.62 mm, height 0.32 mm; a right valve, SUGDMF no. 578, length 0.61 mm, height 0.32 mm.

Occurrence.—Section I.

Family Cytherideidae

Subfamily Cytherideinae

Genus *Neocyprideis* Apostolescu, 1957

Type species.—*Cyprideis (Neocyprideis) durocortoriensis* Apostolescu, 1957.

Neocyprideis raoi (Jain, 1978)

Figure 2.12, 2.13

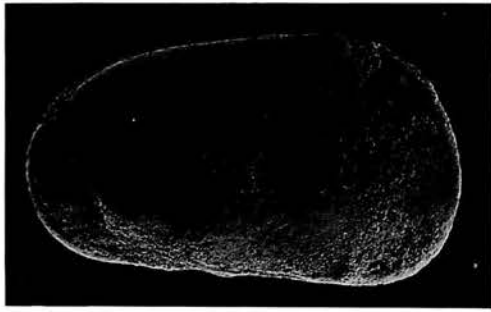
Ovocytheridea raoi Jain, 1978, p. 53, pl. 1, figs. 7–10; Bhandari, 1995, p. 95, 96, pl. 2, figs. 1, 2.

Material.—1134 carapaces and 800 valves.

Remarks.—The species has previously been described as *Ovocytheridea raoi* Jain (1978) from the Inter-trappean beds of Kateru, Rajahmundry and from Duddukuru, West Godavari District, Andhra Pradesh (Bhandari, 1995). This is the most abundant species in our collection and in certain samples it constitutes up to 90 percent of the total ostracode population.

Ovocytheridea is essentially a Cretaceous genus and the majority of the described species of the genus have a trianguloid lateral outline, strongly convex dorsal margin, posterior margin steeply down-sloping and narrowly ventrally rounded, generally smooth valve surface, narrow median hinge element, distinct accommodation groove, and frontal scars that comprise two closely spaced scars. In

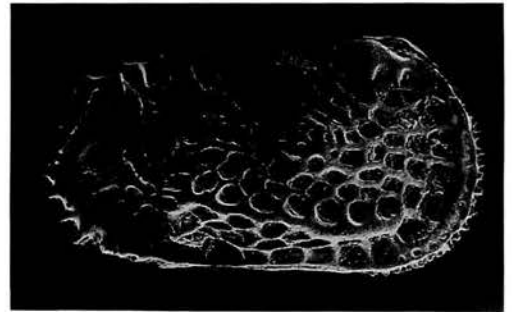
← **Figure 3.** 1, 2. *Neomonoceratina paraoertlii* sp. nov. 1, holotype, SUGDMF no. 574, carapace, right valve view, ×157; 2, paratype, SUGDMF no. 575, carapace, dorsal view, ×152. 3–5. *Paijenborchellini* gen. et sp. indet. A. 3, carapace, SUGDMF no. 576, right valve view, ×102; 4, left valve, SUGDMF no. 577, internal view, ×100; 5, right valve, SUGDMF no. 578, dorsal view, ×105. 6. *Cushmanidea bhatiai* Bhandari, carapace, SUGDMF no. 581, right valve view, ×72. 7, 8. *Krithe bhandarii* sp. nov. 7, holotype, SUGDMF no. 582, male carapace, right valve view, ×142; 8, paratype, SUGDMF no. 583, female carapace, right valve view, ×147. 9–11. *Holcopocythere bassiporosa* Al-Furaih. 9, left valve, SUGDMF no. 584, lateral view, ×111; 10, right valve, SUGDMF no. 585, internal view, ×113; 11, carapace, SUGDMF no. 586, dorsal view, ×120. 12, 13. *Cos-tabuntonia hartmanni* (Jain). 12, female carapace, SUGDMF no. 554, right valve view, ×90; 13, male carapace, SUGDMF no. 557, right valve view, ×87.



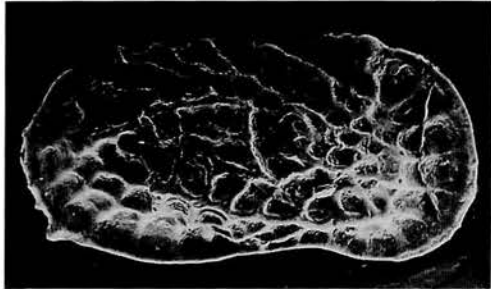
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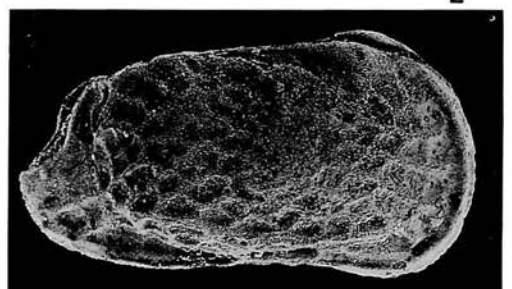
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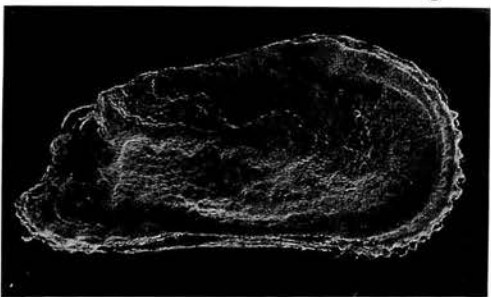
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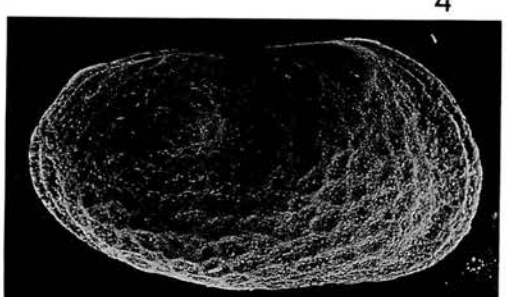
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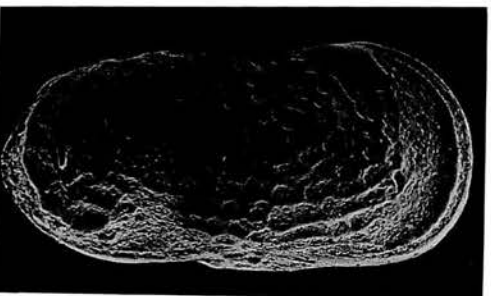
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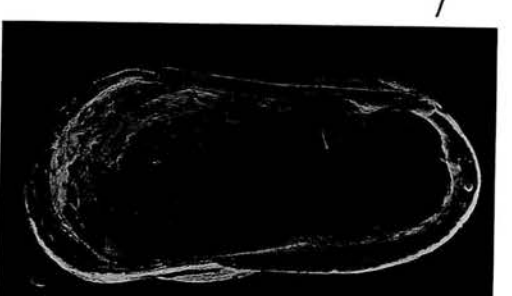
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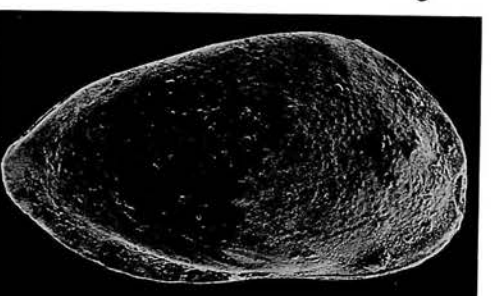
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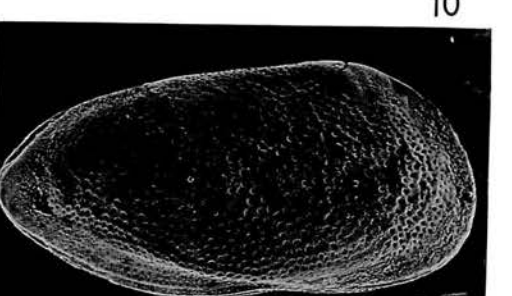
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contrast to this pattern the present species has an elongate and subovate lateral outline, the greatest height slightly anterior to the middle, dorsal margin arched, anterior and posterior margins evenly rounded, median hinge element quite wide, accommodation groove almost lacking, and frontal scar typically v-shaped.

The species is very similar to *Neocyprideis bhupendri* Singh and Mishra (1968) from the Lower Eocene of Rajasthan in all the essential carapace characters (see also Khosla, 1972). This species is also recorded from the Middle Eocene of Kachchh by Khosla and Pant (1988) and the Middle Eocene of Meghalaya by Bhandari (1992). Restudy of the type material of *N. bhupendri* is required to clarify the identity with the present species. The species also closely resembles *Neocyprideis simplex* Siddiqui (2000) from the Lower Eocene of Pakistan in lateral outline and ornamentation. On the basis of the characters given above the present species is transferred to the genus *Neocyprideis*.

Dimensions.—A carapace, SUGDMF no. 579, length 0.75 mm, height 0.48 mm, width 0.40 mm; a left valve, SUGDMF no. 580, length 0.75 mm, height 0.50 mm.

Occurrence.—Sections I and II.

Family Krithidae

Genus *Krithe* Brady, Crosskey and Robertson, 1874

Type species.—*Ilyobates praetexta* Sars, 1866.

Krithe bhandarii sp. nov.

Figure 3.7, 3.8

Etymology.—The species is named in honor of Dr. Anil Bhandari, Chief Geologist, Micropaleontology Laboratory, KDMIPE, ONGC Ltd., Deharadun, India.

Material.—264 carapaces.

Type locality.—Light yellow limestone (Sample SUGDMF no. 3/II), Inter-trappean beds, Paleocene. Section II.

Diagnosis.—Carapace elongate, with greatest height posterior to middle; ventral margin concave anteriorly; posterior margin forming obtuse angle with ventral margin.

Description.—Sexual dimorphism distinct, males being more elongate, less high and wide than females. Carapace

elongate, subrectangular in lateral outline, with greatest height almost half of length posterior to middle; left valve overlaps right valve along dorsal, anterior and mid-ventral margins; dorsal margin asymmetrically convex, merges gradually with anterior margin, and steeply sloping downward from posterior 2/5 of length; ventral margin with a distinct concavity anterior to middle; anterior margin narrow, evenly rounded; posterior obliquely rounded forming obtuse angle with ventral margin; in dorsal view carapace compressed with maximum width near middle. Valve surface smooth.

Dimensions.—Holotype, SUGDMF no. 582, a male carapace, length 0.43 mm, height 0.22 mm, width 0.19 mm; paratype, SUGDMF no. 583, a female carapace, length 0.40 mm, height 0.24 mm, width 0.19 mm.

Discussion.—*Krithe bhandarii* sp. nov. resembles *Krithe oryza* Neale and Singh (1985) and *Krithe* cf. *K. oryza* from the Middle Eocene of Assam in having a vaulted dorsal margin but is readily differentiated in having a distinct concavity along the ventral margin and different outline of the posterior margin.

Occurrence.—Sections I and II.

Family Hemicytheridae

Subfamily Orionininae

Genus *Falsocythere* Ruggieri, 1972

Type species.—*Falsocythere maccagnoii* (Ciampo, 1972) Ruggieri, 1972.

Falsocythere elongata (Bhalla, 1979)

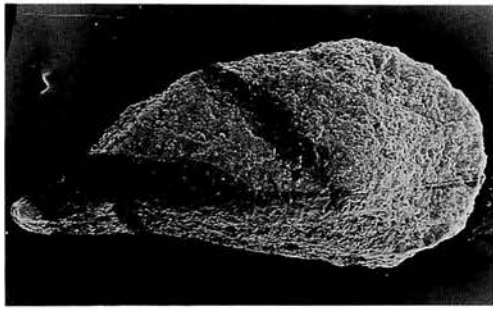
Figure 4.5, 4.6

Occultocythereis elongatum Bhalla, 1979c, p.146–148, figs. A–D.

Material.—40 carapaces.

Description.—Carapace elongate subquadrate in lateral outline, with greatest height about half of length at anterior cardinal angle and greatest length at ventral one-third of height; dorsal margin partly obscured due to overhanging ridge, otherwise straight, sloping down posteriorly; ventral margin slightly concave; anterior margin broadly rounded; posterior margin much narrowed, drawn out ventrally, distinctly concave in upper part and obliquely truncated in lower part; anterior and posterior margins denticulate;

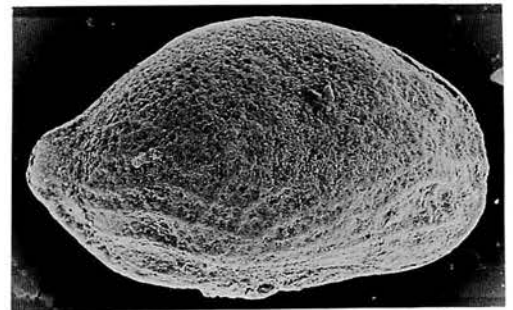
← **Figure 4.** 1. *Nucleolina diluta* Al-Furaih, carapace, SUGDMF no. 587, right valve view, ×84. 2, 3. *Hermanites sastryi* Bhalla. 2, carapace, SUGDMF no. 588, right valve view, ×64; 3, right valve, juvenile, SUGDMF no. 589, lateral view, ×80. 4. *Hornibrookella tewarii* (Bhalla), carapace, SUGDMF no. 590, right valve view, ×86. 5–6. *Falsocythere elongata* (Bhalla). 5, carapace, SUGDMF no. 591, right valve view, ×110; 6, carapace, SUGDMF no. 592, dorsal view, ×119. 7. *Palmoconcha rajui* Bhandari, carapace, SUGDMF no. 593, right valve view, ×122. 8–10. *Hapsicytheridea undulata* sp. nov. 8, holotype, SUGDMF no. 594, carapace, right valve view, ×121; 9, paratype I, SUGDMF no. 595, carapace, dorsal view, ×123; 10, paratype II, SUGDMF no. 596, right valve, internal view, ×122. 11–13. *Cytherura duddukuruensis* sp. nov. 11, holotype, SUGDMF no. 597, female carapace, right valve view, ×157; 12, paratype I, SUGDMF no. 598, female carapace, dorsal view, ×155; 13, paratype II, SUGDMF no. 599, male carapace, right valve view, ×155.



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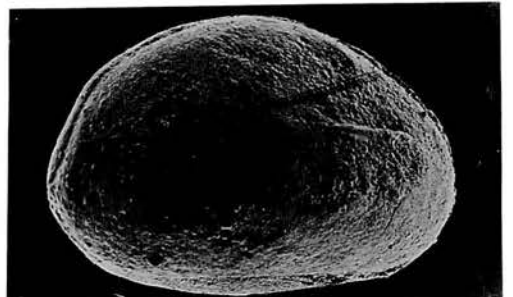
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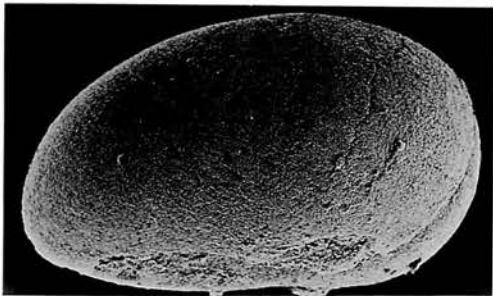
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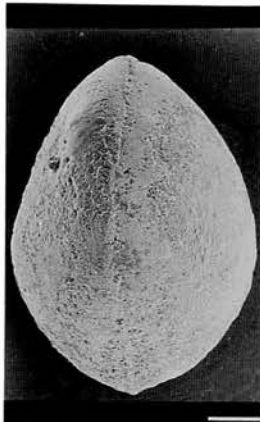
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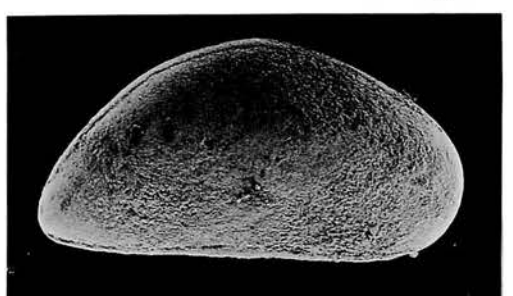
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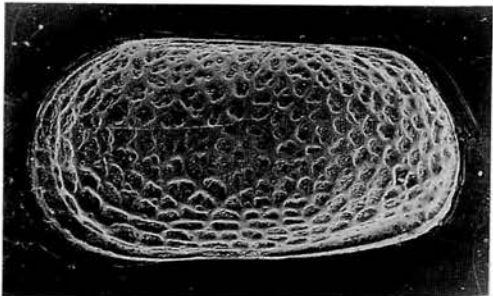
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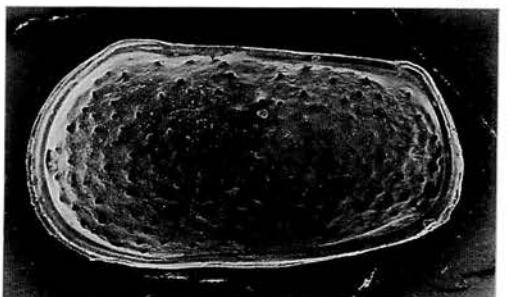
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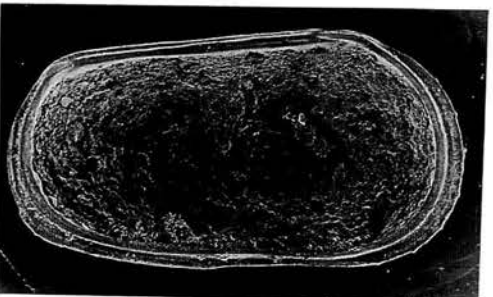
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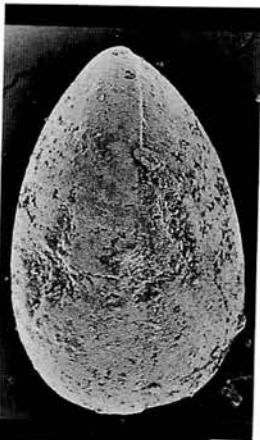
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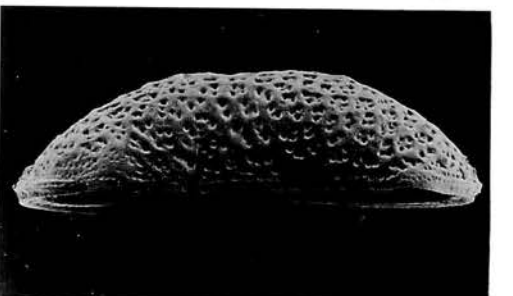
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valve surface ornamented by a high anterior marginal rim which also continues along ventral and posterior margins; an arched dorsal ridge starting from mid-dorsal region overhangs posterodorsal margin and sharply turns forming a U-shaped bend and then continues as a diagonal ridge to anteromedian region; a low vertical ridge extends downwards from the U-shaped bend; area along marginal rim laterally compressed and smooth; faint reticulation over rest of surface

Remarks.—*Occultocythereis elongatum* was described by Bhalla (1979c) from the Inter-trappean beds of Duddukuru. The specimens he illustrated are internal moulds, so that they lack surface reticulation and marginal denticles. The well preserved specimens we newly collected from the type locality allow us to reconsider the generic position of this species.

