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

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1008 *Shako*, a new Miocene stomatopod Crustacea from Japan

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Abstract. The monotypic genus *Shako* (Crustacea, Stomatopoda) is erected with *S. tomidai* sp. nov. from the Miocene Ayugawa and Mizunami Groups (Lower Miocene) of Central Japan. This is the second record of the Stomatopoda from Cenozoic deposits of Japan. It appears that *S. tomidai* preferred a brackish water environment.

Key words: Crustacea, Stomatopoda, *Shako*, Miocene, Japan

Introduction

The order Stomatopoda Latreille, 1817 (Crustacea) contains 15 extant families, the Carboniferous Tyrannophontidae Schram, 1969 and the Jurassic-Cretaceous family Sculdidae Dames, 1886 (Shram, 1986; Müller, 1994). Fossil records of the Stomatopoda are rare in Mesozoic and Cenozoic deposits throughout the world. In the review of fossil records by Holthuis and Manning (1969; R541), four extinct sculdid and four extant squillid genera (i.e. *Gonodactylus* Berthold, 1827, *Hemisquilla* Hansen, 1985, *Squilla* Fabricius, 1787, *Chloridella* Miers, 1880=*Clorida* Eydoux and Souleyet, 1842) are recorded. According to Manning's 1980 classification, *Gonodactylus* belongs to the family Gonodactylidae Giesbrecht, 1910 and *Hemisquilla* to the family Hemisquillidae Manning, 1980.

Secretan (1975) assigned *Squilla antiqua* Münster, 1842, from the Upper Eocene of Italy to *Lysiosquilla* Dana, 1852 (Lysiosquillidae), while *Squilla wetherelli* Woodward, 1879 from the Eocene London Clay of England was assigned to the genus *Bathysquilla* Manning, 1963 (Bathysquillidae) by Quayle (1987). Schram (1968) erected a new monotypic genus, *Paleosquilla* (Gonodactylidae), from the Upper Cretaceous of Colombia, South America. Förster (1982) described three new species, *Squilla hollandi* (Squillidae) and ? *Pseudosquilla wulfi* (Pseudosquillidae), from the Upper Eocene of North Germany, and *Lysiosquilla nkporoensis* from the Upper Cretaceous of Nigeria. Yun (1985) gave detailed descriptions of five fossil species in three genera, *Squilla, Leesquilla* Yun, 1985 and *Pohsquilla* Yun, 1985, of the Squillidae from the Miocene of Korea. Karasawa and Nakagawa (1992) recorded *Oratosquilla* ? sp. (Squillidae) from the Miocene Shimo Formation of Fukui Prefecture. Thus, eleven genera in five extant families have been recognized as fossils.

The purpose of this paper is to describe a new genus and species of squillid from the Ayugawa and Mizunami Groups of Central Japan, and discuss the paleoecology of this species based on the associated decapod fauna.

Systematics

Family Squillidae Latreille, 1803
Genus *Shako* gen. nov.

Type species.—*Shako tomidai* sp. nov. by monotypy; masculine gender; Early Miocene; Japan.

Derivation of name.—The name is derived from the Japanese word for stomatopod.

Diagnosis.—Moderate sized squillid, total length less than 150 mm. Eye small, cornea bilobed, stalk long. Carapace narrowed anteriorly, without median carina; cervical groove distinct; anterolateral angles spined; posterolateral margins strongly convex. Last three thoracic somites with well developed submedian and intermediate carinae; lateral process of 5th thoracic somite developed as single, narrow, gently curved spine, directed anterolaterally; lateral processes of next two somites posterolaterally rounded. Abdomen with submedian, intermediate, lateral and marginal carinae, 4th and 5th somites with median carinule. Telson inflated, slightly broader than long, tapering posteriorly, with dorsal median carina and 6 small, triangular marginal teeth; submedians with fixed apices; intermediate denticles in a sharp oblique, slightly convex row; dorsal surface of telson finely granulated. Dactylus of raptorial claw with 5 teeth on inner margin; outer margin of dactylus sinuate; inner margin of propodus pectinate; dorsal ridge of carpus unarmed.

Discussion.—This new genus is assigned to the Squillidae by having a carinate dorsal body, a pectinate inner margin of the propodus, and the telson with a distinct median carina and 18 intermediate denticles, although the ocular scales, the propodi of 3rd and 4th thoracic appendages and the basal prolongation of the uropod are unknown.

Manning (1968) indicated that there were four generic groups within the Squillidae. *Shako* belongs to his third group in that the lateral process of the 5th thoracic somite is

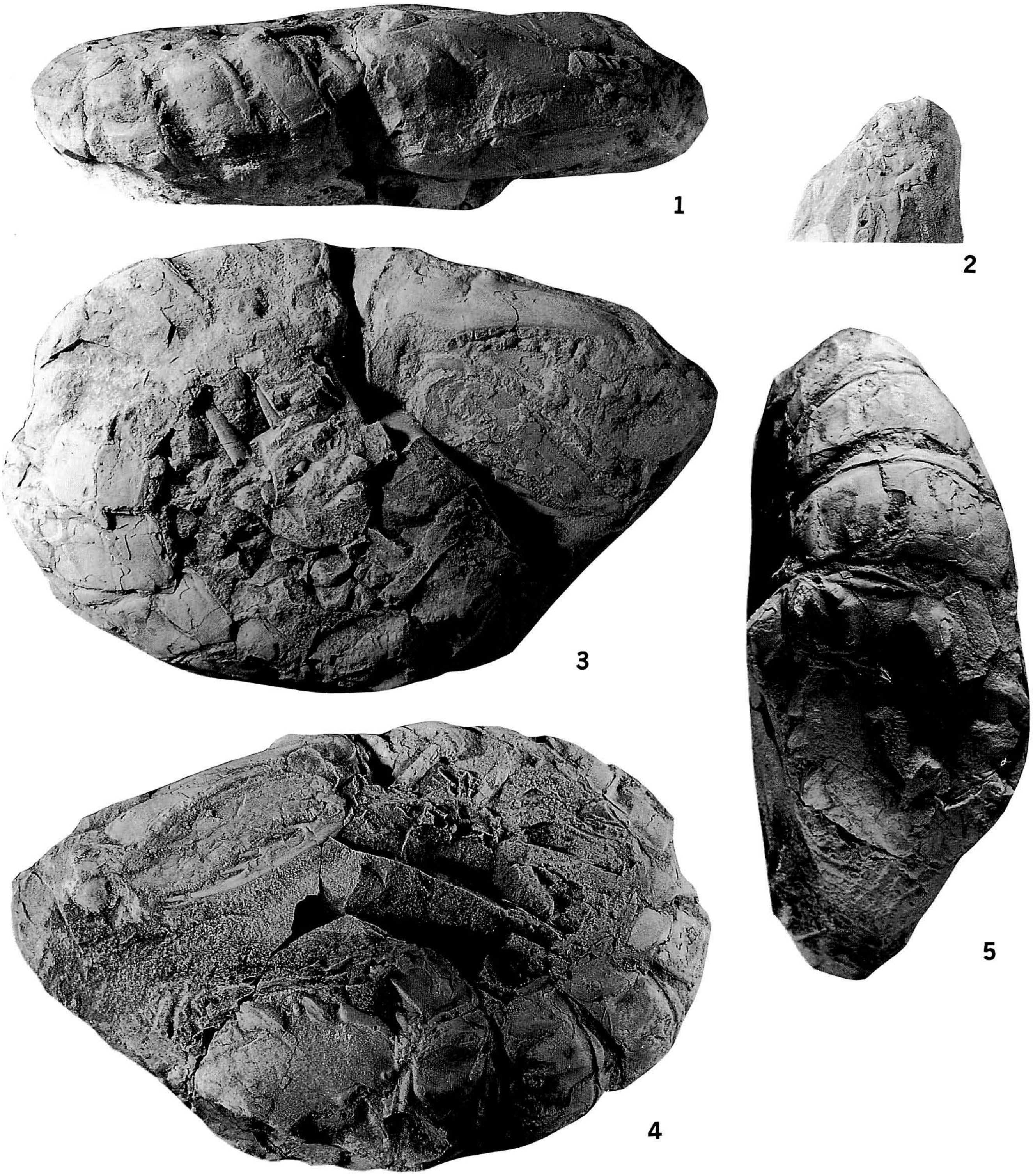

Figure 1. *Shako tomidai* gen. et sp. nov., MFM39013 (holotype). **1.** ×1.5, dorsal view of anterior part of body. **2.** ×2.0, dorsal view of eye and anterior part of carapace. **3, 4.** ×1.5, lateral view. **5.** ×1.5, dorsal view of posterior part of body.

developed as a single spine, the eye is small, and the carapace and an inflated abdomen have a reduced complement of carinae. *Shako* differs from *Clorida* Eydoux and Souleyet, 1842, a typical genus of the group, in having a broad telson with dorsal spines and tubercles, and the submedian teeth without movable apices. *Shako* appears to be related to the Recent genera *Cloridopsis* Manning, 1968, and *Lenisquilla* Manning, 1977, in structure of the lateral process of the 5th thoracic somite and in the telson with fixed apices. The new genus differs from *Cloridopsis* in the lack of a median carina on the carapace, the shape of the lateral process of the 6th and 7th thoracic somites, presence of median carinules on the 4th and 5th abdominal somites, and the dorsal surface of the telson. Presence of median carinules on the 4th and 5th abdominal somites and the prelateral lobe of the telson, and short marginal teeth of the telson readily distinguish *Shako* from *Lenisquilla*.