The lateral outline and surface ornamentation of the species differ from those of the genus *Occultocythereis*. Species of the latter genus generally have a subquadrate lateral outline and a subangular or rounded posterior margin. In addition, they have a valve surface ornamented by 1) a prominent angular massive tubercle at the posterodorsal cardinal angle and a ridge extending from it along the dorsal margin, 2) a prominent anterior rim, 3) a small posteroventral winglike projection with a short vertical ridge posteriorly, and 4) denticles at anterior and posterior margins. Except for having a ventrally drawn-out posterior margin, the present species closely resembles *Falsocythere indica* Khosla and Nagori, 1989, a Lower Miocene species of Kerala, and *F. maccagnoii* (Ciampo, 1972), a Recent species, in overall lateral outline and surface ornamentation. On this basis the species is herein transferred to the genus *Falsocythere*. The difference in the shape of the posterior margin of the present species might be due to the range of variation within the genus.

Dimensions.—A carapace, SUGDMF no. 591, length 0.56 mm, height 0.27 mm, width 0.19 mm; a carapace, SUGDMF no. 592, length 0.53 mm, height 0.27 mm, width 0.19 mm.

Occurrence.—Sections I and II.

Family Loxoconchidae

Genus *Palmoconcha* Swain and Gilby, 1974

Type species.—*Palmoconcha laevimarginata* Swain and

Gilby, 1974.

Palmoconcha rajui Bhandari, 1995

Figure 4.7

Loxoconcha sp. Jain, 1978, p. 56, pl. 2, figs. 6, 7.

Palmoconcha rajui Bhandari, 1995, p. 96, 97, pl. 4, figs. 1–4.

Material.—84 carapaces and 35 valves.

Remarks.—The present species was described from the Paleocene Inter-trappean beds of Duddukuru by Bhandari (1995). It is based on closed carapaces and its generic assignment is highly questionable. The genus *Palmoconcha* is characterised by the presence of flattened, flangelike terminal marginal areas, a gongyodont hinge, a broad vestibule, and numerous closely spaced short marginal pore canals. In contrast, the present species has an anti-merodont hinge structure; in the left valve the hinge comprises loculate terminal sockets that are connected by a finely crenulate median bar, and in the right valve it is complementary, has a few widely spaced, straight, marginal pore canals and lacks flangelike terminal areas and vestibule. Probably a new generic name is required to accommodate this species, but it is deferred unless additional species are found.

Dimensions.—A carapace, SUGDMF no. 593, length 0.51 mm, height 0.29 mm, width 0.29 mm.

Occurrence.—Sections I and II.

Family Cytheruridae

Genus *Hapsicytheridea* Al-Furaih, 1980

Type species.—*Hapsicytheridea binodosa* Al-Furaih, 1980.

Hapsicytheridea undulata sp. nov.

Figure 4.8–4.10

Cytheridella sp. Bhandari, 1995, p. 95, pl. 1, fig. 4.

Etymology.—From Latin, meaning wavy, referring to sinuous venter surface.

Material.—346 carapaces and 18 valves.

Type locality.—Light yellow limestone (Sample SUGDMF no. 8/I), Inter-trappean beds, Paleocene.

← **Figure 5.** 1. *Paijenborchellina indica* (Khosla), carapace, SUGDMF no. 600, right valve view, $\times 105$. 2–4. *Semicytherura diluta* sp. nov. 2, holotype, SUGDMF no. 601, female carapace, right valve view, $\times 150$; 3, paratype I, SUGDMF no. 602, male carapace, right valve view, $\times 137$; 4, paratype II, SUGDMF no. 603, female carapace, dorsal view, $\times 146$. 5, 6. *Uroleberis rasilis* sp. nov. 5, holotype, SUGDMF no. 604, carapace, right valve view, $\times 124$; 6, paratype, SUGDMF no. 605, carapace, dorsal view, $\times 100$. 7, 8. *Xestoleberis subglobosa* (Bosquet). 7, carapace, SUGDMF no. 606, left valve view, $\times 164$; 8, carapace, SUGDMF no. 607, dorsal view, $\times 135$. 9. *Paracypris khuialaensis* Bhandari, carapace, SUGDMF no. 608, right valve view, $\times 71$. 10–13. *Paracandona andhraensis* sp. nov. 10, holotype, SUGDMF no. 609, left valve, lateral view, $\times 129$; 11, paratype I, SUGDMF no. 610, right valve, internal view, $\times 131$; 12, paratype II, SUGDMF no. 611, left valve, internal view, $\times 144$; 13, paratype III, SUGDMF no. 612, right valve, dorsal view, $\times 151$.

Section I.

Diagnosis.—Surface marked by a prominent groove in posteroventral region, an arcuate carina near posterior margin in right valve, and broad shallow reticulation.

Description.—Carapace elongate, subquadrate in lateral view, with greatest height about half of length, at anterior cardinal angle; left valve larger than right valve, overlapping distinctly along anterior and posterodorsal margins; dorsal margin nearly straight; ventral margin sinuate; anterior margin broadly rounded; posterior margin subangulate near mid-height; in dorsal view carapace somewhat inflated, maximum width half of length posteriorly, anterior end narrow, posterior region laterally compressed. Eye tubercle distinct. Valve surface marked by a prominent groove in posteroventral region; a depression posterior to eye tubercle; arcuate carina near posterior margin in right valve; anterior marginal area compressed and smooth; rest of the area ornamented by broad shallow reticulations, arranged in concentric pattern. Inner lamella narrow; line of concrescence and inner margin coincide; selvage distinct near inner periphery; normal pores widely spaced. Hinge antimerodont; in right valve it comprises 8 anterior and 6 or 7 posterior terminal teeth and loculate median groove.

Dimensions.—Holotype, SUGDMF no. 594, a carapace, length 0.53 mm, height 0.26 mm, width 0.27 mm; paratype I, SUGDMF no. 595, a carapace, length 0.53 mm, height 0.26 mm, width 0.26 mm; paratype II, SUGDMF no. 596, a right valve, length 0.51 mm, height 0.26 mm.

Discussion.—The species was originally described as *Cytheridella* sp. by Bhandari (1995) from the Inter-trappean beds of Duddukuru. However, unlike the genus *Cytheridella*, which is characterised by an adont hinge, the new species has a distinct antimerodont hinge structure.

The present species resembles *Hapsicytheridea binodosa* Al-Furaih (1980) from the Lower Paleocene of Saudi Arabia in overall outline and surface ornamentation but differs in the absence of two nodes in the posterolateral region and other ornamental details. The species also lacks a clear caudal process along the posterior margin.

Occurrence.—Sections I and II.

Subfamily Cytherurinae
Genus *Cytherura* Sars, 1866

Type species.—*Cythere gibba* O. F. Müller, 1785.

Cytherura duddukuruensis sp. nov.

Figure 4.11–4.13

Etymology.—After the village of Duddukuru.

Material.—309 carapaces.

Type locality.—Light yellow limestone (Sample SUGDMF no. 3/II), Inter-trappean beds, Paleocene.

Section II.

Diagnosis.—Carapace pear-shaped in lateral outline; surface ornamented by dense fine punctation.

Description.—Sexual dimorphism distinct, males being more elongate, less high and less wide than females; carapace pear-shaped in lateral outline, with greatest height at anterior cardinal angle; valves strongly compressed posteroventrally; overlap indistinct; dorsal margin straight, converging posteriorly; ventral margin distinctly sinuate medially; anterior margin broad and obliquely rounded; posterior margin with a caudal process at mid-height; in dorsal view, carapace biconvex with maximum width near middle, ends compressed. Valve surface ornamented by dense, fine punctation. Internal characters not known.

Dimensions.—Holotype, SUGDMF no. 597, a female carapace, length 0.40 mm, height 0.24 mm, width 0.16 mm; paratype I, SUGDMF no. 598, a female carapace, length 0.40 mm, height 0.24 mm, width 0.18 mm; paratype II, SUGDMF no. 599, a male carapace, length 0.42 mm, height 0.21 mm, width 0.14 mm.

Discussion.—*Cytherura duddukuruensis* sp. nov. resembles *Cytherura interposita* Lyubimova and Guha in Lyubimova *et al.* (1960) from the Miocene of Kachchh in overall shape. The latter species, however, differs from the present species in having an oblong lateral outline, a shallow vertical sulcus and reticulation, and meshes enclosing two or more punctae.

Occurrence.—Sections I and II.

Genus *Semicytherura* Wagner, 1957

Type species.—*Cythere nigrescens* Baird, 1838.

Semicytherura diluta sp. nov.

Figure 5.2–5.4

Etymology.—From Latin *diluta* meaning weakened or thinned; with reference to the faint ornamentation.

Material.—110 carapaces.

Type locality.—Light yellow limestone (Sample SUGDMF no. 1/II), Inter-trappean beds, Paleocene. Section II.

Diagnosis.—Surface ornamented by feeble transverse ridges and reticulation in ventral half.

Description.—Sexual dimorphism distinct, males being more elongate, less high and more wide than females; carapace subovate in lateral outline, with greatest height near middle and greatest length below mid-height; overlap indistinct; dorsal margin strongly convex in females and arched in males; ventral margin concave anteriorly but convex posteriorly; anterior margin narrowly rounded; posterior drawn out in a caudal process slightly below mid-height; in dorsal view carapace biconvex, posterior end compressed,

maximum width near middle in females, posterior in males. Valve surface ornamented by feeble transverse ridges in ventral half, lowermost ridge continuous from anteroventral to posteroventral region, other ridges intersecting each other in ventromedian region forming weak reticulation; fine punctation over rest of area.

Dimensions.—Holotype, SUGDMF no. 601, a female carapace, length 0.42 mm, height 0.26 mm, width 0.22 mm; paratype I, SUGDMF no. 602, a male carapace, length 0.46 mm, height 0.24 mm, width 0.22 mm; paratype II, SUGDMF no. 603, a female carapace, length 0.43 mm, height 0.26 mm, width 0.22 mm.

Discussion.—*Semicytherura diluta* sp. nov. closely resembles *Semicytherura indica*? subspecies described by Neale and Singh (1985, pl. 46, fig. 2) in overall outline and ornamentation. *S. indica*? subspecies is based on a single specimen and inadequately described. It differs from *S. diluta* in having feeble transverse ridges all over the valve surface and a nearly straight ventral margin.

Semicytherura longilinea Bhandari (1995) from the Lower Eocene Khuiala Formation of Jaisalmer resembles *S. diluta* in appearance. However, it differs in having 9 or 10 transverse ridges that extend nearly the entire length of the carapace.

Occurrence.—Section II.

Family Xestoleberididae
Genus *Uroleberis* Triebel, 1958

Type species.—*Eocytheropteron parnensis* Apostolescu, 1955.

Uroleberis rasilis sp. nov.

Figure 5.5, 5.6

Etymology.—From Latin *rasilis*, meaning smoothed; with reference to smooth surface.

Material.—Three carapaces.

Type locality.—Greyish-white limestone (Sample SUGDMF no. 7/II), Inter-trappean beds, Paleocene, Section II.

Diagnosis.—Carapace ovate in lateral outline; posterior margin with an indistinct caudal process.

Description.—Carapace ovate in lateral outline, with greatest height near middle; left valve slightly overlaps right valve along dorsal and posterior margins; dorsal margin arched; ventral margin nearly straight; anterior margin narrowly rounded; posterior margin slightly concave in upper part, rounded in lower part and with indistinct caudal process; in dorsal view carapace biconvex, ends narrowed, maximum width slightly posterior to middle. Valve surface smooth.

Dimensions.—Holotype, SUGDMF no. 604, a carapace,

length 0.45 mm, height 0.30 mm, width 0.30 mm; paratype, SUGDMF no. 605, a carapace, length 0.45 mm, height 0.32 mm, width 0.32 mm.

Discussion.—The species resembles *Uroleberis* sp. aff. *U. sp. 1* described by van den Bold (1988) from the Upper Miocene-Pliocene of the Dominican Republic in lateral outline but differs in the absence of transverse ridges in the ventral region.

Occurrence.—Section II.

Superfamily Cypridacea Baird, 1845
Family Candonidae Kaufmann, 1900
Subfamily Candoninae Kaufmann, 1900
Genus *Paracandona* Hartwig, 1899

Type species.—*Candona euplectella* Brady and Norman, 1889.

Paracandona andhraensis sp. nov.

Figure 5.10–5.13

Etymology.—After the Indian state of Andhra Pradesh.

Material.—Ten valves.

Type locality.—Light yellow limestone (Sample SUGDMF no. 3/I), Inter-trappean beds, Paleocene, Section I.

Diagnosis.—Valve surface marked by dense reticulation, meshes enclosing 3 or 4 punctae.

Description.—Valve subrectangular in lateral outline, with greatest height a little over half of length near anterior cardinal angle; dorsal margin straight; ventral margin slightly concave anterior to middle; anterior margin broad and evenly rounded; posterior margin slightly narrow, sloping down in upper half and rounded in lower; posterior cardinal angle distinct; in dorsal view valve nearly convex, flat medially. Valve surface ornamented by dense reticulation, arranged concentrically, meshes enclosing 3 or 4 punctae; anterior and posteroventral regions laterally compressed. Inner lamella narrow; line of concrescence and inner margin coincide; selvage well developed, near inner periphery. Hinge modified adont; in right valve it consists of a smooth ridge, selvage at its terminal ends raised giving socketlike appearance; hinge complementary in left valve. Central muscle scars not known.

Dimensions.—Holotype, SUGDMF no. 609, a left valve, length 0.45 mm, height 0.24 mm; paratype I, SUGDMF no. 610, a right valve, length 0.45 mm, height 0.22 mm; paratype II, SUGDMF no. 611, a left valve, length 0.43 mm, height 0.22 mm; paratype III, SUGDMF no. 612, a right valve, length 0.42 mm, height 0.22 mm.

Discussion.—The species resembles *Paracandona* aff. *belgica* Tambareau, 1984, described from the Thanetian of the Paris Basin in subrectangular lateral outline and reticu-

lated ornamentation. *Paracandona* aff. *belgica*, unlike the present species, has fine, hexagonal reticules and lacks laterally compressed anterior and posteroventral margins.

Occurrence.—Section I.

Acknowledgments

The authors are highly thankful to P. K. Sarasvati, Indian Institute of Technology, Powai for extending SEM facilities, to S. R. Jakhar for his assistance in photography and other illustrations and to the anonymous reviewers for their useful suggestions to improve the paper.

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Fossil crabs (Crustacea: Decapoda: Brachyura) from the latest Miocene Senhata Formation, Boso Peninsula, Japan

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Received August 27, 2001; Revised manuscript accepted March 15, 2002

Abstract. Two species of fossil decapods, *Maja tomidai* sp. nov. and *Daldorfia* sp. are described from the latest Miocene Senhata Formation of the Boso Peninsula, central Japan. The former species resembles *Maja morii* Kato from the middle Miocene of Japan and *Maja dominoleuae* Hu and Tao from the late Miocene of Taiwan. A large palm of *Daldorfia* sp. is the third fossil record of the genus from Japan. The discovery of *Daldorfia* sp. supports the existence of subtropical to tropical marine conditions in the latest Miocene of the Boso Peninsula indicated previously by molluscan evidence.

Key words: Brachyura, Crustacea, *Daldorfia*, Decapoda, *Maja*, Senhata Formation, Zushi Fauna

Introduction

Decapod Crustacea from the upper Miocene of Japan have previously been reported from the Tano and Aya formations of the Miyazaki Group, Kyushu (4 species; Karasawa, 1993, 1997; Karasawa and Kato, 1996); the Uchiumigawa Group, Kyushu (1 species; Karasawa, 1990); the Itahana Formation of the Tomioka Group, central Japan (8 species; Kato, 2001); the Aoso Formation, north of Sendai (1 species; Karasawa and Kato, 1996), and the Wakkanai Formation, Hokkaido (1 species; Imaizumi, 1952).

Two species of decapod crustaceans were obtained from exposures of the upper Miocene Senhata Formation in the Matsukura Kogyo Quarry in Motona, Kyonan Town, Chiba Prefecture (35° 9' N, 135° 51' E) (Figure 1). A specimen found by S. Tomida represents a new species of the majid genus *Maja*. Several additional fragmentary specimens were subsequently collected from the same locality by N. Kaneko and donated to the Natural History Museum and Institute, Chiba. The other specimen collected by K. Usui is identified as a large palm belonging to the daldorfiid genus *Daldorfia*.

The purpose of this paper is to describe the new species of *Maja* and the undetermined species of *Daldorfia*, and to discuss their phylogenetic and paleobiogeographic implications. The material described herein is deposited in the Mizunami Fossil Museum (MFM) and Natural History

Museum and Institute, Chiba (CBM-PI).

Locality and paleoenvironments

The Senhata Formation exposed at the present locality is up to 130 m in thickness and is composed mainly of coarse-grained sediments, intercalating mudstones and pyroclastics (Yabe and Hirayama, 1998). The formation yields abundant remains of marine animals such as molluscs, hermatypic corals, bryozoans, isopods, echinoids, elasmobranchs and mammals.

The geologic age of the Senhata Formation has been discussed from various viewpoints. Ibaraki and Tsuchi (1980) assigned the formation to Blow's (1969) planktonic foraminifera Zone N17. Kanie *et al.* (1991) reported calcareous nannofossils indicative of the CN9 Zone of Okada and Bukry (1980) from the underlying Amatsu Formation and the CN10b Zone from the overlying Inakozawa Formation. Kasuya (1987) reported a fission-track age of 6.3 ± 0.4 Ma for the Ok tuff bed in the lower part of the Inakozawa Formation. To sum up these data, the geologic age of the Senhata Formation is regarded as the latest Miocene.

O'Hara and Ito (1980) studied the molluscs of the Senhata Formation and noted that the assemblage is a mixture of relatively worn and fragmented shells of shallow-water inhabitants and well preserved shells of deep-water dwellers. They concluded that the shallow-water

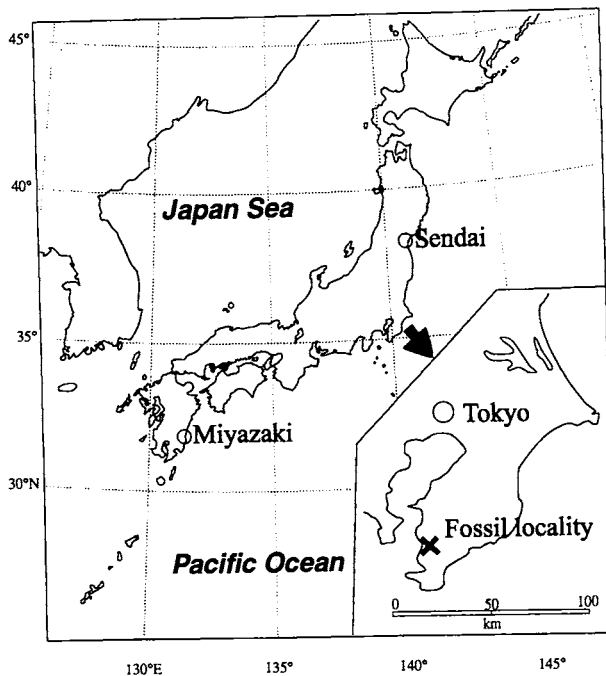


Figure 1. Map showing the fossil locality.

assemblage was mixed with a bathyal assemblage as a result of short distance transportation by bottom currents. Tomida (1989, 1996) recognized seven types of molluscan assemblages in the formation. He also considered the molluscan assemblage of the present locality to be a mixture of both a bathyal assemblage (200–250 m in depth on the continental slope) and mesoneritic to subneritic assemblages that were transported from shallower waters. Based on the occurrences of the isopod *Palaega*, Karasawa *et al.* (1992) suggested an upper bathyal paleoenvironment for the Senhata Formation.

Tomida and Itoigawa (1986) and Tomida (1989) reported the occurrences of the planktonic gastropod *Hartungia* sp. and cephalopods such as *Aturia* and *Argonauta* in various growth stages from the present locality. Based on the presence of these characteristic genera and other subtropical to tropical molluscs, Tomida (1983, 1996), Tomida and Itoigawa (1986) and Ozawa and Tomida (1992, 1996) deduced that the Senhata Formation was deposited under the influence of warm-water currents. In their study of the selachian (shark) assemblage of the Senhata Formation, Yabe and Hirayama (1998) also concluded that this formation was deposited in the upper part of the continental slope under the influence of warm-water currents.

Ozawa and Tomida (1992) and Ozawa *et al.* (1995) proposed the term “Zushi Fauna” for some late Miocene to early Pliocene molluscan assemblages on the Pacific side of Japan which contain molluscan species indicative of tropi-

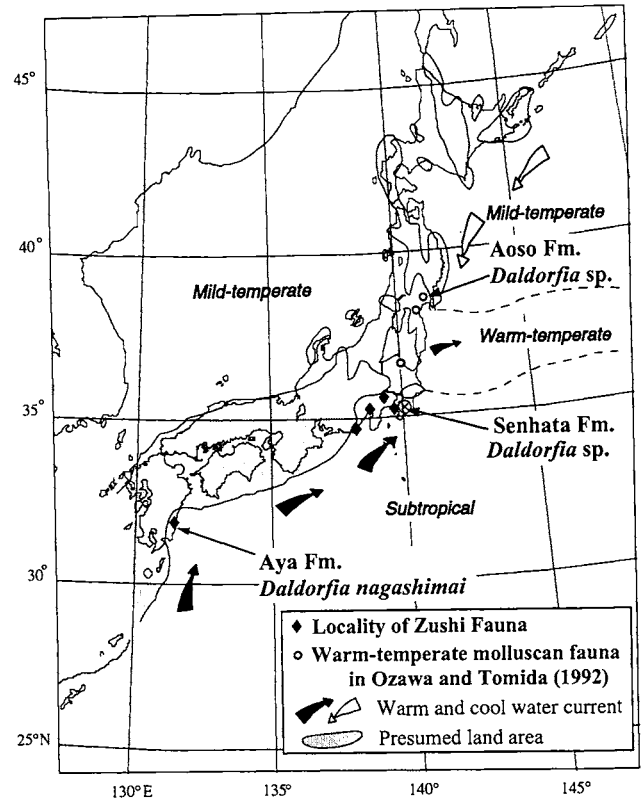


Figure 2. Localities of fossil *Daldorfia* species. Distribution of the Zushi Fauna and reconstruction of paleogeography are modified after Ozawa and Tomida (1992), Ogasawara (1994) and Nakamura *et al.* (1999). The paleoclimatology is based on Ogasawara's (1994) divisions.

cal to subtropical marine climates (Figure 2). They correlated this warmer marine climate with “Climatic Optimum 3” of Barron and Baldauf (1990).

Among the decapod genera here described, the genus *Maja* has 16 living species, of which 13 occur in the Indo-West Pacific (Griffin and Tranter, 1986) and 7 in Japanese warm-temperate to tropical waters south of the Boso Peninsula, central Japan (Sakai, 1976). The genus *Daldorfia* includes 6 living species in tropical to subtropical Japanese waters (Sakai, 1976). Particularly, *D. horrida* (Linnaeus, 1758), the most closely related to *D. sp.* from the Senhata Formation, inhabits tropical to subtropical waters south of the Kii Peninsula in Japan, the area washed by the warm Kuroshio Current (Sakai, 1976). Judging from the distributions of living species, the decapod species found in the Senhata Formation support the view previously suggested by molluscan evidence that a warm marine climate existed along the Pacific coast of Japan in the latest Miocene.

Fossil species of *Daldorfia* have hitherto been recorded from the upper Miocene of Japan and Oligocene of North America. They are *D. nagashimai* Karasawa and Kato,

1996 from the Aya Formation, Miyazaki Group in southwest Japan, *Daldorfia* sp. from the Aoso Formation in northeast Japan (Karasawa and Kato, 1996; Figure 2), and *Daldorfia himaleorhaphis* Schweitzer, 2001a from the Jansen Creek Member of the Makah Formation in the Olympic Peninsula, Washington State, the United States of America.

The Aya Formation yields molluscan species typical of the "Zushi Fauna" (Nakamura *et al.*, 1999). While Ozawa and Tomida (1992) suggested that the "Zushi Fauna" extended north into the Fukuda Formation, south of Sendai, the occurrence of *Daldorfia* sp. from the Aoso Formation indicates that the fauna extended north of Sendai, where a warm-water event is suggested by molluscs (Ogasawara, 1994) and planktonic foraminiferal assemblages correlative with "Climatic Optimum 3" of Barron and Baldauf (1990) (Saito and Isawa, 1995). The occurrences of *Daldorfia* spp. from the Aya, Senhata and Aoso formations provide additional biotic evidence for the warming event in the late Miocene to early Pliocene in northeast Japan. The occurrence of the oldest known species of *Daldorfia*, *D. himaleorhaphis* from the Oligocene of Washington State, is considerably distant geographically from the distribution of living species of this genus. However, the high diversity of the decapod assemblages, including subtropical species from the Eocene to Oligocene of the Pacific North America, indicates a much warmer marine climate in this area than prevails today (Schweitzer, 2001b).

Systematic descriptions

Section Heterotremata Guinot, 1977
 Superfamily Majoidea Samouelle, 1819
 Family Majidae Samouelle, 1819
 Subfamily Majinae Samouelle, 1819
 Genus *Maja* Lamarck, 1801

Type species.—*Cancer squinado* Herbst, 1788. By subsequent designation (ICZN opinion 511).

Discussion.—Based upon larval morphology, Rice (1983) proposed a phylogenetic relationship between genera within the family Majidae, regarding *Maja* as a "primitive" and *Leptomithrax* as an "advanced" form. Several previous studies also supposed the same relationship between the two genera (e.g. Kurata, 1969). The cup-shaped orbit of living species of *Leptomithrax* (three closely spaced orbital spines and the antennal fossa excluded from the orbit) is generally regarded as more "complete" than that of *Maja* (separate spines with an antenna included within the orbit). However, the orbital features of the early middle Miocene *Maja morii* Kato, 1996 from Japan resemble those of *Leptomithrax*, including its postorbital spine which exhibits an excavated anterior surface like that

typically observed in *Leptomithrax* (Griffin, 1966).

With respect to the posterior end of the carapace, the Japanese fossil *Maja* species, *M. morii* and the new species discussed herein have a single tubercle on the posterior end of the carapace as in *Leptomithrax longipes* (Thomson, 1902), a living species found in Australia and New Zealand. In its adult and larval morphologies, *L. longipes* was regarded as unique among the members of the genus *Leptomithrax* (Webber and Wear, 1981; McLay *et al.*, 1995).

Judging from these characters the phylogenetic relationship between *Leptomithrax* and *Maja* should be reconsidered. The oldest fossil record of *Maja* is from the early Miocene (*Maja robinsoni* Jenkins, 1985 from South Australia), while that of *Leptomithrax* extends into the late Eocene (*Leptomithrax griffini* Feldmann and Maxwell, 1990 from New Zealand), suggesting that *Maja* is a more advanced form than *Leptomithrax*.

Geologic range.—Miocene to Recent.

Maja tomidai sp. nov.

Figures 3.1a–c, 4, 5B

Diagnosis.—*Maja* with moderately long, divergent rostrum; lateral and dorsal spines acute. Intercalated and postorbital spines approximated. Dorsal regions densely covered with large, conical tubercles. Posterior end of carapace bearing single conical tubercle.

Description.—Carapace pyriform in outline. Rostrum bifid, acute, widely divergent anterolaterally. Orbit rounded. Supraorbital eave thick, sparsely granulate. Antorbital spine acutely triangular, directed laterally, slightly curved posteriorly. Intercalated spine short, triangular, about half length of antorbital and one-third length of postorbital spines. Postorbital spine triangular, directed anteriorly. Intercalated and postorbital spines closely approximated. Basal antennal article directed forward with anteromedial and anterolateral spines. Anterolateral margin of carapace bears acute, long hepatic spine and three acute branchial spines; posteriormost one lies dorsally. Dorsal regions well defined. Gastric, branchial, and hepatic regions strongly convex, covered with pointed, variable-sized conical tubercles. Frontal region with two longitudinal series of conical tubercles; tubercles extending to base of rostrum, increasing in size posteriorly. Mesogastric region strongly convex with two large, conical tubercles arranged longitudinally. Metagastric region also highly convex with large median tubercle. Urogastric region with conical tubercle markedly smaller than others. Cardiac region strongly convex, defined laterally by broad, plain furrows, and medially by a large, conical tubercle. Intestinal region elevated, forming acute spine. Hepatic region with clustered tubercles, bordered by broad, plain depressions. Branchial re-

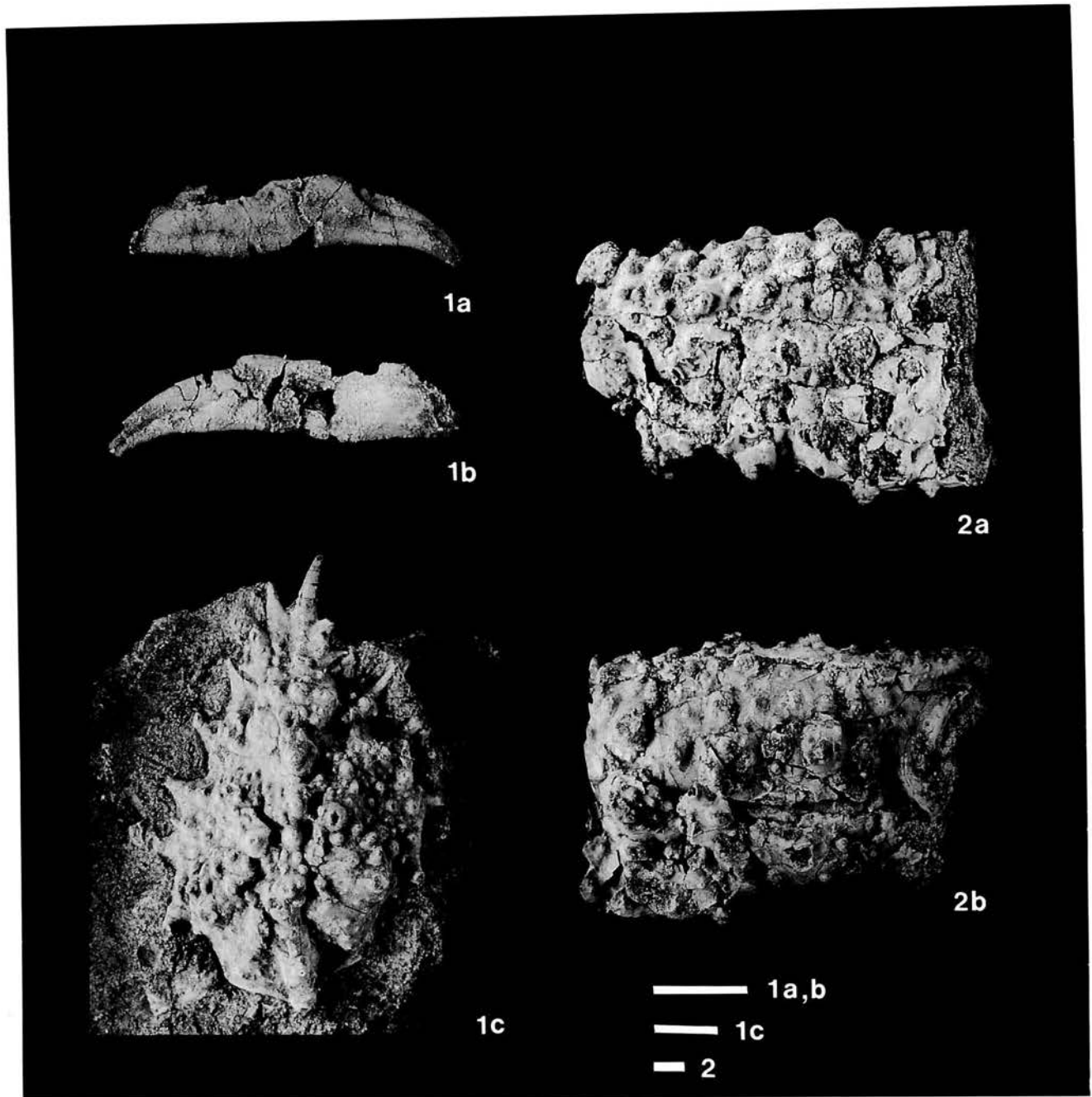


Figure 3. 1. *Maja tomidai* sp. nov., MFM 83053. Holotype. a and b, outer and medial surface of the right chela, $\times 1.5$; c, carapace, $\times 1.0$. 2. *Daldorfia* sp., CBM-PI 01084, manus of right chela; a; outer surface, b; medial surface. CBM-PI 01084, $\times 0.5$. Scale bars = 10 mm.

gions with numerous variable-sized tubercles. Sinuous swellings extending parallel to branchiocardiac groove consisting of large tubercles. Metabranhial region convex with sparse tubercles and granules, less developed than mesobranhial and intestinal swellings. Posterolateral margin rimmed, sinuously convex. Posterior end of carapace bearing one large, conical, axial tubercle. Palm of right cheliped slightly curved upward; preserved part of

outer surface smooth. Fingers acute, slender, obviously curved downward.

Discussion.—In carapace outline, the present species most resembles *Maja dominoleuae* Hu and Tao, 1985 from the upper Miocene of Taiwan. However, *M. tomidai* sp. nov. is easily distinguished from *M. dominoleuae* in that the orbital spines are shorter and slightly curved upward, and the dorsal surface of the carapace is densely covered by

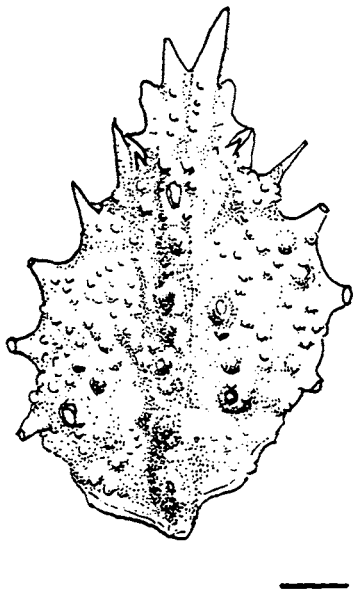


Figure 4. Line drawing showing the dorsal view of carapace of *Maja tomidai* sp. nov. The specimen is compressed obliquely, causing the right half of the carapace to be displaced anteriorly. Scale bar = 10 mm.

large tubercles. *Maja tomidai* sp. nov. resembles *M. morii* Kato, 1996 from the early middle Miocene of the Chichibumachi and Takaku groups, Saitama and Fukushima prefectures, Japan (Kato and Karasawa, 1995) in the general arrangement of tubercles and lateral spines of the carapace, but differs in having denser tubercles and more elongated spines on the dorsal surface. In addition, the antennal fossa of *Maja morii* seems to lie outside the orbit, while that of *Maja tomidai* is included within the orbit like living species of *Maja* (Figure 5).