Shako appears to show an affinity with the Korean Miocene genus, *Leesquilla* Yun, 1985 in the shape of the lateral processes of the 5th-7th thoracic somites, but differs in having a small eye, and lacking a median carina on the carapace and abdominal somites. The lateral process of the 5th thoracic somite in *Shako* is a narrow, gently curved spine, whilst in *Leesquilla* it is a large, acute spine strongly directed anteriorly. The dactylus of the raptorial claw in *Shako* has five teeth, whereas in *Leesquilla* it has four. Short, triangular marginal teeth of the telson readily distinguish *Shako* from *Leesquilla* and the second Korean Miocene genus *Pohsquilla* Yun, 1985.

Shako tomidai sp. nov.

Figures 1-4

Material examined.—MFM39013 (holotype), a road cut of Nishino, Ayugawa, Tsuchiyama-cho, Koga-gun, Shiga Prefecture (34°56′32″N, 136°19′24″E), collected by M. Kametaka; Sendai Sandstone Mudstone Member, Tsuchiyama Formation, Ayugawa Group (Lower Miocene, Zones N7-N8 of Blow's scale by Yoshida, 1992)—MFM9042 (paratype), Loc. 36 of Karasawa (1991), dry riverbed southeast of Shomasamahora, Tsukiyoshi, Akeyo-cho, Mizunami City, Gifu Prefecture (35°22′42″N, 137°14′E), collected by T. Kaede; Tsukiyoshi Member, Akeyo Formation, Mizunami Group.

Repository.—All type specimens are housed in the Mizunami Fossil Museum, Yamanouchi, Akeyo-cho, Mizunami, Gifu, 509-61 Japan.

Derivation of name.—In honor of my friend, Dr. Susumu Tomida (Chukyo Gakuin University, Gifu), a molluscan

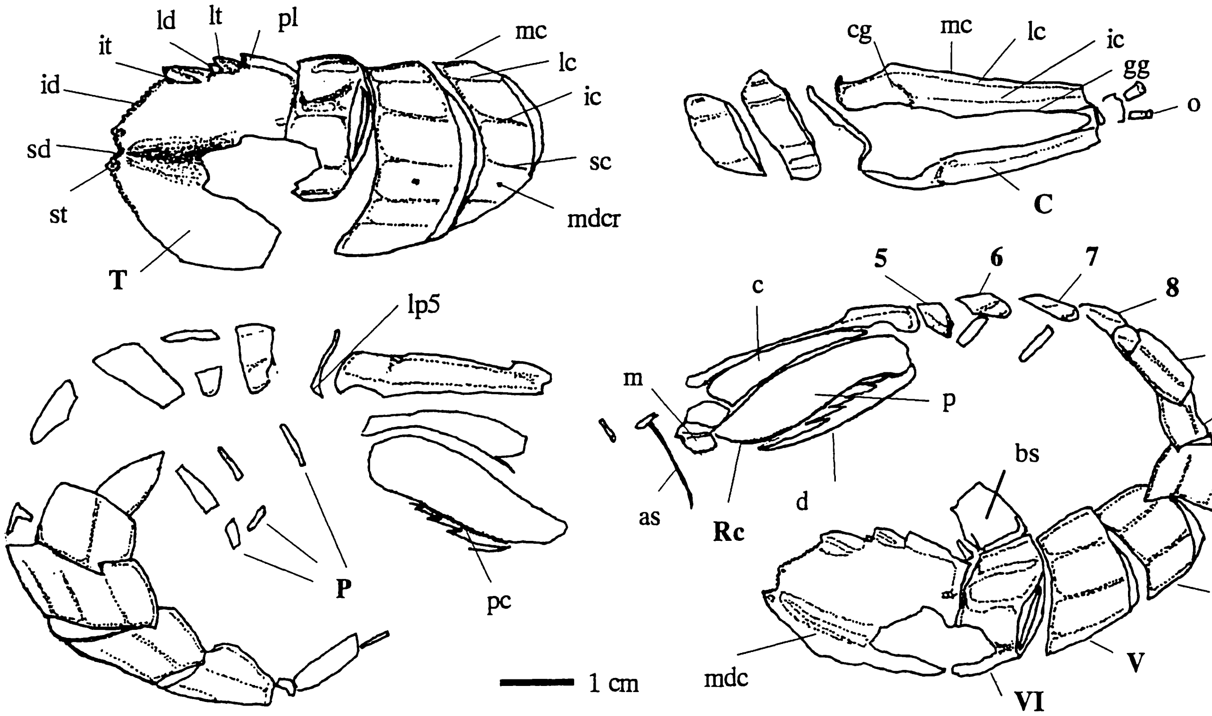

Figure 2. *Shako tomidai* gen. et sp. nov., MFM39013 (holotype). Explanation: 5-8, fifth to eighth thoracic somites; I-VI, first to sixth abdominal somites; as, antennal scale; bs, basal segment of uropod; C, carapace; c, carpus; cg, cervical groove; d, dactylus; gg, gastric groove; ic, intermediate carina; id, intermediate denticle; it, intermediate tooth; lc, lateral carina; ld, lateral denticle; lt, lateral tooth; lp5, lateral process of fifth thoracic somite; m, merus; mc, marginal carina; mdc, median carina; mdcr, median carinule; o, eye; P, pereiopods; p, propodus; pc, pectinations; pl, prelateral lobe; Rc, Raptorial claw; sc, submedian carina; sd, submedian denticle; st, submedian tooth; T, telson.

Figure 3. *Shako tomidai* gen. et sp. nov. **1a, b,** MFM9042 (paratype), ×1.5, a : dorsal view of thoracic and abdominal somites, b : dorsal view of telson. **2.** MFM39013 (holotype), ×2.0, dorsal view of telson.

paleontologist, who studied decapod fossils from the Mizunami Group in his early years.

Diagnosis.—As for genus.

Description.—Size moderate, total length less than about 150 mm. Eye small, cornea bilobed and slightly broader than stalk, stalk length about 0.75 times as long as eye length. Antennal scale less than half as long as carapace. Antennular somite poorly preserved. Ocular scales not preserved. Rostral plate broken.

Carapace narrowed anteriorly. Anterior margins of carapace concave. Anterolateral spine weak, not extending to base of rostral plate. Median carina lacking, intermediate carinae not extending to cervical groove, lateral and marginal carinae well developed. Posterolateral margins strongly convex.

Lateral process of 5th thoracic somite developed as single, narrow, gently curved spine, directed anterolaterally, posterior margin gently convex. Lateral processes of 6th and 7th somites posterolaterally rounded. Somites decreasing in size anteriorly with well developed, unarmed submedian and intermediate carinae, and without median carina.

Abdomen strongly carinate, increasing in width posteriorly, but 6th somite narrower than 5th. Articulated anterolateral plates of abdomen absent. Submedian, intermediate, lateral and marginal carinae distinct; submedian carinae slightly divergent posteriorly on 2nd to 5th somites and inflated, slightly convergent on 6th somite; 4th and 5th somites with interrupted median carinule. None of all abdominal spines armed posteriorly.

Telson longitudinally convex, slightly broader than long, tapering posteriorly. Lateral, intermediate and submedian teeth small, triangular. Submedians with fixed apices. All marginal teeth inflated at the base. Two lateral, 18 intermediate and 6 submedian denticles small, rounded; intermediate denticles in a sharp oblique, slightly convex row. Dorsal surface finely granulated without radial ornamentations, strong median carina well developed without distal spine.

Raptorial claw large. Dactylus slender, about 0.75 times as long as carapace length, with 5 teeth decreasing in size

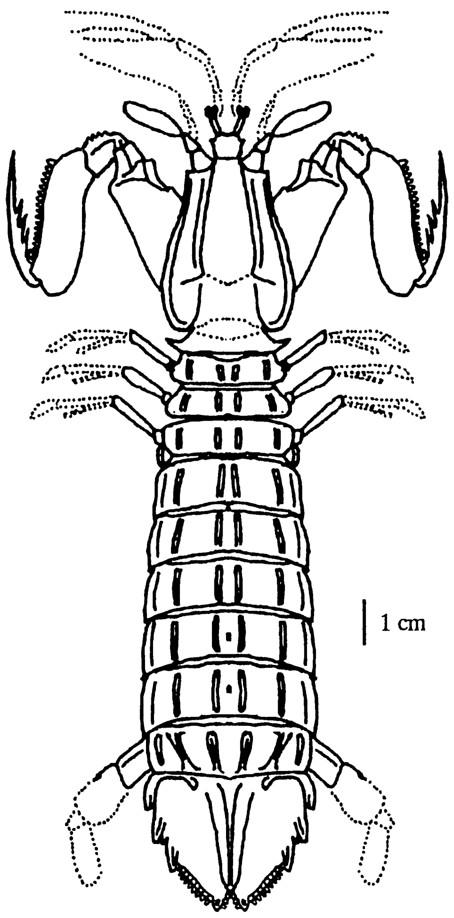

Figure 4. Reconstruction of *Shako tomidai* gen. et sp. nov.

proximally on inner margin, outer margin of dactylus sinuate. Propodus with fine pectinations on inner margin. Carpus bearing 4 small, bluntly triangular teeth on outer margin, dorsal ridge of carpus unarmed.

Paleoecology.—The holotype specimen was collected from mudstone of the Ayugawa Group of Shiga Prefecture, associated with a pelecypod, *Trapezium modiolaeforme* Oyama and Saka (Tanaka and Kimura, per. com.). *T. modiolaeforme* is found in the *Cyclina*-*Vicarya* and *Vicaryella bacula*-*Cyclina* assemblages which represent a shallow estuarine environment from the Ayugawa Group (Shibata, 1975).