Despite these differences, *M. tomidai* sp. nov. shares the following important characters with *M. morii*: (1) the three orbital spines are relatively approximated, and (2) the posterior end of the carapace has a single conical tubercle. Most living species of *Maja* possess a pair of spines or tubercles on the posterior end of the carapace, and no species in this genus has a large, single tubercle on the posterior end of the carapace like *M. tomidai* sp. nov. and *M. morii*. Due to the incompleteness of known specimens, unfortunately, the ventral orbital features and the posterior end of the carapace of *M. dominoleuae* are not available.

The carapace of the holotype is compressed and severely deformed (Figure 4).

Material examined.—MFM 83053 (Holotype: carapace and appendages). CBM-PI 01085-01087.

Etymology.—Named after Susumu Tomida who contributed greatly to the paleontology of the Senhata Formation and discovered the holotype specimen.

Measurements.—Holotype, maximum carapace length

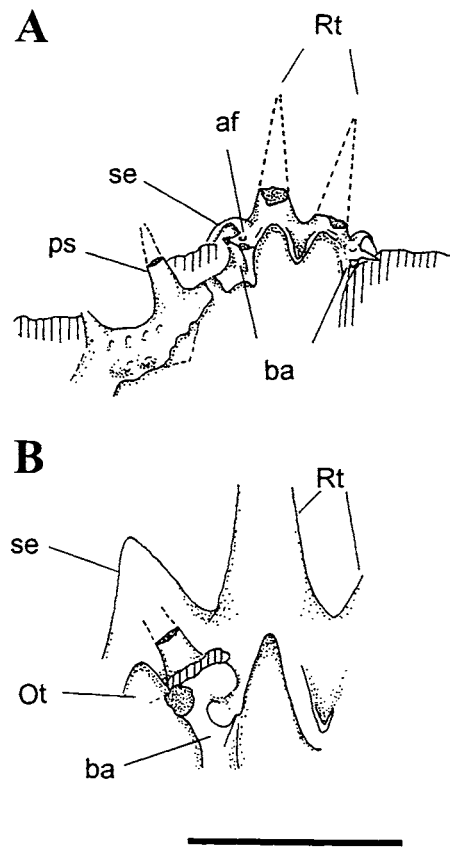


Figure 5. Line drawing showing the ventral orbital features of (A) *Maja morii* Kato, 1996 (CBM-PI 00177, Numanouchi Formation, Takaku Group) and (B) *Maja tomidai* sp. nov. (holotype). Abbreviations: Ot, orbit, Rt, rostrum, af, antennal fossa, ba, basal antennal article, ps, postorbital spine, se, supraorbital eave. Scale bar = 10 mm.

(including rostrum), 78.0 mm; maximum carapace width (excluding the branchial spines), 43.5 mm. Palm length, 37.0 mm.

Superfamily Parthenopoidea MacLeay, 1838
Family Daldorfiidae Ng and Rodriguez, 1986
Genus *Daldorfia* Rathbun, 1904

Type species.—*Cancer horridus* Linnaeus, 1758. By monotypy.

Geologic range.—Oligocene to Recent.

Daldorfia sp.

Figure 3.2a, b

Description.—Manus of right cheliped without fixed finger large (length, 131 mm), strongly compressed; upper and lower margins diverging distally. Lateral and medial surfaces densely nodose. Nodes conical to irregular; variable

in size up to 20 mm in diameter; surface bearing clusters of various-sized tubercles. Furrows between nodes shallow, smooth except for scattered small conical tubercles. Superior socket of articulation, situated near dorsoproximal corner of manus and directed proximally. Proximal margins of lateral and medial surfaces bearing rounded, thick rims along articulation with carpus.

Discussion.—The previously known fossil record of this genus from Japan includes *Daldorfia nagashimai* Karasawa and Kato, 1996 from the latest Miocene Aya Formation, Miyazaki Group in southwest Japan and *D.* sp. from the late Miocene Aoso Formation to the north of Sendai in northeast Japan (Karasawa and Kato, 1996) (Figure 2). *Daldorfia?* sp. from the middle Miocene Aoki Formation in central Japan (Karasawa *et al.*, 1999) is too incomplete to permit generic assignment. It may belong to a species of the Majidae. Therefore, *Daldorfia* sp. described here is the third fossil record for this genus from Japan.

Living species of *Daldorfia* are inhabitants of littoral and sublittoral zones (Sakai, 1976). Judging from the disarticulated and incomplete state of the present specimen, it may have been transported from a littoral or sublittoral zone, together with shallow-water molluscs, to the deeper-water environment of the Senhata Formation.

Material examined.—CBM-PI 01084.

Measurements.—Manus length, 131 mm, manus height, 88 mm.

Acknowledgments

The author is much indebted to Susumu Tomida (Chukyogakuin University) and Kazuyuki Usui (Mito City) for donating the specimens. I wish to express my sincere gratitude to Rodney M. Feldmann (Kent State University, Ohio), Warren C. Blow (National Museum of Natural History, Smithsonian Institution) and Hiroaki Karasawa (Mizunami Fossil Museum) for their critical reading of the manuscript and for providing many valuable comments and discussions. Thanks are also due to Naotomo Kaneko (Geological Survey of Japan), Osamu Fujiwara (Tono Geoscience Center), Yuji Takakuwa (Gunma Museum of Natural History), and Kokichi Inoue (Abiko City) for donating and providing access to the fossil specimens, and giving valuable information and comments.

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Internal test morphology of the genus *Rectobolivina* (Cushman, 1927) from the Late Cenozoic Miyazaki Group, southwestern Japan

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Received September 9, 2001; Revised manuscript accepted March 18, 2002

Abstract. Six species of the genus *Rectobolivina* (benthic foraminifera), *R. asanoi*, *R. bifrons*, *R. clavata*, *R. discontinuosa*, *R. raphana* and *R. striatula* from the Late Cenozoic Miyazaki Group of southwestern Japan were taxonomically studied, particularly focusing on internal test morphology. Two new species of *Rectobolivina*, *R. clavata* and *R. discontinuosa*, and one new replacement name, *Rectobolivina clavatostriatula*, are proposed. Scanning electron microscopic and optical microscopic observations of dissected specimens and thin sections reveal that the chamber wall of the genus *Rectobolivina* is bilamellar, and that the toothplate is an extension of the chamber wall, a twisted plate strongly folded at both edges and connecting successive foramina. The toothplate constantly attaches with one of its sides to the axial side of the inner margin of the preceding foramen. It exhibits a lamellar structure, showing that the extension of the outer lamella of the chamber wall is covered by two thin inner lamellae on both axial and peripheral sides.

The six species of *Rectobolivina* display a clear stratigraphically separated distribution during the period from latest Miocene to earliest Pleistocene.

Key words: benthic foraminifera, internal morphology, lamellar structure, Miyazaki Group, *Rectobolivina*, toothplate

Introduction

The current classification scheme of benthic foraminifera requires examination of the internal test morphology (Loeblich and Tappan, 1987). This is mainly caused by the development of scanning electron microscopy (SEM) since the 1960's and of techniques for dissecting specimens.

The genus *Rectobolivina* proposed by Cushman (1927) differs from the genus *Siphogenerina* Schlumberger, 1882 by its biserial chamber arrangement in the earlier stage, in contrast to the triserial one in *Siphogenerina*. Hofker (1951a) indicated the importance of the toothplate of *Rectobolivina* at generic level, and Hofker (1951b) pointed out the difference of toothplate orientation between *Rectobolivina* and *Siphogenerina*. The current classification (Loeblich and Tappan, 1964, 1987) adopted the significance of the toothplate orientation. Although Revets (1993) briefly described the monolamellar structure in the toothplate of the genus *Siphogenerinoides* Cushman, 1927,

which shows the same toothplate orientation as *Rectobolivina*, the structure of the toothplate in *Rectobolivina* has not yet been described.

The present paper deals with the taxonomy of *Rectobolivina* species from the Late Cenozoic Miyazaki Group, with emphasis on the nature of the toothplate.

Geologic settings

On the coastal region of Miyazaki Prefecture, southeast Kyushu, Late Cenozoic marine deposits named the Miyazaki Group are widely distributed. The Miyazaki Group unconformably overlies the Paleogene unit of the Shimanto Supergroup. Shuto (1952) divided the Miyazaki Group into three facies, the Aoshima, the Miyazaki, and the Tsuma facies from south to north, based on lithological differences and on their geographic distribution. The relationship among these facies has been thought to be contemporaneous. Shuto (1952) divided the Tsuma facies into three members, the Kawabaru, the Tsuma, and the

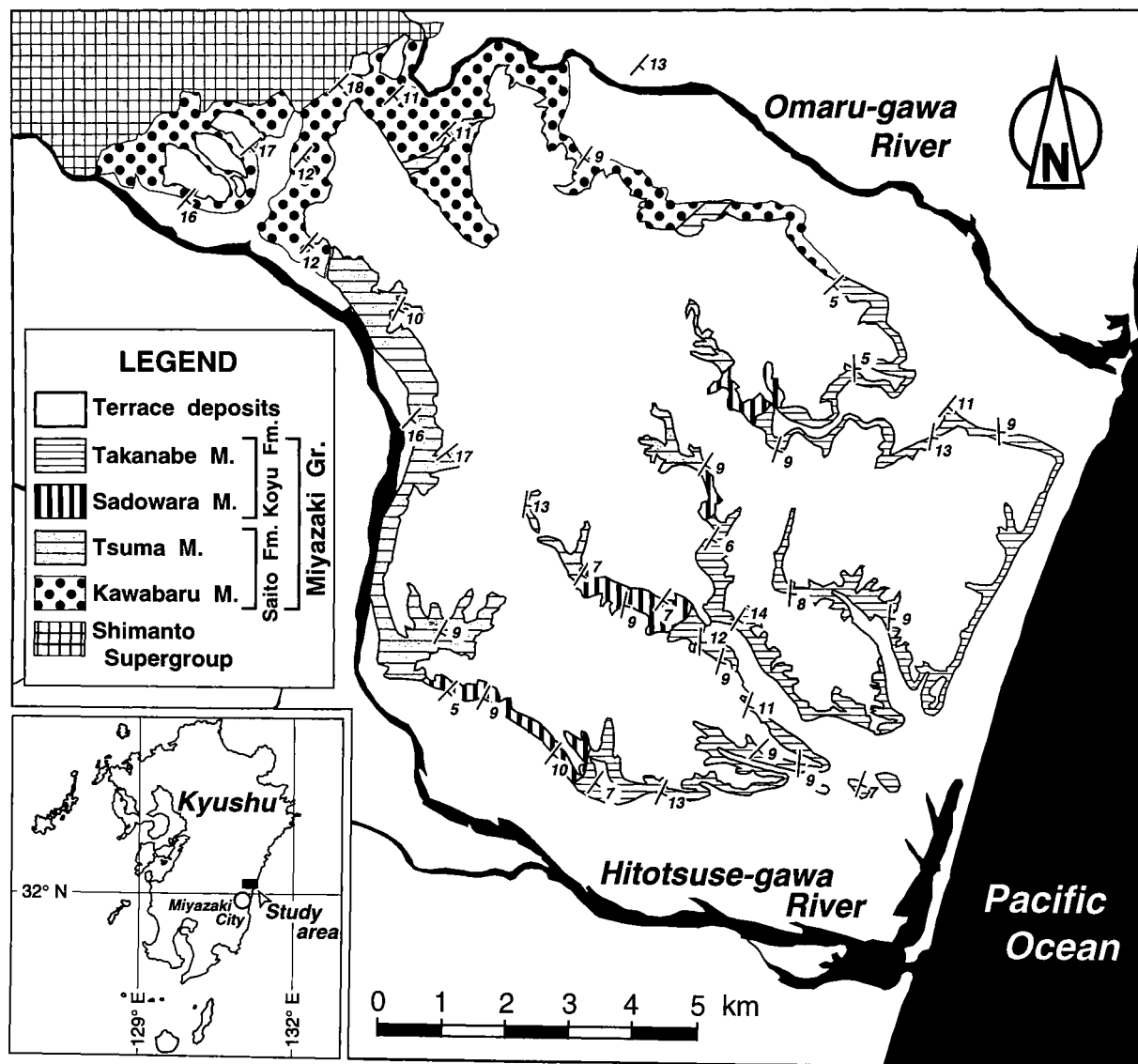


Figure 1. Geologic map of the study area (modified after Suzuki, 1987).

Takanabe Member in ascending order. The Tsuma facies was reclassified and subdivided into four members by Suzuki (1987) as follows: the Kawabaru and Tsuma Members of the Saito Formation, and the Sadowara and Takanabe Members of the Koyu Formation in stratigraphic order (Figure 1). The geologic age of the group was previously assigned to latest Miocene to earliest Pleistocene based on planktonic foraminifera by Natori *et al.* (1972) and calcareous nannoplankton by Nishida (1980).

The Tsuma facies is well exposed at the terrace cliffs along the Hitotsuse-gawa River. We collected 59 sediment samples for this study from this section (Figure 2).

Materials and methods

Lithology and horizons of foraminifera-bearing rock samples in the section along the Hitotsuse-gawa River are shown in Figure 3. The pelitic layers in a siltstone/sandstone alternation were selected for sampling. Rock samples were disintegrated with an oversaturated sodium sulfate (Na_2SO_4) solution following the method of Ujié *et al.* (1977) and were washed using a 74 μm sieve.

Rectobolivina specimens were picked out from the sediment residue on the sieve and identified with optical and scanning electron microscopes (SEM). A number of megalospheric specimens were dissected and observed under SEM following Nomura's (1983) Canada balsam-

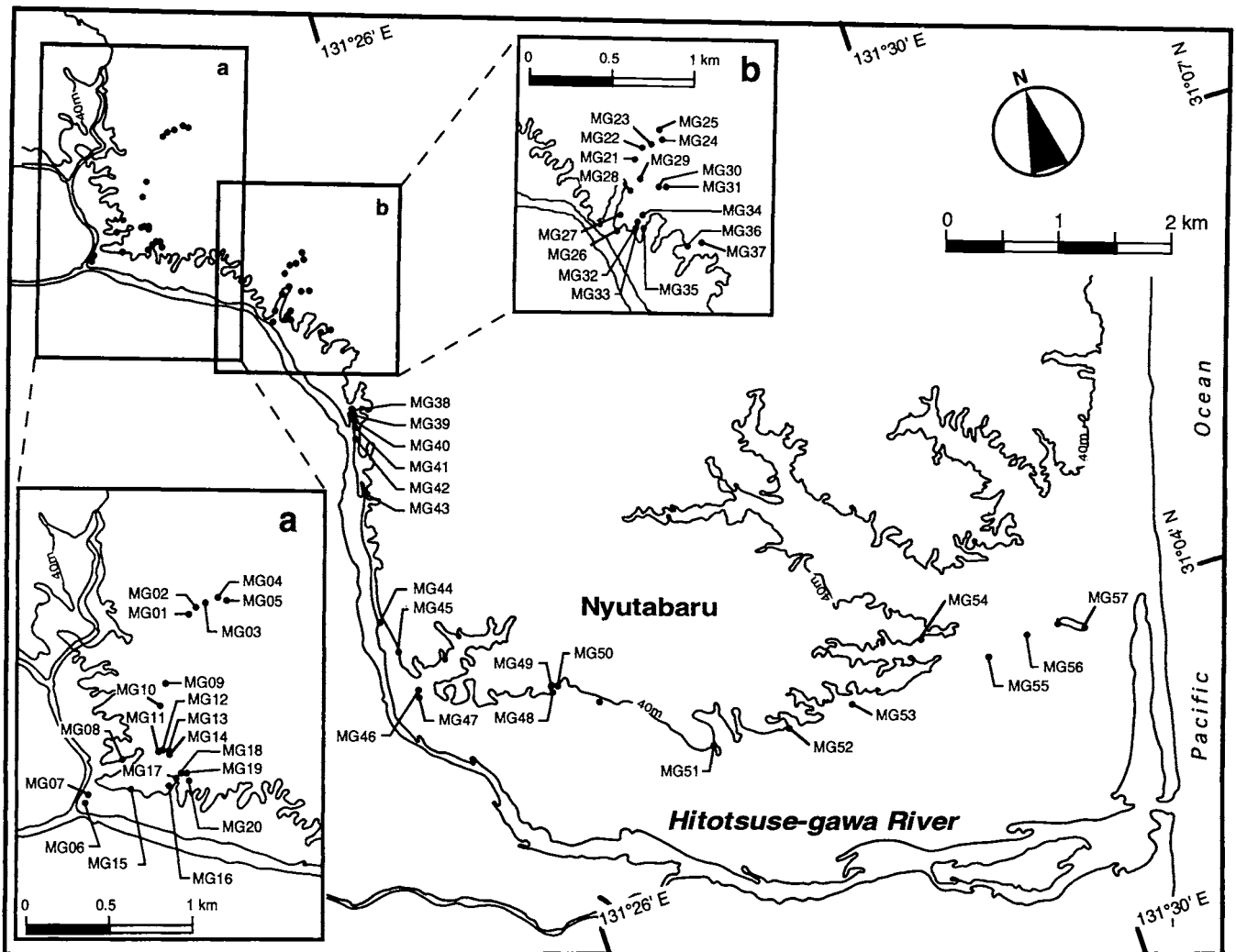


Figure 2. Map showing sampling localities.

xylene embedding method to examine the internal test structures.

All the illustrated specimens are deposited in the collections of the University of Tsukuba with catalog number prefixed IGUT.

Brief note on stratigraphic occurrence

Rectobolivina asanoi Murata, 1951, *R. bifrons* (Brady, 1881), *R. clavata* sp. nov., *R. discontinuosa* sp. nov., *R. raphana* (Parker and Jones, 1865), and *R. striatula* (Cushman, 1913) were recognized in 35 sampling horizons (Figure 4). As shown in Figure 5, the stratigraphic distribution and the frequency of occurrence of these species are different in the study section. *R. asanoi* characteristically occurs only in the Kawabaru Member of uppermost Miocene age. *R. bifrons* and *R. striatula* occur at two ho-

rizons in the upper part of the Kawabaru Member and in the lower part of the Tsuma Member, while *R. clavata* sp. nov. is characteristic at two horizons, one in the upper part of the Tsuma Member and another in the lower part of the Sadowara Member. *R. raphana* occurs in the Takanabe Member. *R. discontinuosa* sp. nov. is restricted to the lowest Pleistocene horizon of the Takanabe Member. Possibly, these stratigraphic distributions of the species may offer clues for the restricted but detailed correlation of strata in a further study.

Previous studies on toothplate of *Rectobolivina*

Although Brady (1881, 1884) did not mention the existence of the toothplate in the original description of *Sagrina bifrons* (type species of *Rectobolivina*), Cushman (1913) described "the internal tubular connection" of *R. bifrons*

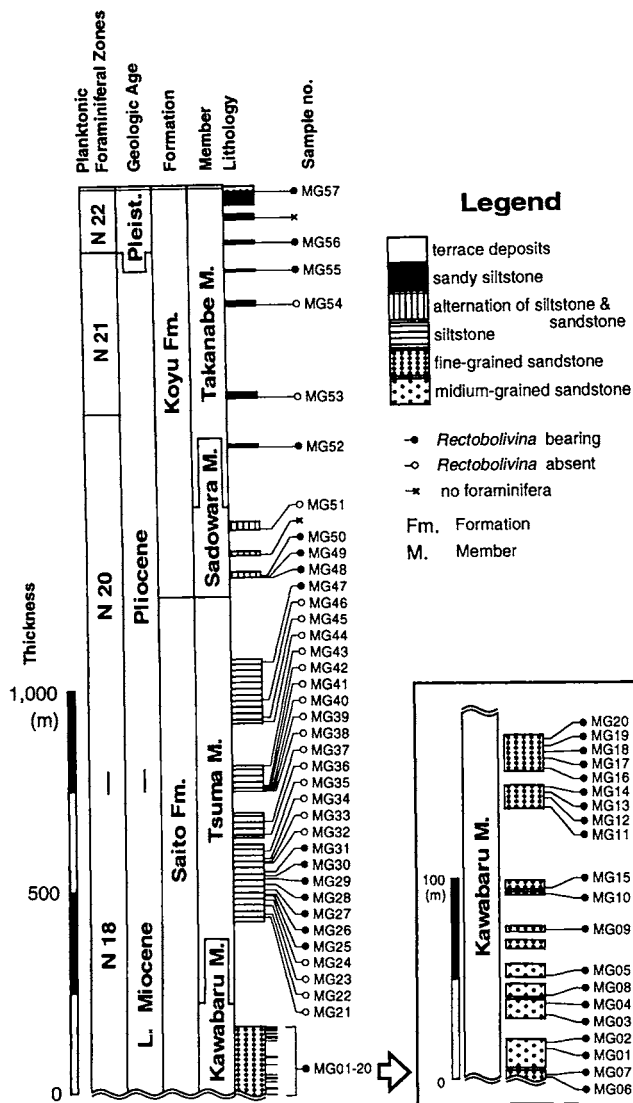


Figure 3. Geologic columnar section with the sampling levels. Stratigraphic division and thickness calculation are based on Suzuki (1987), and geologic age and planktonic foraminiferal zones are after Natori *et al.* (1972).

(his *Siphogenerina bifrons*) based on observations by optical microscopy. Cushman (1927, 1937) described the toothplate as “tube” or “tubular”, and Hofker (1933) called it an “internal tube”. Later, Hofker (1951a) examined toothplates of foraminifera including *Rectobolivina* species, and stated, “...in the biserial part of *Rectobolivina*, this plate is fastened at one side of the aperture of the former chamber, and is erected in such way, that, by contorting itself, it is attached to the opposite side of the chamber itself, giving rise to a tooth by means of its folded and flaring side...”. He (fig. 35) illustrated in detail the schematic succession of toothplates in relation to the chamber arrangement for some

Rectobolivina species, particularly for *Rectobolivina columellaris* (Brady). He first showed that the toothplate of the genus is not a cylindrical tube but is a hemicylindrical plate. Hofker (1951b) showed the different modes of toothplate orientation in *Rectobolivina* and its related genus *Siphogenerina*; the angle between successive toothplates in *Rectobolivina* is constantly 180°, whereas it is 120° in *Siphogenerina*. Thus, the morphology and succession of the toothplates are now regarded as important taxonomic features. Loeblich and Tappan (1964) adopted Hofker’s (1951b) opinion in their classification scheme of foraminifera and placed *Rectobolivina* into the family Bolivinitidae Cushman, 1927. They used the term “toothplate” only for the superfamily Buliminioidea (= their Buliminacea). Later, Loeblich and Tappan (1987) moved *Rectobolivina* into the subfamily Siphogenerinoidinae Saidova, 1981. The Siphogenerinoidinae consists of 11 genera, including *Rectobolivina* but not *Siphogenerina*, which are characterized by biserial chamber arrangement in earlier stage becoming uniserial in later stage, associated with the toothplate rotating 180° between chambers. Loeblich and Tappan (1987) defined the toothplate as an extension of the chamber wall and a contorted plate extending within the chamber lumen. Recently, Revets (1989, 1993, 1996) pointed out that the toothplate of the Buliminioidea (= his Buliminacea) (including *Rectobolivina*) originated from the inner layer of a bilamellar chamber wall, and he distinguished it from the so-called “toothplate” in the Rotalioidea, which shows a more complicated structure.

Toothplate in *Rectobolivina*

Megalospheric specimens were vertically sectioned in two ways (Figure 6); i.e. cut through the broader diameter of test (Section A) and perpendicularly (section B).

The following description can be applied to all species treated here. The relationship among toothplate, foramen and chamber lumen is schematically shown in Figure 7.

The aperture of *Rectobolivina* species is elliptical to circular in outline and its top fuses to the apertural lip, which never distinctly protrudes (Figure 4). The toothplate is apparently thin and trough-shaped, strongly folded at its side edges as seen in section A (e.g. Figures 8.2, 11.7). The plate in the uniserial stage descends straight into the chamber lumen towards the preceding foramen, along the center of the test (e.g. Figure 10.5), whereas it extends in a zigzag way in the biserial stage, according to the biserial chamber arrangement (e.g. Figure 10.5). The trough-shaped concavity (tc) of the toothplate appears alternately from chamber to chamber in both biserial and uniserial stages (e.g. Figure 8.2). This indicates that the toothplate retains the early ontogenic biserial (= 180°) rotation, although cham-

bers become uniserial.

After slight etching with dilute hydrochloric acid solution, the chamber wall of *R. bifrons* (type species of the genus) shows a lamellar structure (Figure 8.5). The later chamber wall entirely covers the preceding ones, causing the thickening of the test wall in the earlier portion. The final chamber wall of *R. raphana* (Figure 11.4) is bilamellar, consisting of a thin inner lamella (il) and a thick outer lamella (ol). A similar lamellar structure can be seen in the toothplate (tp) of *R. bifrons* (Figure 9.2, 9.3), where a thick outer lamella (ol) is covered by a thin inner lamella (il) at both the axial and peripheral sides. In conclusion, it can be stated that the lamellae of the toothplate do not originate in the preceding toothplate nor septal wall, but represent an extension of the chamber wall (Figures 8.1, 9.2, 9.3, 9.5, 9.6). These observations on the lamellar structure of the toothplate differ from those by Revets (1989, 1993), who regarded the toothplate as an extension of the inner lining (= inner lamella in this study) of the chamber wall.

Our observation of the internal, lamellar structure in the genus *Rectobolivina* is summarized in Figure 12, and supports Hofker's (1951a) idea that the toothplate is a part of the chamber wall.

Systematic description

Family Siphogenerinoidea Saidova, 1981

Subfamily Siphogenerinoidinae Saidova, 1981

Genus *Rectobolivina* Cushman, 1927

Rectobolivina asanoi Murata, 1951

Figures 4.1a-c, 4.2a-c; 10.1, 10.2; 13.1a, b

Rectobolivina asanoi Murata, 1951, p. 96, pl. 1, text-figs. 2a, b; Asano, 1952, p. 13, figs. 70, 71; Kawagata, 2001, p. 88, figs. 8-13a, b.

Rectobolivina bifrons striatula (Cushman) (non *Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917). Asano, 1950, p. 12, figs. 48, 49; Matsunaga, 1963, pl. 41, figs. 9a, b.

Material.—IGUT14488, sample MK07 (Figure 4.1a-c); IGUT14489, sample MK07 (Figure 4.2a-c); IGUT14490, sample MK07 (Figure 10.1); IGUT14491, sample MK07 (Figure 10.2).

Remarks.—Since Murata (1951) described *Rectobolivina asanoi* from the Miocene part of the Miyazaki Group, this species has been reported only from the late Neogene Shimajiri Group in Kume-jima Island, southwestern Japan (Kawagata, 2001). Comparing the original figure of *R. asanoi* Murata, 1951 (Figure 11.1a) to other costate *Rectobolivina* species, the former species is characterized in having a much wider test, and being elliptically rounded

in cross section. *R. bifrons* var. *striatula* (Cushman, 1917) of Suzuki (1987) from the lower part of the Miyazaki Group, south of the present study area, of Asano (1950) from the Pliocene Kakegawa Group, central Japan, and of Matsunaga (1963) from the Pliocene in Niigata Prefecture, northeastern Japan, are all probably identical to *R. asanoi*. The specimens treated here resemble those described as *R. striatula* (Cushman, 1917) from the late Neogene of New Zealand (Hornibrook, 1968; Hayward and Buzas, 1979) and from the Miocene of Victoria, Australia (Carter, 1964), and those described as *R. striatula* (Cushman, 1913) of Kennett (1966) from the late Neogene of New Zealand. However, these Southern Ocean species show cylindrical tests with numerous fine longitudinal striations (Carter, 1964; Kennett, 1966) or with fewer costae (Hornibrook, 1968; Hayward and Buzas, 1979), in contrast to the rather compressed test with a number of raised longitudinal costae in *R. asanoi*.

The megalospheric form of *R. asanoi* shows a bluntly rounded initial end and approximately four to five pairs of chambers in the biserial stage (Figure 4.1a, c), whereas the microspheric form has a rather tapered initial end and more chamber pairs in the earlier stage (Figure 4.2a, c). There is no distinct size difference between the forms.

Rectobolivina bifrons (Brady, 1881)

Figures 4.3a-c, 4.4a-c; 8.2-8.5; 9.1-9.6; 13.2-13.4b

Sagrina bifrons Brady, 1881, p. 64; Brady, 1884, p. 582, pl. 75, figs. 18-20.

Siphogenerina bifrons (Brady). Cushman, 1913, p. 103, pl. 45, figs. 1a-2, 5-7; Cushman, 1921, p. 277, pl. 56, figs. 2, 3; Cushman, 1926, p. 16, pl. 3, figs. 7-9, pl. 4, fig. 4.

Rectobolivina bifrons (Brady). Cushman, 1927, p. 68, pl. 14, fig. 11; Cushman, 1937, p. 204, pl. 23, figs. 13, 14a, b; Asano, 1938, p. 606, pl. 16, figs. 11a, b; Asano, 1950, p. 11, figs. 46, 47; Asano, 1958, p. 28, pl. 5, figs. 10, 11; Kuwano, 1962, pl. 21, fig. 6; Huang, 1964, pl. 2, fig. 28; Ishiwada, 1964, pl. 4, fig. 68; Kikuchi, 1964, pl. 3, fig. 23; Belford, 1966, p. 45, pl. 9, figs. 13, 14; Inoue, 1989, pl. 28, fig. 6.

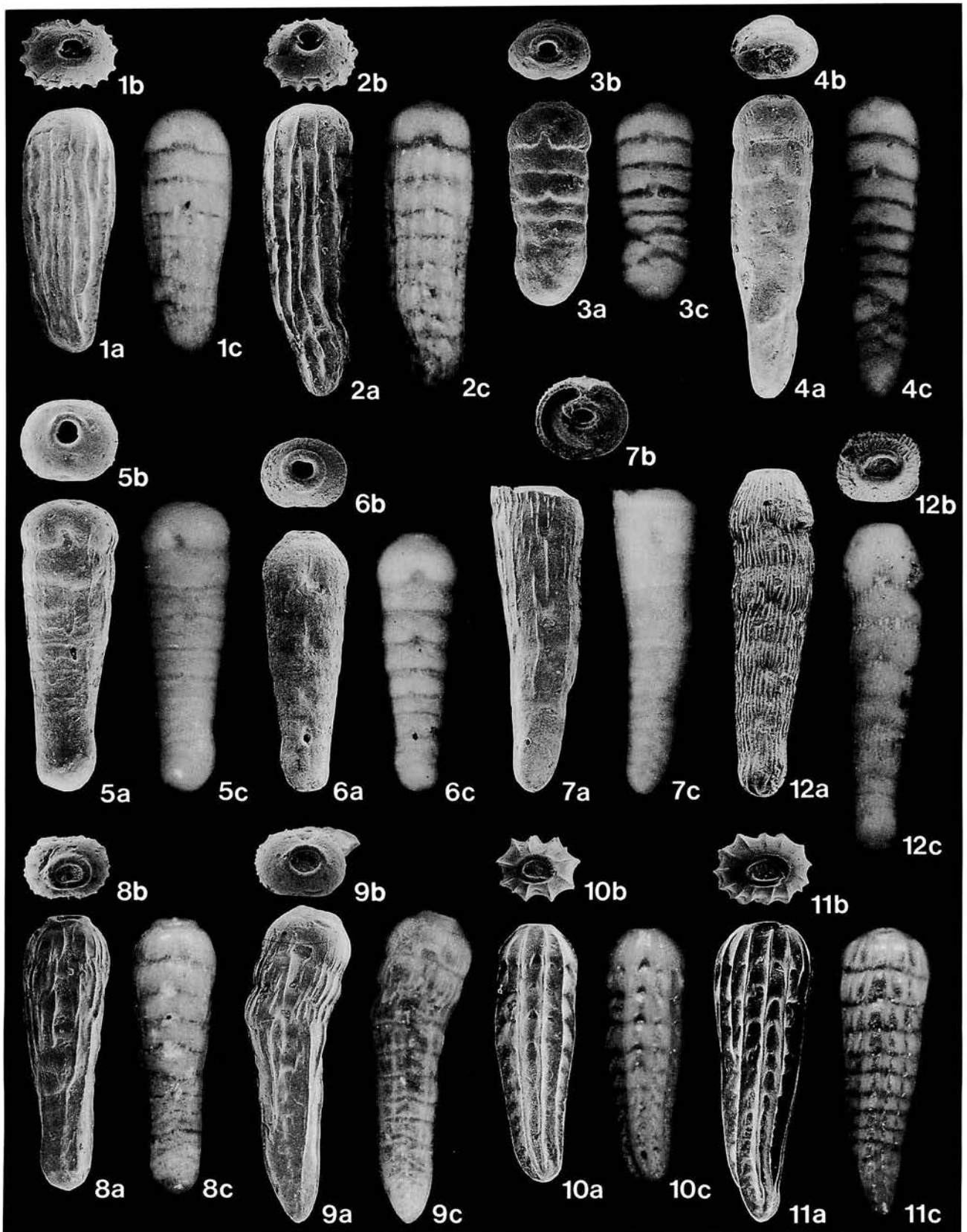
? *Siphogenerina* (*Sagrina*) *bifrons* (Brady). Egger, 1893, p. 317, pl. 4, figs. 25, 26, 29.

? *Rectobolivina bifrons* (Brady). Matsunaga, 1963, pl. 41, figs. 8a, b; Saidova, 1975, pl. 86, figs. 9, 10.

not *Rectobolivina bifrons* (Brady). LeRoy, 1964, p. F34, pl. 3, figs. 1, 2; Loeblich and Tappan, 1964, p. C553, fig. 438, nos. 2a-5b.

not *Rectobolivina* cf. *bifrons* (Brady). McCulloch, 1977, p. 259, pl. 107, figs. 17a, b.