Karasawa (1991; 1993) reported six species of decapod from the Mizunami Group of the fossil-bearing locality within Mizunami City, Gifu Prefecture. The decapod assemblage is dominated by *Upogebia mizunamiensis* Karasawa and *Laurentiella imaizumii* Karasawa. Associated with them, *Laomedia praeastacina* Karasawa, *Scylla ozawai* Glaessner, *Miosesarma japonicum* Karasawa, and Varuninae gen. et sp. indet. occur rarely.

The depositional environment of the localities was interpreted as an intertidal zone of muddy bottom (Karasawa, 1991). The brackish-water molluscs *Cyclina japonica* Kamada, *Vicarya yokoyamai* Takeyama, *Batillaria mizunamiensis* Itoigawa and *Vicaryella ishiiana* Yokoyama were found at the decapod-bearing localities (Karasawa, 1991). Thus, it appears that *S. tomidai* preferred to inhabit a muddy bottom in the intertidal zone under the influence of low-salinity water.

Acknowledgments

I thank Dr. R.B. Manning (Smithsonian Institution, Washington, D.C.) for critically reading the manuscript, Prof. J. Itoigawa (Sugiyama Jogakuen University) for advising me on the generic name, and Mr. M. Kametaka (Nagoya University) and Mr. T. Kaede (Inazawa City) for offering their fossil stomatopod specimens.

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1009 Larval paleoecology of the late Pleistocene naticid gastropod *Cryptonatica* with two protoconch types from the Oga Peninsula, northern Japan

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Abstract. Gastropod fossils from the upper Pleistocene marine sequence in the Oga Peninsula, northern Japan, were analyzed, with special reference to the larval paleoecology and taxonomic relationships of *Cryptonatica* with two different protoconch types. The frequency of warm-water species increases towards the top of the section, with a gradual decrease in the frequency of cold-water species, suggesting gradual warming of the ambient sea water under the influence of the Tsushima currents from the south during 100-134 Ka. Available data on the relationship between protoconch morphology and mode of development in extant naticids strongly suggest that the two morphotypes of *Cryptonatica*, whose teleoconch morphologies are comparable to *C. andoi*, probably underwent different modes of development, *i.e.* planktotrophy for the type with a smaller protoconch (S-type) and non-planktotrophy for the type with a larger protoconch (L-type). The taxonomic relationships of the two morphotypes of *Cryptonatica* can be interpreted as closely allied different species (cryptic species) rather than dimorphs of a single species with different developmental modes (poecilogony), since the latter phenomenon is quite rare in modern marine invertebrates. Comparison with type and figured specimens of *C. andoi* and related species of the same genus shows that specimens of S-type are referable to *C. andoi* (Nomura), while those of L-type may belong to a new species; here I provisionally treat them under *C.* sp. aff. *C. andoi*. According to this interpretation, the transition of developmental modes from non-planktotrophy to planktotrophy may have occurred in association with a speciation event of the "*Cryptonatica andoi*" lineage at least before late Pleistocene time.

Key words: *Cryptonatica*, Naticidae, Pleistocene, Oga area, larval ecology, cryptic species, evolution

Introduction

A major goal of paleontology is to understand how the biological characteristics of fossil organisms have influenced their success on the earth (Emlet, 1989). Many marine invertebrates undergo a larval stage during a limited interval between hatching and metamorphosis. Developmental mode may influence autecology, modes of selection, and rates of speciation and extinction (Wary and Raff, 1991). The excellent fossil record of marine molluscs allows us to examine the life history and the tempo and mode of morphological evolution by the comparison of fossil remains with related living representatives.

Gastropods secrete a protoconch shell that formed during embryogenesis and/or during the post-hatching larval stage before metamorphosis. Since the early studies of Thorson (1950), Shuto (1974) and Jablonski and Lutz (1980) on the relationship between protoconch morphology and mode of development in extant species, microscopic studies of the protoconch have become one of the useful approaches to the study of larval ecology and paleoecology of gastropods.

Until now, it has been generally thought that larval ecology is stable throughout a given gastropod lineage. Jablonski (1986) emphasized the species-level invariability of the mode of development in gastropods. Protoconch morphology has been frequently utilized as a reliable basis for phylogenetic reconstruction. For example, two turrid genera, *Guraleus* and *Antiguraleus*, are distinguished based on differences in protoconch morphology that reflect larval ecological differences (Shuto, 1994). The idea that larval ecology is invariant at the species level may influence or be influenced by the definition of taxa. This can lead to circular arguments. On the other hand, some taxonomists have made allowance for polarity of changes in protoconch morphology. Bouchet (1990) suggested the possibility that protoconch morphology in the Turridae exhibits polarity from multispiral type to pauspiral type reflecting planktotrophy and non-planktotrophy respectively. Nevertheless, the relationship between developmental modes and phylogeny in gastropods has not yet been sufficiently elucidated.

The family Naticidae possess unique egg masses called egg collars (e.g. Giglioli, 1955; Amio, 1955). The larval ecology in some species of this family has been studied experimentally (e.g. Amio, 1955). Furthermore, fossils of this family are found abundantly in marine Cenozoic strata in the northern Pacific region including Japan (Marincovich, 1977; Majima, 1989). In this study, larval ecology and taxonomy of a naticid, "*Cryptonatica andoi* Nomura, 1935" with two protoconch morphotypes are examined based on upper Pleistocene and Recent specimens. The purpose of this

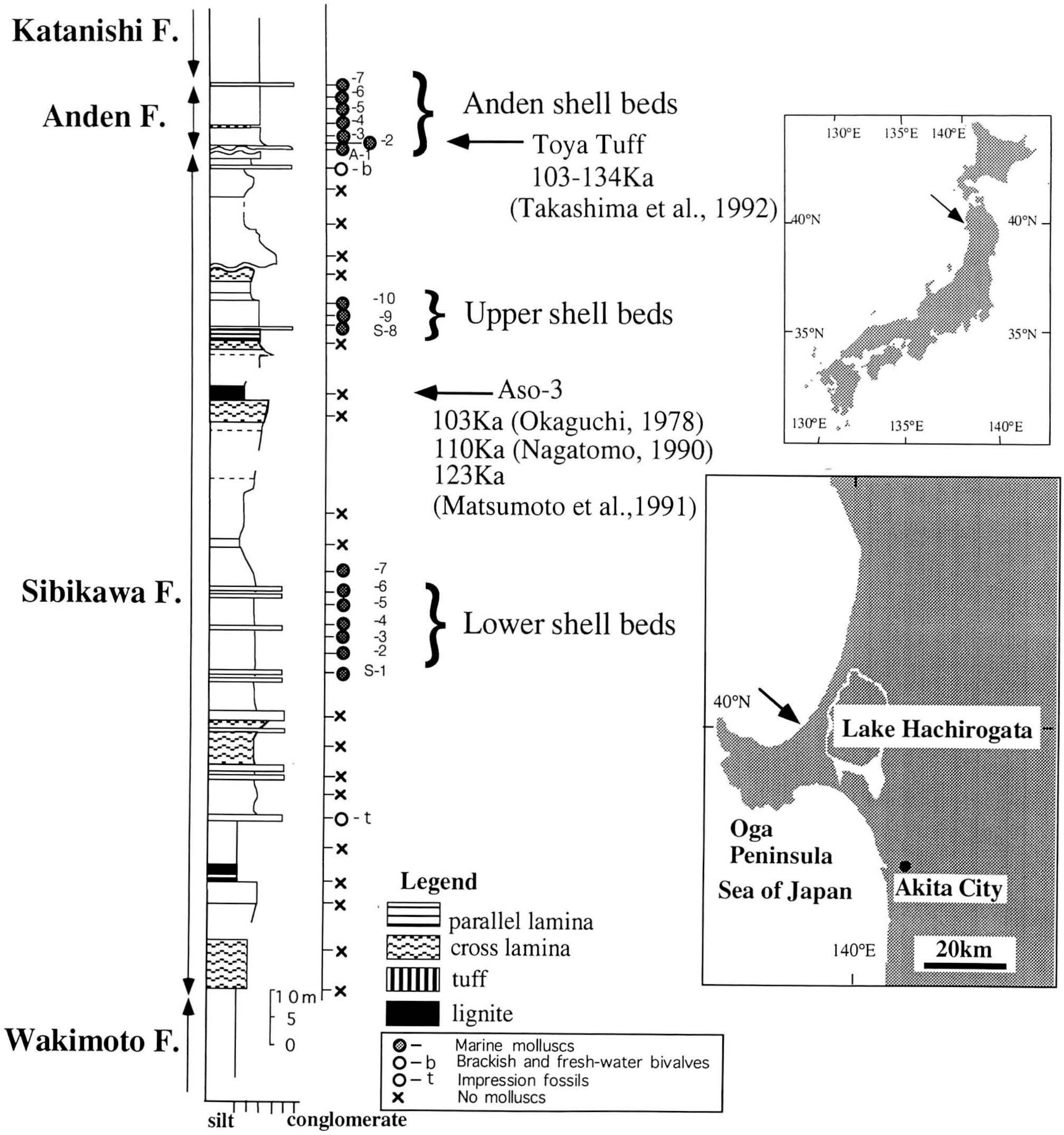


Figure 1. Geological column of the upper Pleistocene sequence exposed along the Anden coast, north of the Oga Peninsula, northern Japan (arrow on index map), showing the stratigraphic positions of fossil localities.

paper is to demonstrate how developmental mode in gastropods is affected by paleoenvironmental change and to examine the stability of developmental modes within a lineage.