Material.—IGUT14492, sample MK19 (Figure 4.3a-c); IGUT14493, sample MK19 (Figure 4.4a-c); IGUT14494, sample MK19 (Figure 8.2); IGUT14495, sample MK19



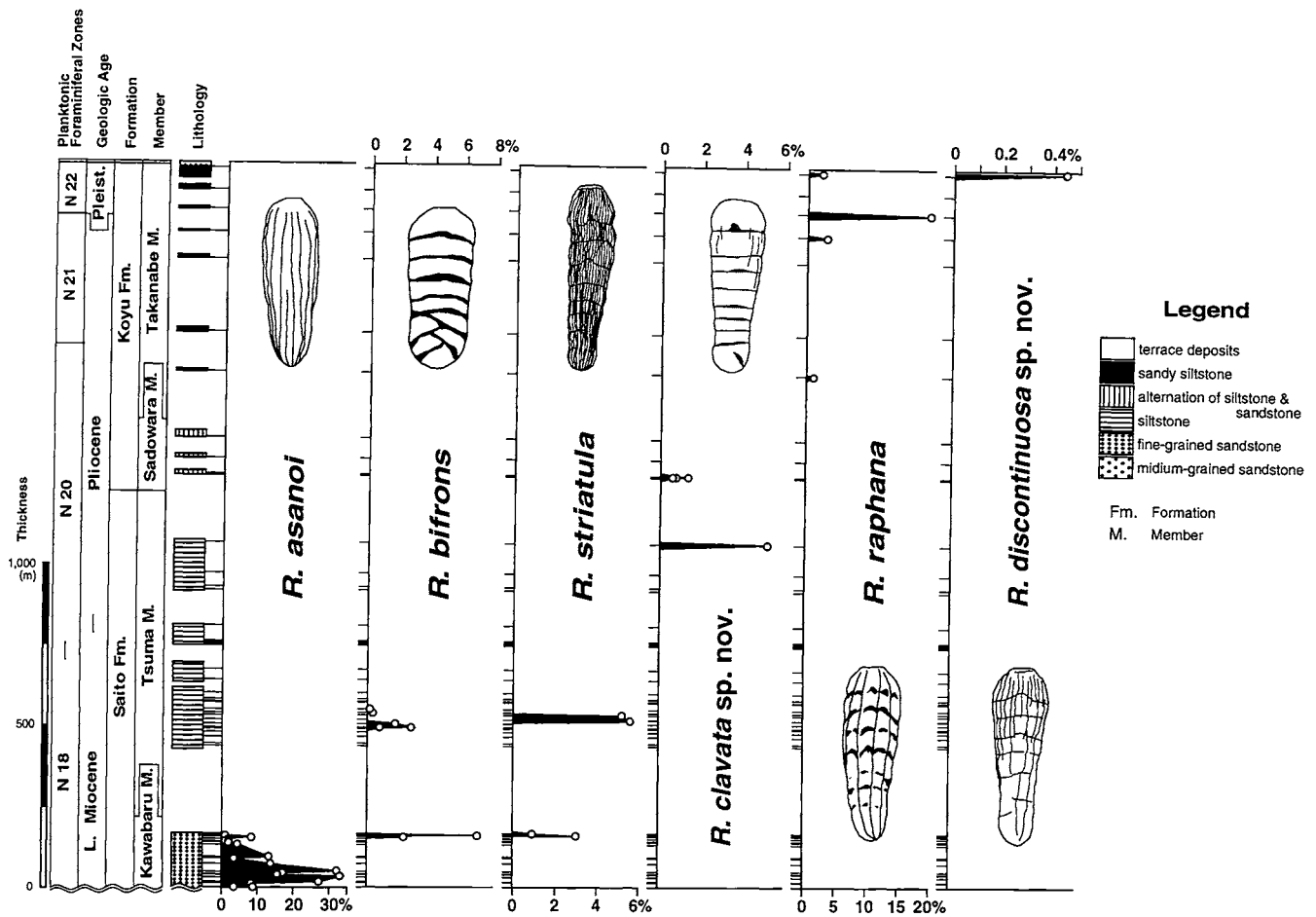


Figure 5. Stratigraphic occurrence and percentage abundance of six *Rectobolivina* species in the study section of the Miyazaki Group.

← **Figure 4.** 1a–c. Megalospheric form of *Rectobolivina asanoi* (Murata), IGUT14488, 1a: side, 1b: apertural views, $\times 60$. 1c: Optical microphotograph of 1a, $\times 60$. 2a–c. Microspheric form of *Rectobolivina asanoi* (Murata), IGUT14489, 2a: side, 2b: apertural views, $\times 60$. 2c: Optical microphotograph of 2a, $\times 60$. 3a–c. Megalospheric form of *Rectobolivina bifrons* (Brady), IGUT14492, 3a: side, 3b: apertural views, $\times 60$. 3c: Optical microphotograph of 3a, $\times 60$. 4a–c. Microspheric form of *Rectobolivina bifrons* (Brady), IGUT14493, 4a: side, 4b: apertural views, $\times 60$. 4c: Optical microphotograph of 4a, $\times 60$. 5a–c (holotype), IGUT14499, and 6a–c (paratype), IGUT14500. Megalospheric form of *Rectobolivina clavata* sp. nov., 5a: side, 5b: apertural views, $\times 60$. 5c: Optical microphotograph of 5a, $\times 60$; 6a: side, 6b: apertural views, $\times 50$. 6c: Optical microphotograph of 6a, $\times 50$. 7a–c. Microspheric form of *Rectobolivina clavata* 2p. nov., IGUT14501, 7a: side, 7b: apertural views, $\times 50$. 7c: Optical microphotograph of 7a, $\times 50$. 8a–c. Megalospheric form of *Rectobolivina discontinuosa* sp. nov. (holotype), IGUT14504, 8a: side, 8b: apertural views, $\times 50$. 8c: Optical microphotograph of 8a, $\times 50$. 9a–c. Microspheric form of *Rectobolivina discontinuosa* sp. nov. (paratype), IGUT14505, 9a: side, 9b: apertural views, $\times 50$. 9c: Optical microphotograph of 9a, $\times 50$. 10a–c and 11a–c. Megalospheric form of *Rectobolivina raphana* (Parker and Jones), IGUT14508 and IGUT14509, 10a: side, 10b: apertural views, $\times 50$. 10c: Optical microphotograph of 10a, $\times 50$; 11a, IGUT14509: side, 11b: apertural views, $\times 50$. 11c: Optical microphotograph of 11a, $\times 50$. 12a–c. Megalospheric form of *Rectobolivina striatula* (Cushman), IGUT14513, 12a: side, 12b: apertural views, $\times 50$. 12c: Optical microphotograph of 12a, $\times 50$.

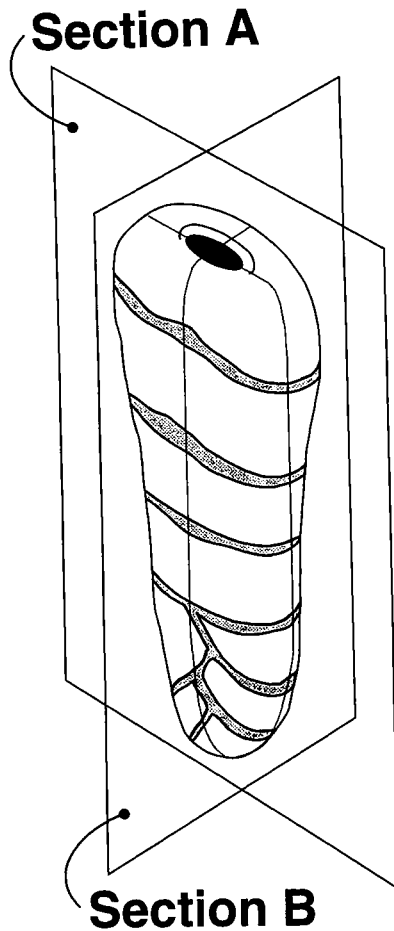


Figure 6. Diagram showing the two sections of a foraminiferal test used in this study.

(Figure 8.3); IGUT14496, sample MK19 (Figure 8.4); IGUT14497, sample MK19 (Figures 8.5, 9.1–9.2); IGUT 14498, sample MK19 (Figures 9.4–9.5).

Remarks.—This species was first described by Brady (1881) from off the Pacific coast of central Japan, and the original figures by Brady (1884) are reproduced in Figure 13.2–13.4b. Cushman (1913) examined both megalospheric and microspheric forms of the species and pointed out that all Brady's original figures represent megalospheric forms. Many specimens treated here are megalospheric forms (e.g. Figure 4.3a–c), which compare well with Brady's original figures. The megalospheric form is much shorter than the microspheric one, because of the reduced chamber number at the biserial stage.

***Rectobolivina clavata* sp. nov.**

Figures 4.5a–c, 4.6a–c, 4.7a–c; 10.3, 10.4

? *Rectobolivina bifrons* (Brady). LeRoy, 1964 (non *Sagrina*

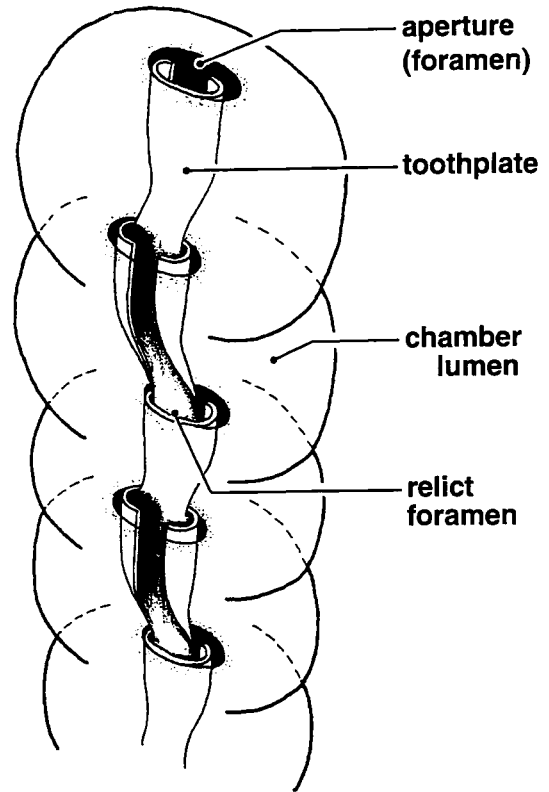


Figure 7. A schematic sketch of the *Rectobolivina* species showing the relationship among toothplate, foramina and chamber lumina in the uniserial stage. Terms follow Revets (1989, 1993).

bifrons Brady, 1881), p. F34, pl. 3, figs. 1, 2.

Diagnosis.—A species of *Rectobolivina* with a clavate-shaped and inornate test.

Description.—Test free, moderate size, approximately four times as long as broad, straight, clavate in shape, elliptical in being laterally depressed in cross section, initial end bluntly rounded in megalospheric form, whereas initial end pointed in microspheric form; chambers numerous, breadth twice the height, gradually increasing in size added changing from uniserial to biserial, after the third chamber in megalospheric form or after the tenth chamber in microspheric form; wall calcareous, optically radial, transparent or semitransparent, finely perforate, rather thick, sometimes very weakly striate in later part of test; sutures distinct, moderately thick, slightly depressed; aperture terminal, nearly circular to elliptical opening, with a distinct but slightly protruding lip; intercameral septa thick as well as the wall, parallel to slightly arched; toothplate folded at the lateral edge, extending into the preceding aperture (foramen), its folded face arranged alternately in planes 180° apart.

Material.—Holotype: IGUT14499 (1.03 mm in length,

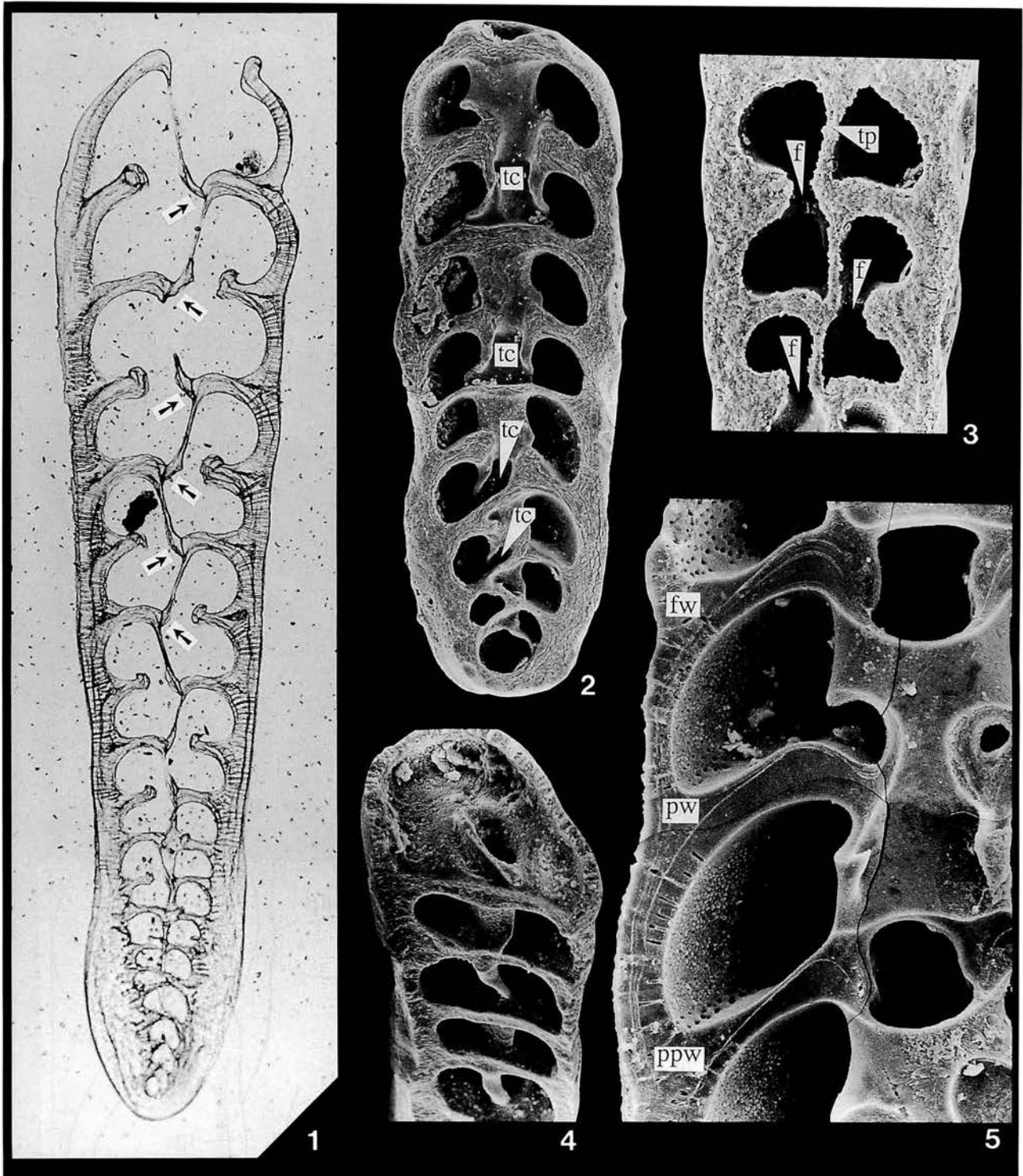


Figure 8. Sections of the microspheric form of *Rectobolivina raphana* (Parker and Jones) (8.1) and the megalospheric forms of *Rectobolivina bifrons* (Brady) (8.2–8.5), IGUT14494–IGUT14497. **1.** Overall view of Section B (Figure 6). Arrows indicate the attached portion of the toothplates, which never continuously extend from the preceding toothplate or septa, $\times 143$. **2.** Overall view of Section A. Concave side of trough-shaped plate (tc) which rotates 180° between chambers, $\times 180$. **3.** A part of the uniserial stage in Section B. Foramen (f) opens alternately along toothplate (tp). Toothplate always runs along the centre of chamber lumen, $\times 350$. **4.** Oblique section showing relationship between foramen and toothplate, $\times 250$. **5.** A part of test wall showing lamellar development of test wall according to test growth. Final chamber wall (fw) covers wall of penultimate chamber (pw), and pw covers over the pre-penultimate chamber wall (ppw), $\times 500$.

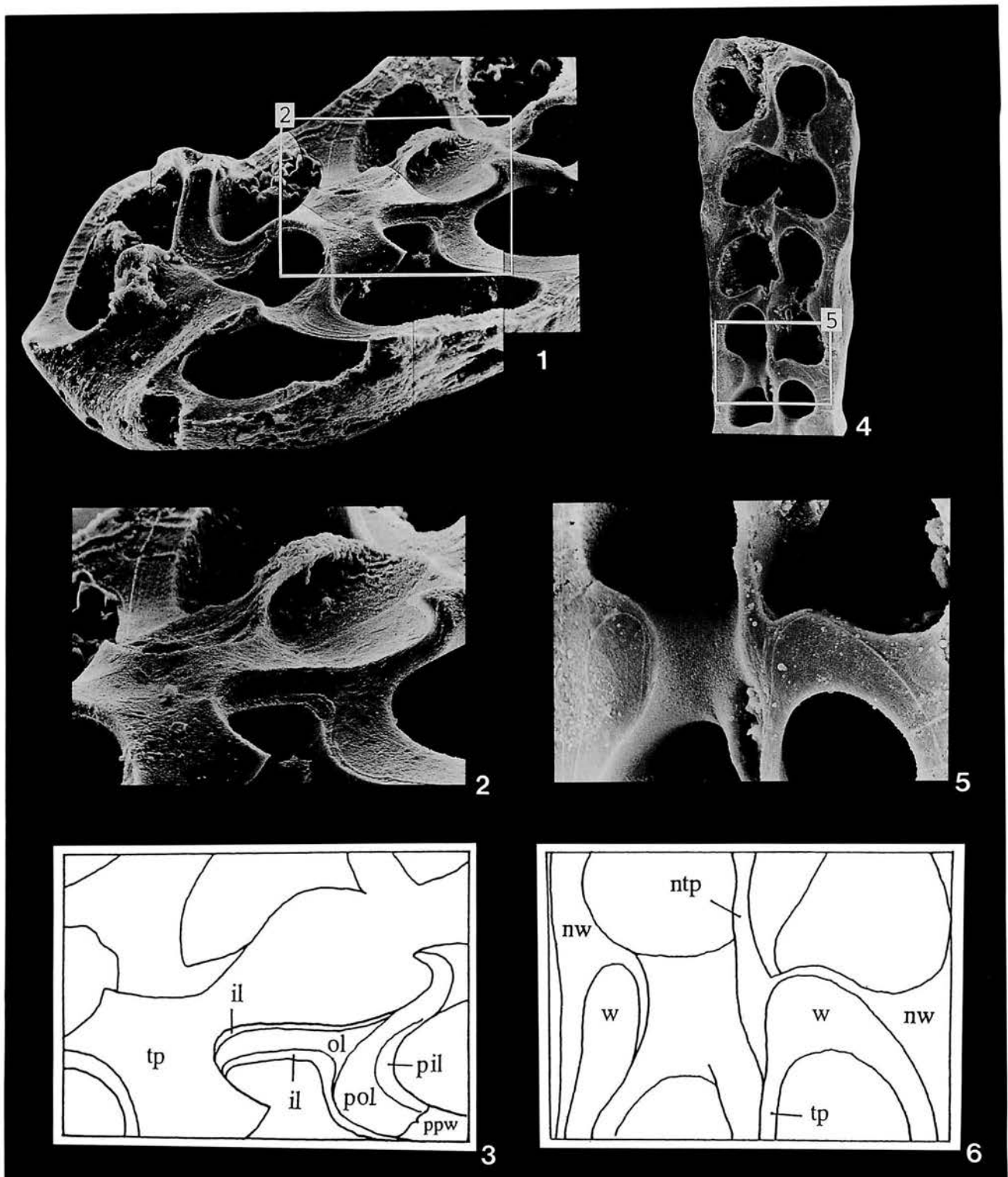


Figure 9. Megalospheric forms of *Rectobolivina bifrons* (Brady). 9.1, 9.2, IGUT14497. 1. Oblique view of later part of test of the same specimen shown in Figure 8.5, $\times 450$. 2, 3. Close-up photograph and its sketch, showing lamellar structure of toothplate (tp) in the penultimate chamber. A thick outer lamella (ol) is intercalated with two inner lamellae (il), and attaches to pre-penultimate chamber wall (ppw) composed of previous outer (pol) and inner layers (pil), $\times 800$. 4, 5. IGUT14498. 4. A part of the uniserial stage in Section B (Figure 6), $\times 180$. 5, 6. Close-up photograph and its sketch, are showing the attachment portion of toothplate (tp). Toothplate (tp), a part of chamber wall (w), is separated from next toothplate (ntp) which is a part of next chamber wall (nw), $\times 700$.

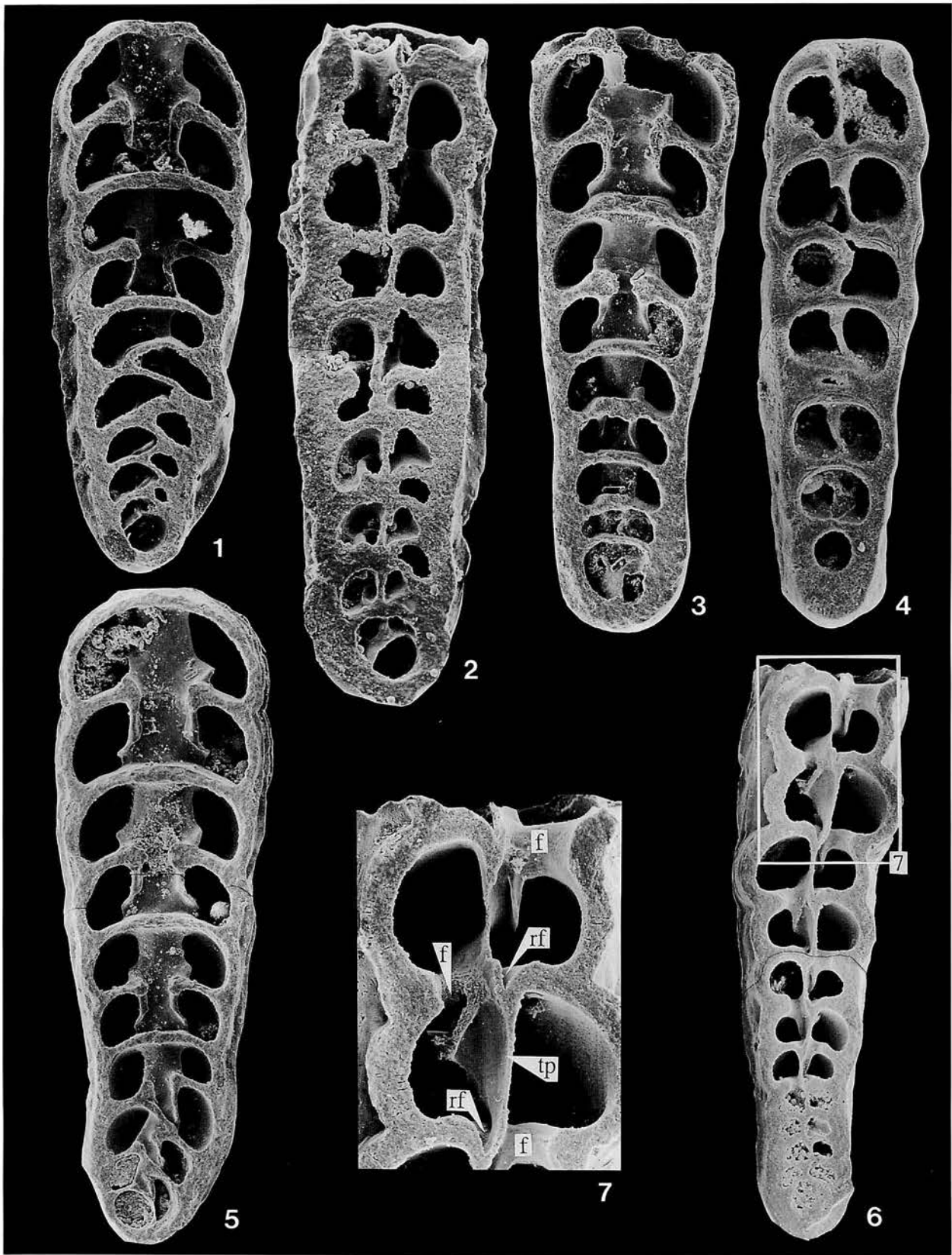
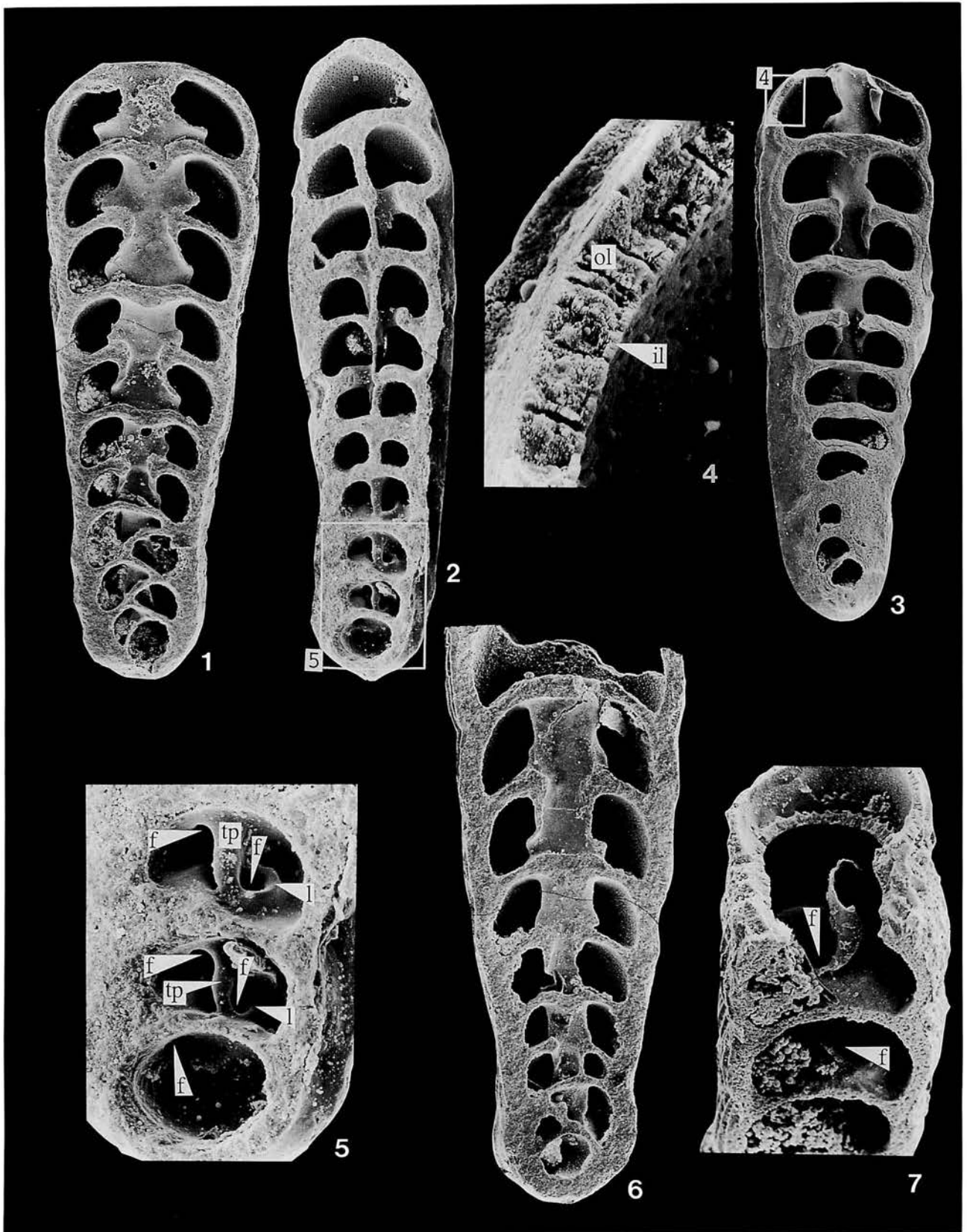


Figure 10. All dissected specimens are the megalospheric forms. **1, 2.** Sections A and B (see Figure 6) of *Rectobolivina asanoi* (Murata), respectively, IGUT14490 and IGUT14491, $\times 150$ and 200 . **3, 4.** Sections A and B of *Rectobolivina clavata* sp. nov., respectively, IGUT14502 and IGUT14503, $\times 150$ and 200 . **5, 6.** Sections A and B of *Rectobolivina discontinuosa* sp. nov., respectively, IGUT14506 and IGUT14507, $\times 120$. **7.** Close-up of a part of 6, showing the relationship among toothplate (tp), foramen (f) and relict foramen (rf), $\times 250$.



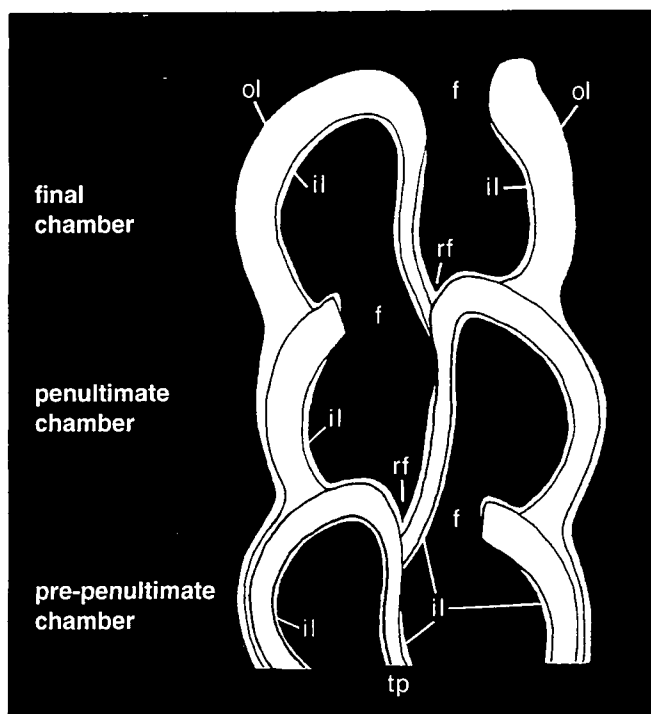


Figure 12. A schematic figure of the lamellar structure of the test wall and the toothplate in Section B (see Figure 6), showing foramen (f), toothplate (tp), outer lamella (ol), inner lamella (il), and relict foramen (rf). The terms used in the figure mostly follow Revets (1989, 1993).

0.36 mm in maximum breadth), sample MK48 (Figure 4.5a–c). Paratypes: IGUT14500 (0.92 mm in length, 0.32 mm in maximum breadth), sample MK48 (Figure 4.6a–c); IGUT14501 (1.08 mm in length, 0.34 mm in maximum breadth), sample MK48 (Figure 4.7a–c); IGUT14502, sample MK48 (Figure 10.3); IGUT14503, sample MK48 (Figure 10.4).

Etymology.—The specific name, *clavata*, is derived from the clavate-shape of the test.

Remarks.—This new species has a more slender and more clavate-shaped test than *R. bifrons* (Brady). According to measurements of the test width (TW) in megalospheric forms of *R. bifrons* and *R. clavata* (Figure 14), the test width of *R. clavata* becomes narrowest at the fourth chamber, whereas that of *R. bifrons* constantly increases (Figure 15). Furthermore, the former has a single pair of biserial chambers, whereas the latter has several

pairs of biserial chambers. *R. clavata* differs from *Rectobolivina columellaris* (Brady, 1881) in having a more compressed test, in contrast to the cylindrical test of the latter species. An Australian *Rectobolivina* species, described as *Sagrina sydneyensis* by Goddard and Jensen (1907), differs from *R. clavata* in having ornamentation with minute spines and some large pores.

Rectobolivina striatula (Cushman, 1913)

Figures 4.12a–c; 11.6, 11.7; 13.11a, b

Siphogenerina striatula Cushman, 1913, p. 108, pl. 47, fig. 1.

Rectobolivina bifrons (Brady) var. *striatula* (Cushman, 1917).

LeRoy, 1964 (non *Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917, nomen nudum), p. F34, pl. 3, figs. 5, 6.

? *Rectobolivina bifrons* (Brady) var. *striatula* (Cushman, 1917).

LeRoy, 1941a (non *Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917, nomen nudum), p. 35, pl. 2, figs. 7, 8.

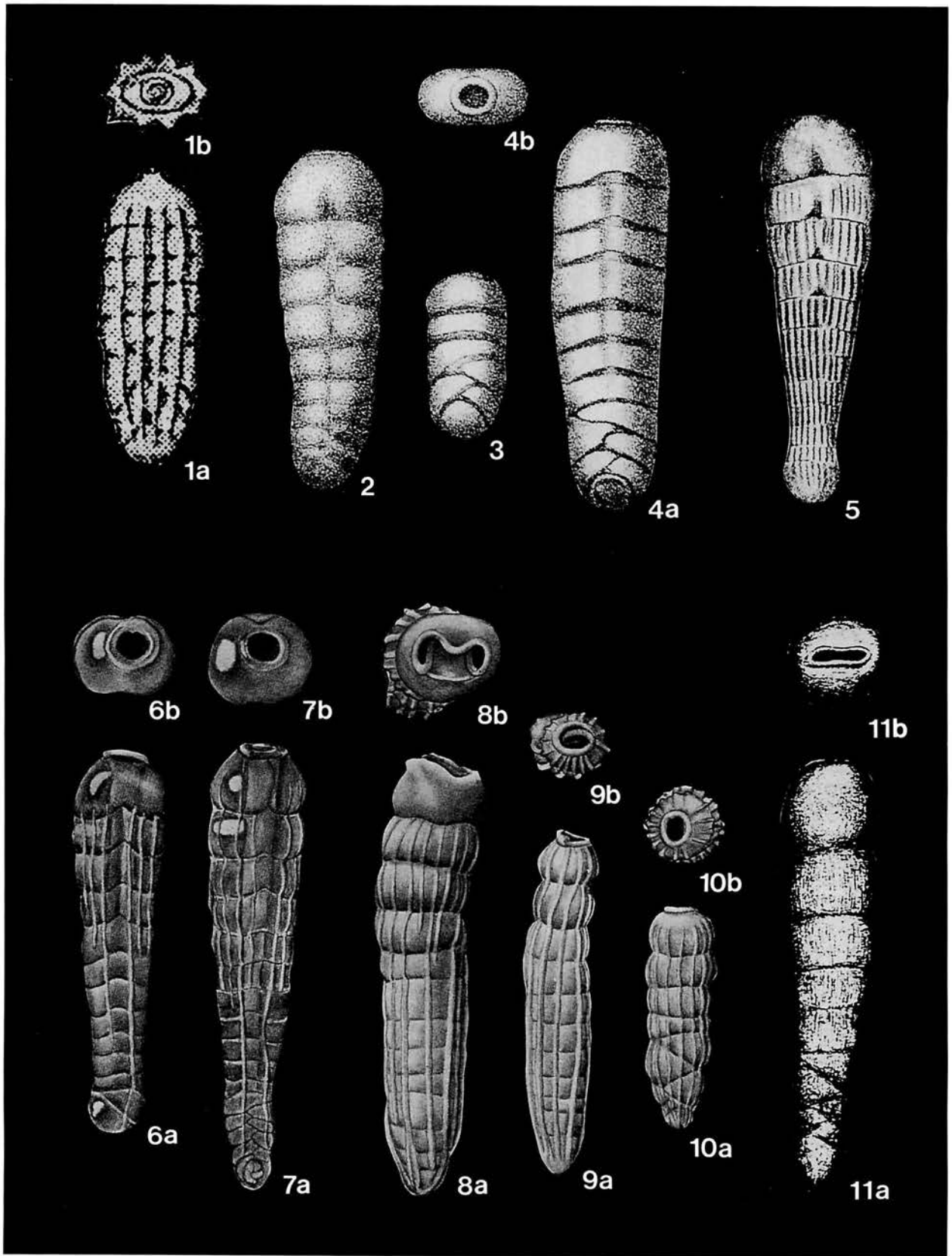
not *Rectobolivina striatula* (Cushman, 1917) (non *Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917, nomen nudum). Carter, 1964, p. 69, pl. 2, figs. 35, 36; Hornibrook, 1968, p. 73, fig. 13 (part), Hayward and Buzas, 1979, p. 72, pl. 26, figs. 320, 321.

not *Rectobolivina striatula* (Cushman, 1913). Kennett, 1966 (non *Siphogenerina striatula* Cushman, 1913), p. 47, fig. 59.