Materials and methods

Geological settings of fossil-bearing strata

Naticid fossils from the late Pleistocene marine strata exposed at the Anden Coast, Oga City, were used for the study of change in larval paleoecology (Figure 1). The strata are divided into the Wakimoto, the Shibikawa, the Anden, and the Katanishi Formation based on lithostratigraphy (Kitazato, 1975). The Shibikawa Formation overlies the massive mudstone of the Wakimoto Formation. It attains about 120 m in thickness in the studied section. Two sedimentary cycles are recognized in the Shibikawa Formation : coarse sand or granule-sized gravel beds grading upwards into medium to fine sand and silt and terminating in a lignite bed. The age of the lignite bed in the upper cycle is 103-123 Ka based on fission track analysis of an enclosed volcanic ash layer (Aso-3) (Okaguchi, 1978 ; Nagatomo, 1990 ; Matsumoto *et al.*, 1991).

The Anden Formation clinounconformably covers the Shibikawa Formation. It attains about 10 m in thickness and consists of sand and sandy silt with an intercalation of massive pink tuff. The pink tuff has been identified as the Toya Tuff, which has fission track ages of 103-134 Ka (Takashima *et al.,* 1992). The Katanishi Formation, more than 15 m thick, conformably covers the Anden Formation. It consists mainly of alternating fine and modium sand beds with a shell bed containing disarticulated *Glycymeris* at the base. It also contains a tuff correlated with the Aso-4 Tuff (86-90 Ka fission track age, Oba, 1991).

In both Shibikawa and Anden Formations, the lower and middle parts of the cycle are rich in shallow-marine invertebrate fossils (molluscs, brachiopods and echinoids), while the uppermost part contains brackish to freshwater bivalves (ostreids and corbiculids) and water nuts (*Trapa* sp.). Molluscan shell beds are intercalated at two horizons in the Shibikawa Formation ; I will refer to them as the lower and upper shell beds. Recent studies on the sequence and oxygen isotope stratigraphy in combination with the faunal analysis have suggested that lithologic and faunal changes in the upper Pleistocene sequence in the Oga Peninsula were controlled by global glacial eustatic sea-level changes (Matoba, 1992 ; Shirai, 1995MS).

Materials

5,000 cm^3 of fossil bearing sediment was collected at each of the ten horizons in the Shibikawa Formation [7 horizons in the lower shell beds (S-1 to S-7) and 3 horizons in the upper shell beds (S-8 to S-10)] and each of the seven horizons in the Anden Formation (A-1～A-7) (Figure 1). Each sediment sample was sieved with a 2 mm mesh screen, and gastropod fossils in the residue were picked and identified. A total of 1640 specimens belonging to 75 species were idetified (see Appendix I).

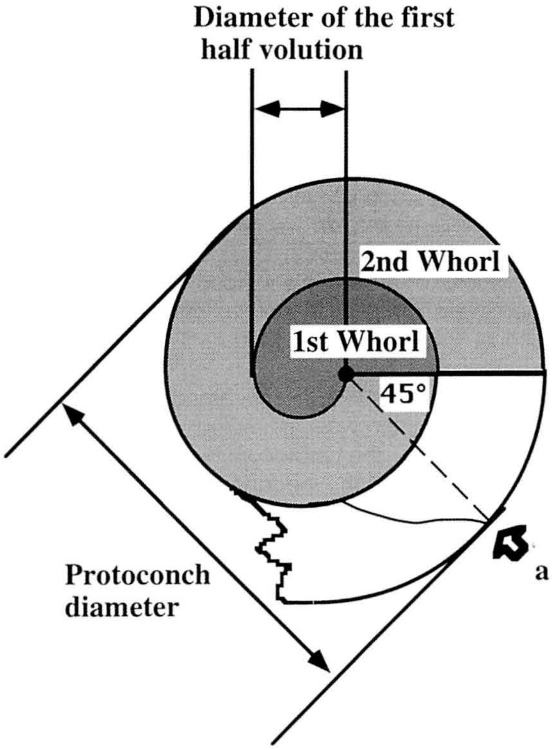


Figure 2. Terminology and measurements of protoconch used in this paper. The arrow a points to the protoconch-teleoconch boundary. The illustrated gastropod has $2^{1}/_{8}$ volutions.

Table 1. Recent and fossil specimens of *Cryptonatica* species used for comparison of protoconch morphology.

Species	Locality and age	No. of specimens and repository (UMUT)
Cryptonatica andoi (Nomura)	Mikawaissiki, Aichi Prefecture, central Japan, Recent	4 (RM 19865-1～4)
C. ciausa (Broderip and Sowerby)	Oga Peninsula, Akita Pref., northern Japan, Shibikawa F. (upper Pleistocene)	2 (CM 19866-1～2)
	Toyama Bay, Toyama Pref., central Japan, Recent	1 (RM 19867)
C. janthostoma (Deshayes)	Muroran, Utiura Bay, Hokkaido, Recent	5 (RM 19868-1～5)
C. wakkanaiensis (Habe and Ito)	Off wakkanai, Hokkaido, Recent	7 (RM 19869-1～7)
C. hirasei (Pilsbry)	Off Wakkanai, Hokkaido, Recent	4 (RM 19870-1～4)

After having determined the taxonomic relationships, faunal characteristics of each sample were analyzed. Almost all gastropod species identified are extant. The biogeographic distributions of the species were determined according to the data of living species in the north Pacific (Higo and Goto, 1994). Species living south of N35° are considered warm-water species and those north of N35° are cold-water species. Species occurring in both realms were treated as moderate-water species. These criteria were used to examine historical changes of the gastropod fauna. For determination of developmental types in *Cryptonatica* from the Oga Pleistocene, protoconch morphology and morphometry of several species of *Cryptonatica* from the Japanese coast were examined and compared with fossil specimens. All the specimens utilized are housed in the University Museum, University of Tokyo (UMUT).

Furthermore, the type of *C. andoi* and other specimens which have been described as *C. andoi* were examined for comparison. They are stored in the Institute of Geoscience, University of Tsukuba (IGUT), Institute of Geology and Paleontology, Tohoku University (IGPS), and Geological Institute, Yokohama National University (GIYU).

Laboratory methods

Observations of the early shell portion of each gastropod specimen were made with optical and scanning electron microscopy (SEM) (Hitachi Model S-2400). The protoconch-teleoconch boundary can be recognized easily under the SEM by the sudden appearance of growth lines. Protoconch diameter was measured after the removal of later whorls from the protoconch region exposing the protoconch-teleoconch boundary (Figure 2). Because abrasion or dissolution has removed the protoconch surface in many specimens, whorl volutions of protoconch were counted at the point that the outer lip and suture line crossed. Likewise, because of poor preservation, it is difficult to distinguish the protoconch I (PI)-protoconch II (PII) boundary in most specimens. For this reason, the shell diameter at the first half volution (f.v.) was measured and used as a relative size of protoconch I. Measurements were made by means of a micrometer (accuracy±0.025 mm) attached to an optical microscope.

Determination of the mode of development

Developmental types in marine benthic invertebrates including gastropods fall into three main categories; pelagic (planktic) development, direct development, and ovoviviparity (Thorson, 1946, 1950). Pelagic (planktic) development is further classified into planktotrophic (larvae) feeding on phytoplankton during the veliger stage) and lecithotrophic (larvae feeding on egg yolk during a relatively short pelagic stage) (Thorson, 1950). Jablonski and Lutz (1980) summarized and modified Thorson's (1946, 1950) categories, grouping lecithotrophic, direct, and ovoviviparous development into non-planktotrophy, so that the modes of development in molluscs are classified into two major categories, planktotrophy and non-planktotrophy. Their classification is adopted in this paper.

The modes of development of Pleistocene samples of *Cryptonatica* have been examined on the basis of culture experiments of living species (Table 1) and the morphological characteristics of the protoconch with species whose early life histories have been well documented. The family Naticidae is known to include both planktotrophy and non-planktotrophy (Thorson, 1950; Giglioli, 1955; Bandel, 1975; Amio, 1955, 1963; Appendix 2).