Material.—IGUT14513, sample MK19 (Figure 4.12a–c); IGUT14514, sample MK19 (Figure 11.6); IGUT14515, sample MK19 (Figure 11.7).

Remarks.—All specimens of the present species from the Miyazaki Group are regarded as megalospheric forms because they are characterized in having a bluntly rounded initial end (Figure 4.12a, c) and three pairs of biserial chambers at the earliest part (Figure 11.6). This species is distinguished from the other *Rectobolivina* species in having numerous, fine, and longitudinal striations covering the test surface (Figure 4.12a). Compared with Cushman's (1913) original figure of the type specimen (here reproduced in Figure 13.11a, b), our specimens have a slightly rhomboidal outline in section and an elliptically rounded aperture, in contrast to the rounded outline and rather narrow slit-like aperture in the type specimen.

← **Figure 11.** All dissected specimens are megalospheric forms. 1, 2. Sections A and B (see Figure 6) of *Rectobolivina raphana*, respectively, IGUT14510 and IGUT14511, $\times 120$ and 150 . 3. Section A of *R. raphana*, IGUT14512, $\times 120$. 4. Close-up of final chamber wall of figure 3, $\times 1,500$. ol: outer layer, il: inner layer. 5. Close-up view of the biserial part in *R. raphana*, $\times 400$. f: foramen, tp: toothplate, l: lip. 6. Section A of *Rectobolivina striatula* (Cushman), IGUT14514, $\times 180$. 7. Oblique view of foramen and toothplate in *R. striatula*, IGUT14515. The toothplate extends into the chamber lumen. Its lateral edges strongly fold towards the opposite side of the preceding foramen opening (f), but it never shows the tube-like structure, $\times 180$.



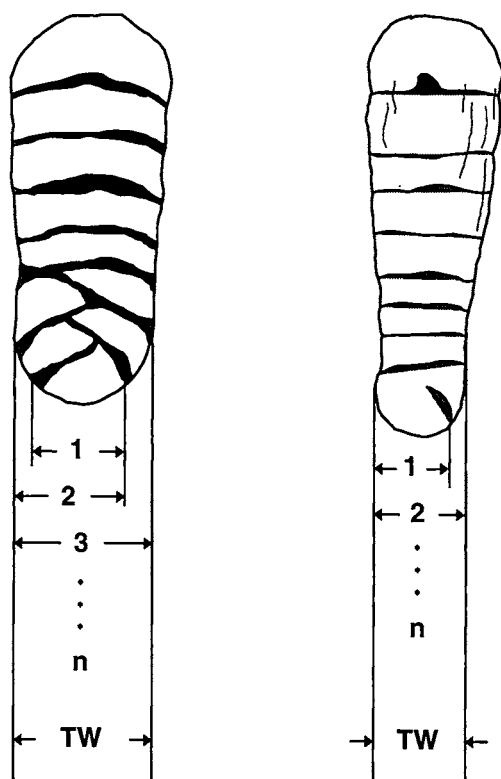
*R. bifrons**R. clavata* sp. nov.

Figure 14. Definition of measurements. TW: Test width including the distal chambers, n: Number of chambers from the initial to final chamber.

Rectobolivina clavatostriatula nom. nov.

Figure 13.5

Siphogenerina bifrons (Brady) var. *striatula* Cushman, 1917, p. 662 (nomen nudum); Cushman, 1919, p. 620; Cushman, 1921, p. 278, pl. 56, fig. 4; Cushman, 1926, p. 18, pl. 2, fig. 6, pl. 4, figs. 1-3.

Rectobolivina bifrons (Brady) var. *striatula* (Cushman, 1917). Cushman, 1937, p. 205, pl. 23, figs. 17, 18.

Diagnosis.—A species of *Rectobolivina* with a clavate-shaped test covered by distinct longitudinal striations.

Etymology.—The new specific name, *clavatostriatula*, represents clavate test shape and distinct striations of this species.

Remarks.—Cushman (1917) reported this species from the Sogod Bay (~1,000 m water depth), Philippines, under the name of *Siphogenerina bifrons* (Brady) var. *striatula* Cushman. Later, Cushman (1921, pl.56, fig.4) illustrated it (here reproduced in Figure 13.5). However, *S. bifrons* var. *striatula* Cushman, 1917 is a junior primary homonym of *Siphogenerina striatula* Cushman, 1913 (the original figure of the holotype is reproduced in Figure 13.11a, b), reported from the western Pacific Ocean. The former can clearly be distinguished from the latter in having a clavate-shaped test with fewer but more raised striations on the test surface. Consequently, *Rectobolivina clavatostriatula* is proposed as a new name to replace *S. bifrons* var. *striatula* Cushman, 1917.

Rectobolivina discontinuosa sp. nov.

Figures 4.8a-c, 9a-c; 10.5-10.7; 13.6a, 13.7b

Rectobolivina bifrons (Brady) (non *Sagrina bifrons* Brady, 1881). Loeblich and Tappan, 1964, p. C553, fig. 438, nos. 2a-5b; Loeblich and Tappan, 1987, p. 517, pl. 567, figs. 11-14 (not figs. 15-17).

? *Rectobolivina bifrons* (Brady) var. *striatula* (Cushman). LeRoy, 1941b (non *Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917, nomen nudum), p. 80, pl.1, fig. 9.

Diagnosis.—A species with a clavate-shaped test, whose surface is covered by numerous and discontinuous striations mainly on the later portion of the test.

Description.—Test free, moderate size, approximately four times as long as broad, straight, clavate-shaped, elliptical in being laterally depressed in cross section, initial end bluntly rounded in megalospheric form, pointed in microspheric form; chambers numerous, breadth twice the height, gradually increasing in size, changing from biserial to uniserial after the seventh chamber in megalospheric forms or after the thirteenth chamber in microspheric forms; wall calcareous, optically radial, transparent or semitransparent, finely perforate, rather thick, striae numerous in the later part of the test but much sparser in the earlier part of the test; sutures distinct, moderately thick, slightly depressed or flush; aperture terminal, nearly circular to elliptical, with a distinct lip; intercameral septa thick as well as the wall, parallel to slightly arched; toothplate folded at the side edge, extending into the preceding aperture (foramen), its folded face arranged alternately in position in planes 180° apart.

← **Figure 13.** Reproduction of original figures of the studied species. 1a, b. *Rectobolivina asanoi* Murata, 1951, ×135. 2-4b. *Rectobolivina bifrons* (Brady, 1881), after Brady (1884), ×71. 5. *Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917, after Cushman (1921) = *Rectobolivina clavatostriatula* nom. nov., ×66. 6a-7b. *Rectobolivina bifrons* (Brady, 1881) of Loeblich and Tappan (1964) = *Rectobolivina discontinuosa* sp. nov., ×66. 6a, b: megalospheric, 7a, b: microspheric forms. 8a-10b. *Rectobolivina raphana* (Parker and Jones, 1865) of Loeblich and Tappan (1964), ×55. 11a, b. *Siphogenerina striatula* Cushman, 1913, ×75.

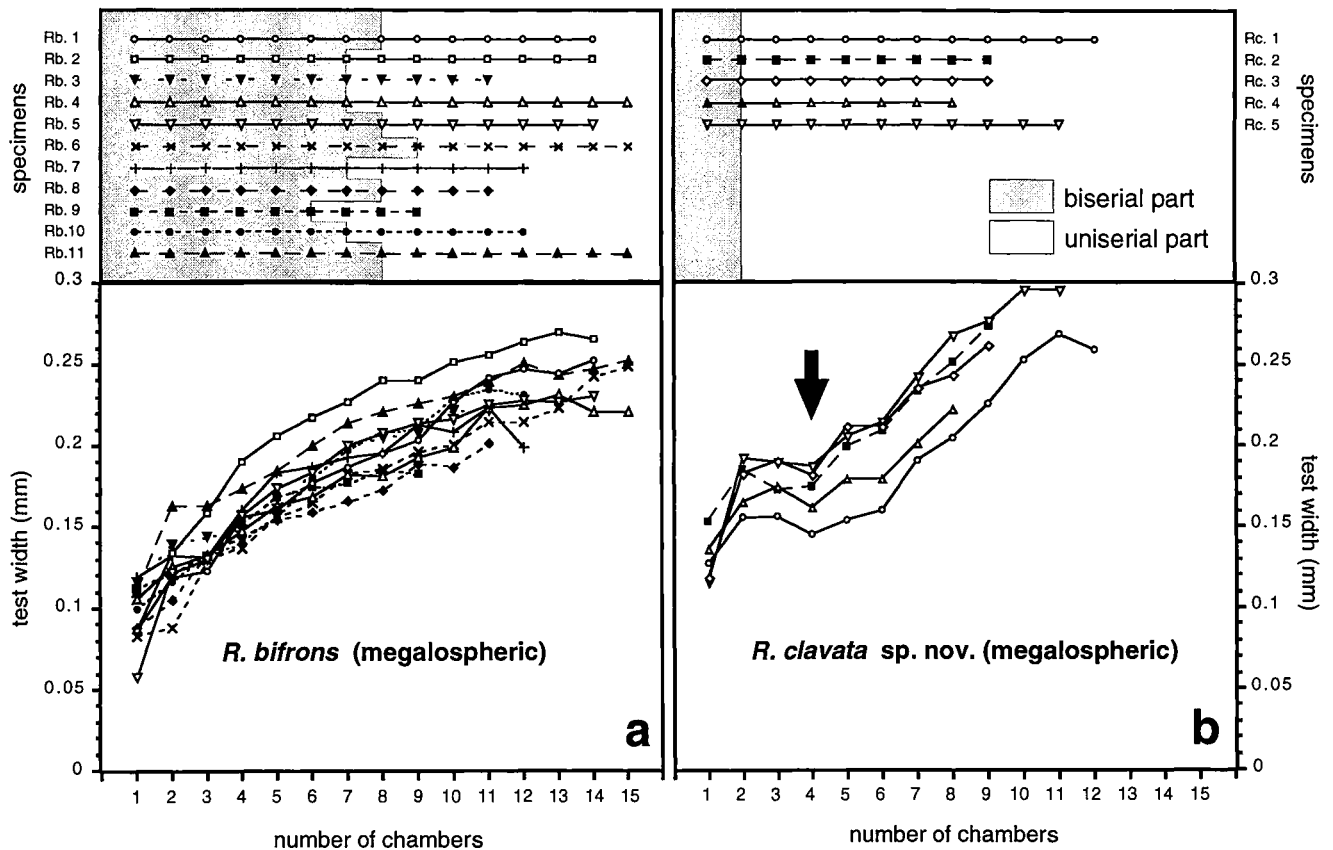


Figure 15. Test width changes in the megalospheric forms of *Rectobolivina clavata* sp. nov. ($n = 5$) and *R. bifrons* ($n = 11$) through ontogeny. Arrow indicates the position where the test width of *R. clavata* becomes the narrowest.

Material.—Holotype: IGUT14504 (0.98 mm in length, 0.31 mm in maximum breadth), sample MK57 (Figure 4.8a–c). Paratypes: IGUT14505 (1.05 mm in length, 0.31 mm in maximum breadth), sample MK57 (Figure 4.9a–c); IGUT14506, sample MK57 (Figure 10.5); IGUT14507, sample MK57 (Figure 10.6, 10.7).

Etymology.—The new specific name, *discontinuosa*, comes from the discontinuous striations of the test.

Remarks.—The specimens treated here (Figures 4.8a–c, 9a–c) are compared well with those of Loeblich and Tappan's (1964, 1987) *Rectobolivina bifrons* (here reproduced in Figures 13.6a–7b) in having a clavate-shaped test ornamented by distinct, discontinuous striations. This discontinuous striation is clearly distinguished from the completely continuous striation in typical *Rectobolivina clavatostriatula* (Figure 13.5) and from the inornate test of *Rectobolivina clavata* (Figure 4.5a–c, 4.6a–c, 4.7a–c). Therefore, we judge our specimens to belong to a new species and not to either of the latter two species. This new species differs from *Rectobolivina asanoi* Murata, 1951 by its more slender and clavate-shaped test with less raised striations on the test surface.

Rectobolivina raphana (Parker and Jones, 1865)

Figures 4.10a–c, 4.11a–c; 8.1; 11.1–11.5; 13.8a–13.10b

Uvigerina (*Sagrina*) *raphanus* Parker and Jones, 1865, p. 364, pl. 18, figs. 16, 17.

Sagrina raphanus (Parker and Jones). Brady, 1884, p. 585, pl. 75, figs. 21–24.

Siphogenerina (*Sagrina*) *raphanus* (Parker and Jones). Cushman, 1913, p. 108, pl. 46, figs. 1–5.

Siphogenerina raphanus (Parker and Jones). Cushman, 1921, p. 280, pl. 56, fig. 7; Cushman, 1926, p. 4, pl. 1, figs. 3, 4 (? figs. 1, 2), pl. 2, figs. 1–3, 10, pl. 5, figs. 1, 2; Cushman, 1942, p. 55, pl. 15, figs. 8, 9 (not figs. 6, 7); Hofker, 1951a, p. 233, figs. 155, 156; LeRoy, 1964, p. F35, pl. 3, fig. 35.

Siphogenerina raphana (Parker and Jones). Hada, 1931, p. 134, text-figs. 91a, b; Asano, 1950, p. 14, figs. 56, 57; Asano, 1958, p. 30, pl. 7, figs. 8–10; Kuwano, 1962, pl. 22, fig. 5; Ishiwada, 1964, pl. 5, fig. 81.

Rectobolivina raphana (Parker and Jones). Loeblich and Tappan, 1964, p. 533, fig. 438–9–11; Matoba, 1970, p. 60, pl. 3, fig. 31; Whittaker and Hodgkinson, 1979, p. 56, fig. 8; Matoba and Honma, 1986, pl. 4, figs. 6a, b; Matoba and Fukusawa,

1992, p. 218, fig. 9-6.

? *Siphogenerina (Sagrina) raphanus* (Parker and Jones). Egger, 1893, p. 317, pl. 9, fig. 36.

Material.—IGUT14508, sample MK56 (Figure 4.10a-c); IGUT14509, sample MK56 (Figure 4.11a-c); sample MK56 (Figure 8.1); IGUT14510, sample MK56 (Figure 11.1); IGUT14511, sample MK56 (Figure 11.2, 11.5); IGUT14512, sample MK56 (Figure 11.3, 11.4).

Remarks.—All specimens treated in this study are elliptically rounded in section, and in this respect, they are distinguished from the paratypes of this species designated by Loeblich and Tappan (1964) (here reproduced in Figure 13.8a-13.10b). Unfortunately, they did not show a figure of the lectotype. As was shown in many previous descriptions (see the above synonym list), strongly raised costae on the entire test surface are recognized in all specimens examined (e.g. Figure 4.10a-4.11c).

Acknowledgments

We express our deep gratitude to Hiroshi Ujiié, Takushoku University, for his critical reading of the manuscript and many useful taxonomic comments. We gratefully acknowledge Stefan A. Revets, University of Western Australia and Johann Hohenegger, Geozentrum Universität Wien for their kind pre-reviewing of the manuscript and constructive comments. We are sincerely indebted to Shuko Adachi of University of Tsukuba for her kind technical support in making thin sections of foraminiferal tests. Reviews by George H. Scott of Institute of Geological and Nuclear Sciences, New Zealand, and an anonymous referee improved the manuscript. Parts of samples utilized in this study were collected by Yoshiaki Yoshimura and Hiroshi Oi, who are former students of A. Hatta.

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行事予定

◎第152回例会は、2003年1月24日（金）～26日（日）に横浜国立大学教育人間科学部にて開催の予定です。1月24日（金）にシンポジウムとして「白亜紀海洋無酸素事件の解明：世話人 平野弘道・北里 洋・西 弘嗣」が、また1月25日（土）にシンポジウム「中・古生代微化石研究の現状と将来－テレーン解析後の使命－：世話人 指田勝男」が開催されます。なお、講演の申し込み締め切りは、2002年11月29日（金）です。講演申し込みの予稿集原稿送付の際には発表で使用する機器（液晶プロジェクター、OHP、スライドなど）の希望について明記して下さい。

◎2003年年会総会は、2003年6月下旬に静岡大学理学部で開催されます。シンポジウム「生物多様性を古生物学から考える：世話人 塚越 哲・北村晃寿・生形貴男」を開催予定です。講演の申し込み締め切りは2003年5月2日（金）の予定です。このほか、夜間小集会などの希望予定がありましたら、2002年12月初旬までに行事係までお知らせ下さい。

個人講演・シンポジウム案の申し込み方法

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

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本誌の発行に要する費用は、会員の会費以外に、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。

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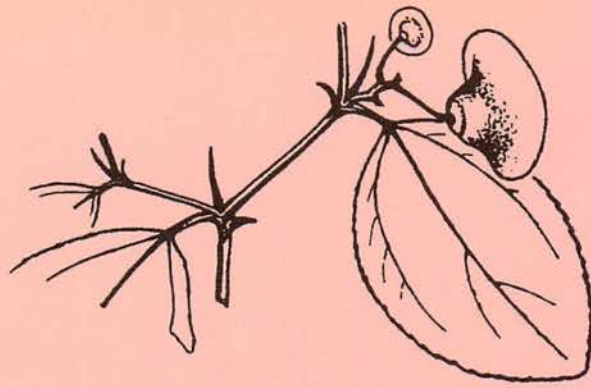
2002年6月25日 印刷
2002年6月28日 発行

ISSN 1342-8144
Paleontological Research

第6巻、第2号

2,500円

発行者 日本古生物学会
〒113-8622 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 棚部一成・加瀬友喜
編集幹事 遠藤一佳・重田康成・佐々木猛智
印刷者 学術図書印刷株式会社 富田 潔
〒176-0012 東京都練馬区豊玉北2の13の1
電話 03-3991-3754



ISSN 1342-8144

Paleontological Research

Vol. 6, No. 2 June 28, 2002

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