Results

Historical changes in faunal composition

The frequency of warm-water species increases towards the top of the section, with a gradual decrease in the

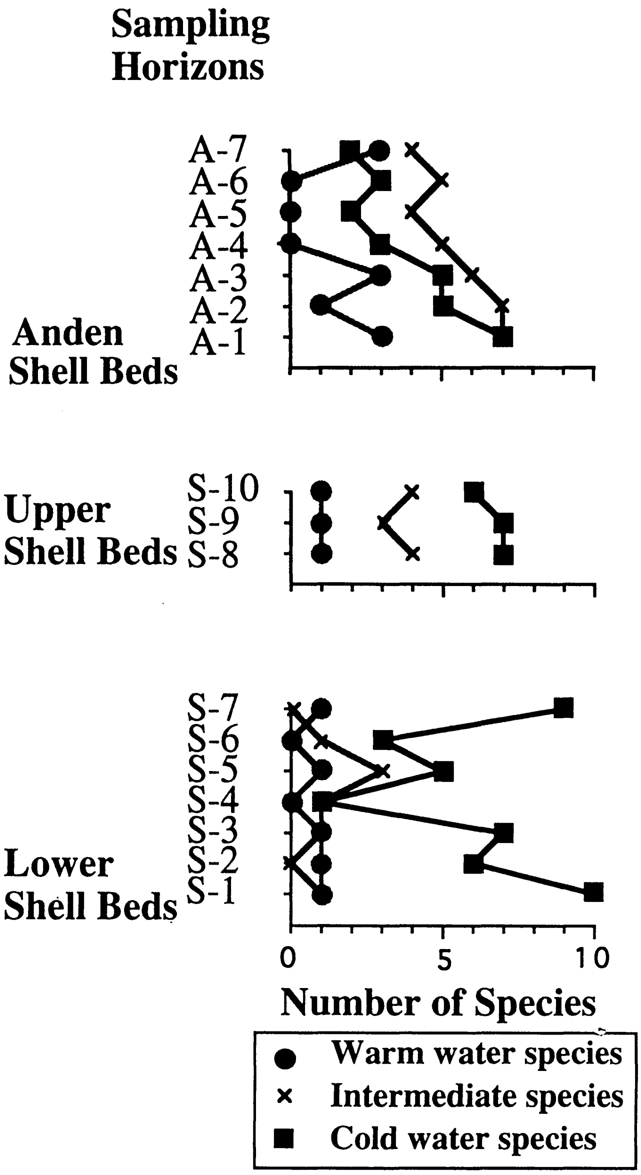


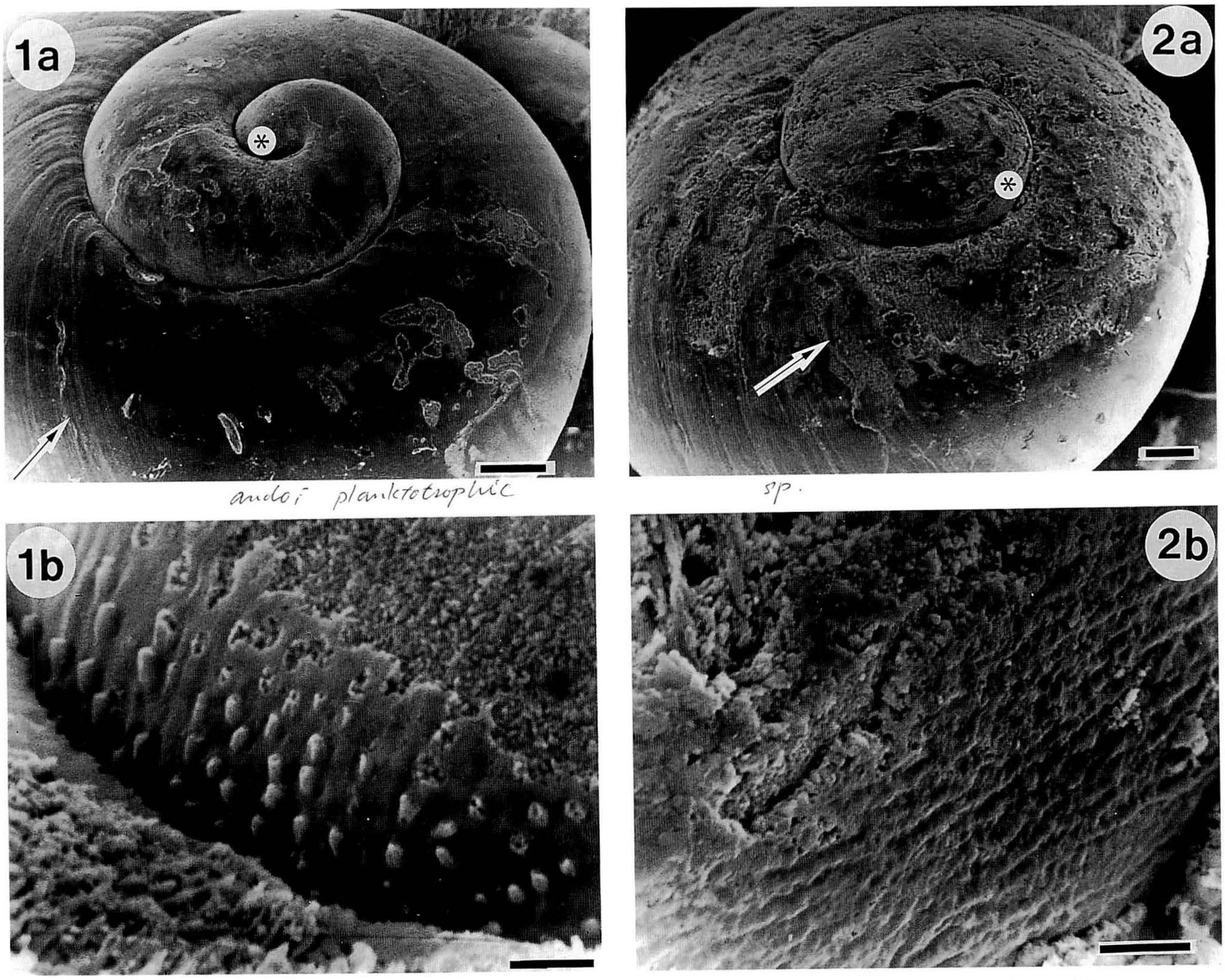
Figure 3. Historical change of gastropod faunal composition in the upper Pleistocene sequence of the Oga Peninsula.

frequency of cold-water species (Figure 3). No major change in litho- and biofacies is recognized in the marine shell beds studied, suggesting that the sediments were mostly deposited under a similar environmental setting of shallow shelf to intertidal zone. These lines of evidence correlate well with the results of molluscan faunal analysis by Takayasu (1962) and both strongly suggest a gradual increase in the influence of the warm Tsushima currents from the south during 100-134 Ka.

Protoconch morphology and variation in *Cryptonatica*

There are two protoconch morphotypes in the specimens of *Cryptonatica* from the upper Pleistocene sequence in the Oga Peninsula. One morphotype here named S-type, has a smaller protoconch (0.8 to 1.13 mm in diameter) and a larger number of volutions (2 to 2.5) (Figures 4-1a, b). The other morphotype here termed L-type, is characterized by a larger protoconch (0.95 to 1.4 mm in diameter) with a smaller number of volutions (1.5 to 2) (Figures 4-2a, b). No intermediate specimen has been found in the material examined (Figure 5). These two morphotypes cannot be distinguished by other shell features. L-type occurs abundantly in the Shibikawa Formation and the lower part of the Anden Formation (A-1), but is rare in the middle to upper part of the Anden. In contrast, S-type is rare in the Sibikawa Formation, although it occurs abundantly in the Anden Formation (Figure 6).

Specimens of L-type exhibit remarkable variations in the diameter and number of volutions of protoconch at each horizon. The protoconch diameter of specimens from the



andoi planktotrophic

sp.

Figure 4. Scanning electron micrographs of the protoconch region of *Cryptonatica*. **1.** A specimen of S-type (*C. andoi*), UMUT CM 19863-1, Loc. A-3, Anden Formation, a: overall view, b: close-up of the apical part marked by an asterisk in a. **2.** A specimen of L-type (*C.* sp. aff. *C. andoi*), UMUT CM 19864-1, Loc. S-1, Shibikawa Formation, a: overall view, b. close-up of the apical portion marked by an asterisk in a. Arrows in 1a and 2b point to the protoconch-teleoconch boundary. Scale bars: 100 μm for 1a, 2a; 10 μm for 1b, 2b.

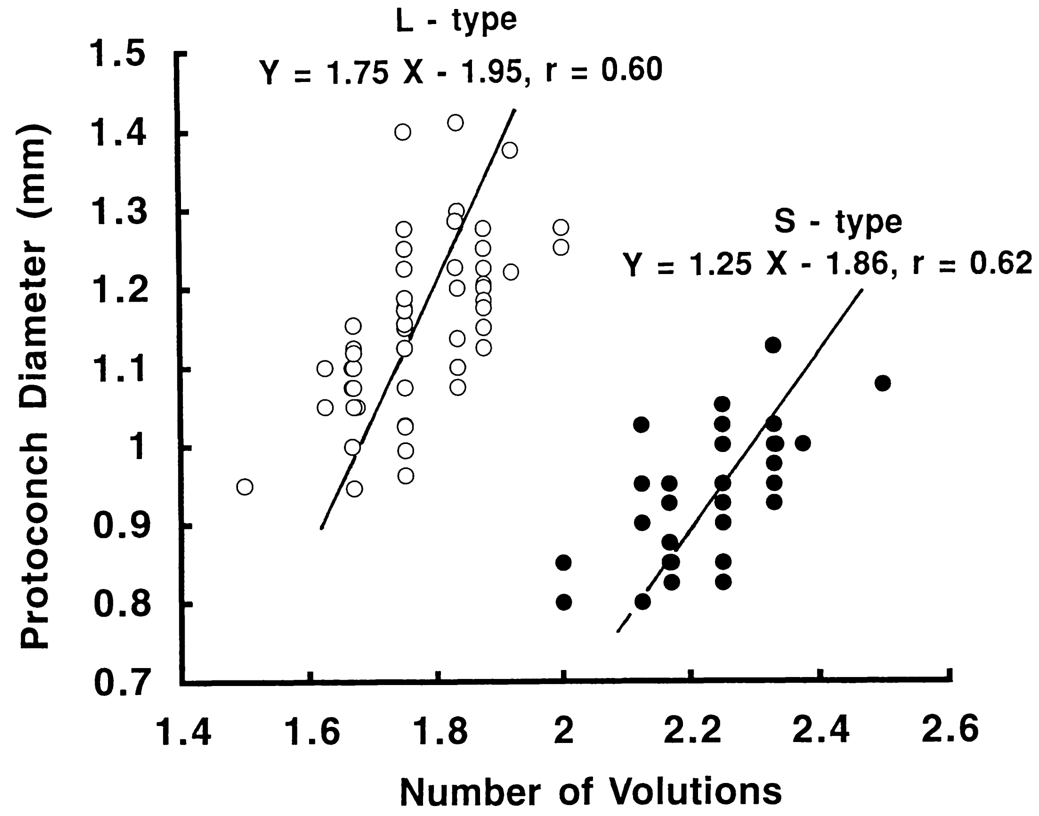


Figure 5. Scatter plots of protoconch diameter versus protoconch volutions in the late Pleistocene specimens of *Cryptonatica* from the Oga Peninsula. Black circles : S-type (*C. andoi*), white circles : L-type (*C.* sp. aff. *C. andoi*). Regression lines by least-squares fit.

upper shell beds of the Shibikawa Formation (S-8~S-10) is generally larger than that of specimens from other horizons (Figure 6). There is a positive linear relationship between the diameter and the number of volutions in the protoconch of specimens of this type from each horizon (r=0.6) (Figure 5). There is, however, little variation in the average diameter of the first volution in L-type specimens from different horizons. There is no significant variation in protoconch size or volutions in the S-type specimens.

Inferred mode of development in *Cryptonatica*

Culture experiments of snails from Hokkaido have shown that larvae of *C. andoi* are planktotrophic (Amio, 1955 ; Table 2). Amio (1955) described a distinct granulation on the protoconch surface that formed during incubation. Recent specimens of this species from off the Mikawaisshiki area, Pacific coast of Central Japan, also have this granulated ornamentation on the PI surface (Figure 7-2). Four specimens from this area have a relatively small Protoconch I (mean f.v. value=0.12 mm), a larger number of protoconch volutions (mean value=2.38) and a small protoconch diameter (mean value=1.20 mm) (Table 2).

The late Pleistocene S-type specimens of *Cryptonatica* from the Oga Peninsula are very similar to the specimens of *C. andoi* shown by Amio (1955, fig. 8) and those from off Mikawaisshiki (Figures 7-1, 2), in the size, shape, and ornament of protoconch and teleoconch, suggesting a planktotrophic mode of development in the former.

In contrast, the upper Pleistocene *Cryptonatica* specimens of L-type from the Oga Peninsula are similar in the size and shape of protoconch to those of *C. clausa*, *Polinices josephina*, and *Neverita vesicalis*, all of which have non-planktotrophic development (Bandel, 1975 ; Giglioli, 1955 ; Amio, 1955). These observations suggest that *Cryptonatica* of L-type had a non-planktotrophic development. No distinct granulated ornamentation is observed on the protoconch surface of L-type under the SEM (Figures 4-2a, b).

Distinct granulation also occurs on the protoconchs of *C. janthostoma* (Figures 7-3, 4) and *C. wakkanaiensis* (Figures 7-5, 6), whose size and volution numbers are compared with those of S-type specimens of *Cryptonatica* from the Oga Pleistocene and of extant specimens of *C. andoi*. In view of these morphological data, the former two species may have a planktotrophic development (Table 2).

Discussion

Taxonomic and ecological relationships of L- and S-types

Two protoconch types, L- and S-types, have been distinguished in specimens of *Cryptonatica* from the upper Pleistocene deposits in the Oga Peninsula. Available data on the relationships between protoconch morphology and mode

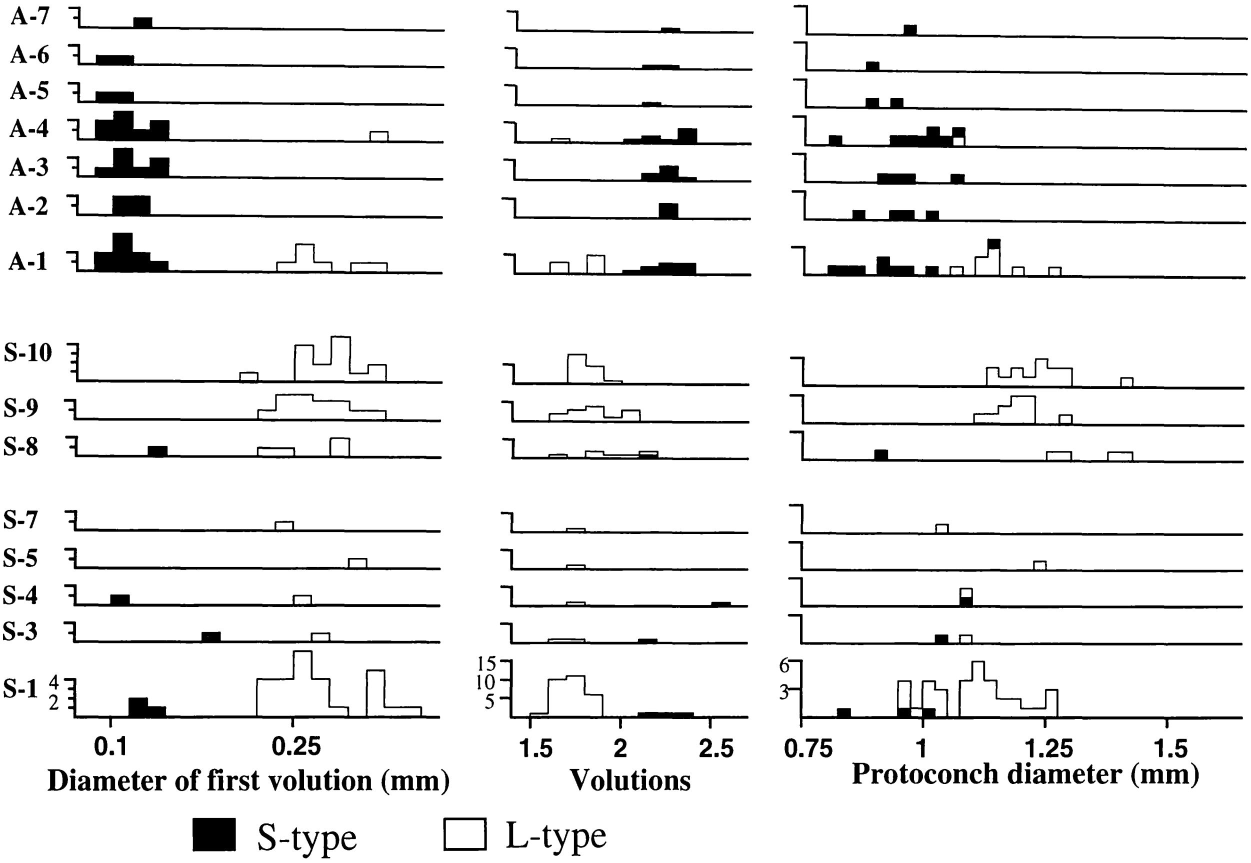


Figure 6. Variation of the number of volutions and size of protoconch in two morphotypes of *Cryptonatica* in the upper Pleistocene sequence of the Oga Peninsula. Specimens of L-type (*C.* sp. aff. *C. andoi*) have been replaced by those of S-type (*C. andoi*) toward the top of the sequence.

Table 2. Measurements of protoconch and mode of development in six species of *Cryptonatica*. All specimens excluding *C. clausa* are Recent specimens. f.v.: diameter of the first half volution. Number of specimens is shown in parentheses. Measurements are shown by sample means for those species which represented by more than two specimens. Developmental modes of *C. clausa*, *C. andoi* and *C. adamsiana* were determined by culture experiments and those of other three species were inferred from comparison of protoconch morphology with naticid species whose developmental modes are known (see Appendix 2).

Species	f.v. in mm	Number of volutions	protoconch diam. (mm)	Mode of development
C. andoi	0.12 (4)	2.38 (4)	1.20 (4)	Planktotrophy (Amio, 1955)
C. clausa	0.28 (3)	1.81 (3)	1.38 (3)	Non-planktotrophy (Thorson, 1950)
C. janthostoma	0.14 (5)	2.39 (3)	1.16 (3)	Planktotrophy (this study)
C. wakkanaiensis	0.12 (1)	2.25 (1)	0.94 (6)	Planktotrophy (this study)
C. adamsiana				Planktotrophy (Amio, 1955)
C. hirasei	0.26 (4)	2.23 (4)	1.76 (3)	Non-planktotrophy (this study)

of development in extant naticids strongly suggest that the two morphotypes probably underwent different modes of development; namely planktotrophy for S-type and non-planktotrophy for L-type. They, however, cannot be distinguished by the teleoconch morphology.

Two interpretations are possible for the taxonomic relationship of these two morphotypes. One is that they represent discontinuous variation in a single biological species with two different modes of development. This kind of discontinuous variation in which two or more modes of reproduction exist within a single species was termed poecilogony (Giard, 1905). If we accept this interpretation, the stratigraphic occurrences of L- and S-types in the Pleistocene section of the Oga Peninsula indicate that non-planktotrophic development was replaced by planktotrophic development in a single species lineage during a relatively short interval between 130-100 Ka.

The other interpretation is that L- and S-types belong to two different species. If this interpretation is correct, the similarity of teleoconch morphology between the two morphotypes must be explained by convergence. In this case, the two morphotypes may represent cryptic species, since they cannot be distinguished morphologically except for the difference in protoconch size and shape.

The genus *Cryptonatica* was established by Dall (1892) for naticids with a semicircular callus entirely or largely filling the umbilicus and a smooth operculum in association with a few grooves along its outer shell margin. He designated *Natica clausa* Broderip and Sowerby, 1892 as the type species. Majima (1989) recently summarized the systematics and stratigraphic distribution of *Cryptonatica* from Japan and described five species, *C. ichishiana, C. clausa, C. janthostoma, C. adamsiana,* and *C. andoi*, among which *C. andoi* is most similar in the overall shell features to the two late Pleistocene morphotypes of *Cryptonatica* from the Oga Peninsula. *C. andoi* ranges from Early Pliocene to Recent and is characterized by having a relatively shallow sulcus, commonly narrow umbilical callus, and an operculum sculptured with two marginal grooves on the exterior surface. Of the five Japanese *Cryptonatica* species, only *C. andoi* and *C. adamsiana* are known to occur in late Pleistocene age in the northwestern Pacific region, and they are easily distinguished by the differences in the development of callus and umbilicus (see Majima, 1989). *C. andoi* was established by Nomura (1935, p. 201, pl. 9, figs. 35a-36b) based on a specimen (holotype) from the Upper Pliocene of Taiwan. My observation of this specimen (IGPS 52295) reveals that it has a small protoconch, measuring 2.5 volutions and 0.15 mm in the diameter of the first half volution, which is similar to the protoconch of S-type specimens from the Oga Peninsula. The S-type specimens of late Pleistocene *Cryptonatica* from the Oga Peninsula are, therefore, identified as *C. andoi*. Living samples of this species from off Mikawaisshiki, Central Japan, and Muroran Bay, southern Hokkaido (Amio, 1955), consist of S-type only, and no extant specimens of L-type have been found in this species around the Japanese coast.

According to Majima (1989), *C. andoi* exhibits a relatively wide but continuous variation in callus development at maturity, and no discontinuous variation has hitherto been reported in teleoconchs. Of the specimens described as *C. andoi* by Majima (1988), the following four early Pleistocene specimens are similar to L-type specimens from the Oga area: GIYU 531-3 and 4, both from the Sawane Formation, and IGUT 16004-3 and IGUT 16004-3, both from the Omma Formation.

We have at present no data on the genetics or soft anatomy which would allow us to determine whether L- and S-types are dimorphs of a single species (*C. andoi*) or represent two different species, but current knowledge of early life history of extant marine invertebrates may provide some useful comparisons. Recently it has become clear that poecilogony is rare in marine invertebrates (Hoagland and Robertson, 1988; Bouchet, 1989). Many examples of "poecilogony" have been shown to be two reproductively isolated, cryptic species. Levin *et al.* (1991) demonstrated that the polychaete *Streblospio benedicti* is a rare case of true poecilogony, and that the traits associated with the two developmental modes have a clear genetic basis.

It is not easy to maintain two developmental modes in a population. Therefore, it appears that shifts in mode of reproduction usually occur rapidly and completely within populations, leading to reproductive isolation and hence speciation (Hoagland and Robertson, 1988; Bouchet, 1989). Judging from these lines of indirect evidence, it can be postulated that L- and S-types of *Cryptonatica* represent closely allied, but different species, though the ancestral-descendant relationship between them is still uncertain. L-type is assigned to an undescribed species, but in this paper, it is provisionally placed under *Cryptonatica* sp. aff. *C. andoi* until an adequate taxonomic survey of large samples is made.

Summary and conclusions

1. Faunal analysis of gastropod assemblages from the upper Pleistocene marine sequence in the Oga Peninsula, northern Japan, shows that the frequency of warm-water species increases towards the top of the sequence, with a gradual decrease in the frequency of cold-water species. This reflects a gradual increase in the influence of the warm Tsushima currents from the south during 100-134 Ka.
2. The upper Pleistocene specimens of *Cryptonatica* from the Oga area consist of two morphotypes that can only be distinguished by the difference in size and shape of the protoconch. They are comparable in teleoconch morphology to *C. andoi*. The relationship between protoconch morphology and mode of development in extant species of the Naticidae strongly suggests that the two morphotypes underwent different modes of development; *i.e.* planktotrophy for the type with a smaller protoconch (S-type) and non-planktotrophy for the type with a larger protoconch (L-type). The non-planktotrophic form was replaced by the planktotrophic form in the Oga Pleistocene during a relatively short interval between 130-100 Ka.
3. The two morphotypes of *Cryptonatica* can be interpreted as closely allied different species (cryptic species) rather than dimorphs of a single species with different develop-

Figure 7. Scanning electron micrographs of the protoconch region of the three species of *Cryptonatica*. Overall apical views (1, 3, 5) and close-up of the granulated ornament on the apical portion (2, 4, 6; pointed by short arrows). 1-2. *C. andoi*. Two specimens from off Mikawaisshiki, Central Japan. UMUTRM 19865-1, 2. 3-4. *C. janthostoma*. Two specimens from off Muroran, southern Hokkaido. UMUT RM 19868-1, 2. 5-6. *C. wakkanaiensis*. Two specimens from off Wakkanai, northern Hokkaido. UMUT RM 19869-1, 2. Arrows in 1, 3, and 5 point to the protoconch-teleoconch boundary. Scale bars: 500 μm (1, 3, 5) and 50 μm (2, 4, 6).

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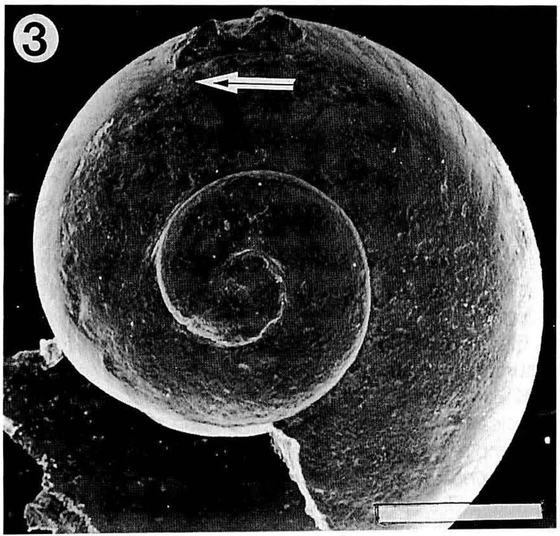

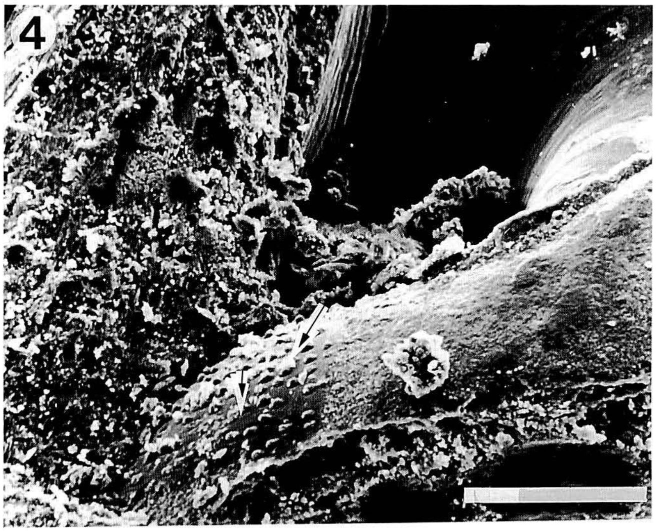

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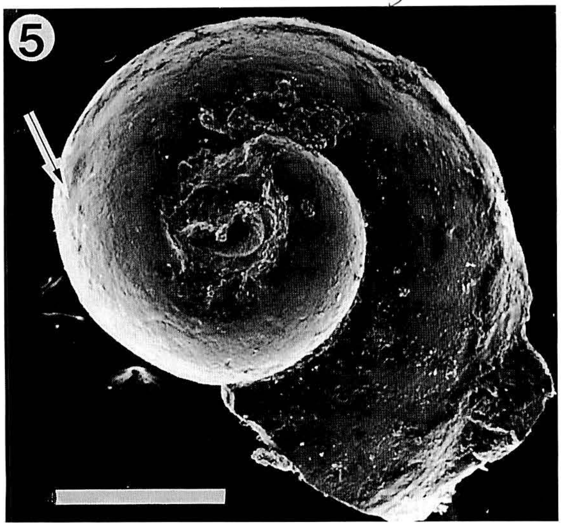

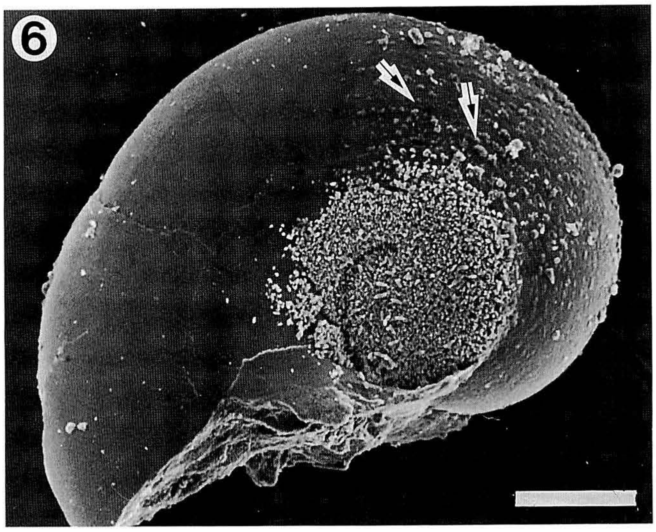

mental modes (poecilogony). Comparison with the type and figured specimens of *Cryptonatica* indicates that S-type specimens are identified as *C. andoi*, whereas those of L-type belong to a new species, here provisionally described as *C.* sp. aff. *C. andoi.*

Acknowledgments

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Appendix 1. List of gastropod species from the upper Pleistocene of the Oga Peninsula. c : cold-water species, w : warm-water species, i : intermediate species.

Family	Species	S-3	S-4	S-5	S-6	S-7	S-8	S-9	S-10	A-1	A-2	A-3	A-4	A-5	A-6	A-7		
Acmaeidae	*Notoacmea concinna* (Lischke)						2			178	4				2			i
Buccinidae	*Buccinum* sp.																	?
	Siphonalia sp.						1											?
Cerithiopsidae	*Notoseila laqueata* (Gould)								1									i
Cocculinidae	*Cocculina kuragiensis* (Yokoyama)		17	22	3	4		6	4									?
	Cocculina japonica Dall						1	10	3									c
Eulimidae	*Eulima ozawai* Yokoyama											1						w
Fissurellidae	*Emarginula fragilis* Yokoyama							2										w
	Punctrella nobilis A. Adams	5	1	13	1	1	15	19	10	18	3	2	1		1			c
Lacunidae	*Epheria decorata* (A. Adams)	1				1			6	4	4	3						c
Lamellariidae	*Velutina conica* Dall							1										?
Lepetidae	*Acmaea (Niveotectura) pallida* (Gould)	5		4		1	3	11	9	52	3	1						c
Liotiidae	*Liotina semiclathratura* (Schrenck)								1									w
Muricidae	*Boreotrophon candelabrum* (Reeve)	1								1								i
	Pteropurpura adunca (Sowerby)						1											i
	Pteropurpura adunca (Sowerby)			2														i
Nassaridae	*Reticunassa multigranosa* (Dunker)										4	2	2	1				i
Naticidae	*Cryptonatica andoi* Nomura							6	2	8	3	3	2		2	1		i
	Cryptonatica clausa (Broderip and Sowerby)					1												c
	Eunaticina papilla (Gmelin)															1		w
	Euspira pila (Pilsbry)	1			6	2	1											c
	Glossaulax didyma didyma (Roding)										1							?
Olividae	*Olivella fulgurata* (A. Adams and Reeve)						9	5	10	155	2	12	1	2	3	2		i
Pyramidellidae	*Leucotina gigantea* (Dunker)	1																w
	Odostomia sp.					1												?
	Turbonilla subplanicostata Yokoyama						1			9					1			w
	Turbonilla sp.																	?
Pyrenidae	*Mitrella bicincta* (Gould)						1	9	3	3	1	2				2		i
Retusidae	*Rhizorus cylindrella* (A. Adams)			1		1												c
	Rhizorus radiolus (A. Adams)			2														i
	Rhizorus sp.																	?
Ringiculidae	*Ringicula doliaris* Gould		1	1	1					16	1	77	39	31	13	44		i
	Ringicula sp.																	?
Scaphandridae	*Cylichna consobrina* Gould					1		1										c
Trichotropidae	*Trichamathina nobilis* (A. Adams)																	c
Triphoridae	*Triphora* sp.	1		1														?
Trochidae	*Calliostoma multiliratum* (Sowerby)										1							w
	Calliostoma sp. 1								1									?
	Calliostoma sp. 2			1														?
	Calliostoma sp. 3							1										?
	Cantharidus jessoensis (Schrenck)									1								c
	Cantharidus callichroa (Philippi)															3		w
	Cantharidus sp.								2									?
	Lirularia pygmaea (Yokoyama)							12	11									c
	Lirularia sp.	2							5									?
	Minolia punctata A. Adams									5		2				2		w
	Margarites laudatus (Yokoyama)	2	1	2	1	2												?
	Trochidae sp. 1							8										?
	Trochidae sp. 2							1										?
	Trochidae sp. 3		1											1				?
Turbinidae	*Homalopoma amussiatum* (Gould)	5		7	2	2	13	15	198	39	22	6	4	1	3	14		c
	Homalopoma sp.										2							?
Turridae	*Etremopa subauriformis* (E. A. Smith)											1	1	1				i
	Clathrodrillia sp.1						1											?
	Mangelia semicarinata (Pilsbry)						1											w
	Mangelia tabatensis Tokunaga									1		2						w
	Mangelia sp.									2					1	1		?
	Oenopota okudai Habe	1																c
	Ophiodermella miyatensis (Yokoyama)									2								i
	Ophiodermella psedopannus (Yokoyama)	4		9		1				1								w
	Ophiodermella sp.																	?
	Propebella yokoyamai (Onoyama)	1					2	5		25	7	15	10	10	2	1		c
	Propebella sp.								1									?
	Pseudoetrema fortilirata (E. A. Smith)														3	1		i
	Turritomella candida (Yokoyama)			1		2	1											c
	Turridae sp. 1									2								?
	Turridae sp. 2									2								?
	Turridae sp. 3									1								?
	Turridae sp. 4										2							?
	Turridae sp. 5		1	1														?
	Turridae sp. 6					1												?
	Turridae sp. 7	1		1														?
Turritellidae	*Neohaustator andenensis* (Otuka)									8								c
	Turritella otukai Kotaka	4		12														?
	Turritellidae, gen. et sp. indet. 1			1						3	1							?
	Turritellidae, gen. et sp. indet. 2																	?
	Number of specimens	35	22	81	14	21	53	112	267	536	61	129	60	47	31	72	1589	
	Number of cold-water species	7	1	5	3	9	7	7	6	7	5	5	3	2	3	2		
	Number of intermediate species	1	1	3	1	0	4	3	4	7	7	6	5	4	5	4		
	Number of warm-water species	1	0	1	0	1	1	1	1	3	1	3	0	0	0	3		

Appendix 2. Mode of development and measurements of protoconch in 14 species of the Naticidae. f.v.: diameter of the first half volution, Pt: planktotrophic, P: planktic either planktotrophic or lecithotrophic, D: direct development. Species with a small f.v. value (<0.21) indicate planktotrophic or at least planktic. *P. sagamiensis* is thought to have a lecithotrophic larval stage in view of its relatively short planktic period.

Species	Author	Hatching shell size (mm)	Diameter of f.v. (mm)	Development type	Pelagic period
Polinices hepaticus	Bandel, 1975	0.28	0.10	Pt	Unknown
P. lactes	Bandel, 1975	0.40	0.10	Pt	Unknown
P. triseriata	Giglioli, 1955	0.52	0.16	P	Unknown
P. sagamiensis	Amio, 1963	0.46-0.64	0.21	P	2 weeks
P. josephina	Giglioli, 1955	0.78	0.20	D	—
P. heros	Giglioli, 1955	0.13-0.15	0.093	P	Unknown
P. duplicata	Giglioli, 1955	0.18	0.10	P	Unknown
Natica pallida	Thorson, 1950	1.7	0.31	D	—
N. canrena	Bandel, 1975	0.56	0.17	Pt	Unknown
N. maculosa	Amio, 1955	0.26-0.28	0.11	P	3-4 weeks
Neverita vesicalis	Amio, 1955	1.0	0.31	D	—
N. rainiata	Amio, 1955	0.32	0.13	P	3 weeks
N. didyma	Amio, 1955	0.45	0.17	P	3 weeks
Sinum papilla	Amio, 1955	0.16-0.22	0.09	P	3-4 weeks

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1010 The first reliable record of *Beremendia* (Insectivora, Mammalia) in East Asia and a revision of *Peisorex* Kowalski and Li, 1963

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Abstract. Well preserved large shrew remains with pigmented teeth were recovered from early Pleistocene fissure sediments at Haimao, Dalian, northeast China. They are assigned to the genus *Beremendia* on the basis of their morphological characters. The monospecific genus *Peisorex* previously described from the early Pleistocene of north China is synonymized with *Beremendia*, because no basic morphological differences indicative of generic distinction exist between them, and its sole species, *P. pohaiensis*, therefore becomes *Beremendia*. Comparison with the holotype of this species reveals that the remains from Haimao belong to *Beremendia pohaiensis*. Moreover, it is newly recognized that "*Peisorex pliocaenicus*" recently described from the middle Pliocene of north China is conspecific with *B. pohaiensis*.

The remains from Haimao provide us with much knowledge on the morphological characters of *B. pohaiensis*, which is distinct from other known species of *Beremendia*. The occurrence of *B. pohaiensis* is the first reliable record of the genus in East Asia, because previous records of *Beremendia* from East Asia lack sufficient grounds in identification. *Beremendia* has been known mainly from the early Pliocene to middle Pleistocene of Europe. *B. pohaiensis* indicates that *Beremendia* was distributed both in Europe and East Asia from the middle Pliocene to early Pleistocene. This genus had probably migrated from Europe to East Asia by the middle Pliocene.

Key words : *Beremendia, Peisorex*, early Pleistocene, northeast China, systematics, paleobiogeography

Introduction

Beremendia, a large extinct shrew with pigmented teeth, was first established by Kormos (1934) on the basis of specimens from Villány, south Hungary. It has been recorded from a number of Pliocene to middle Pleistocene fossil localities in Europe, but is unknown in East Asia except for three questionable records from north China, which are too insufficient to prove its distribution greatly remote from Europe.

In June 1989, fossiliferous fissure sediments were found in a limestone quarry at Haimao (Figure 1). The sediments were preserved in two small pockets at different altitudes (Sun *et al.*, 1992). The excavations conducted in 1989 and 1990 revealed that the sediments of the lower pocket yielded abundant micro-mammalian remains of early Pleistocene age, including well preserved large shrew remains with pigmented teeth. The morphological characters of the remains indicate that they are assignable to the genus *Beremendia*. This occurrence is, therefore, the first reliable record of the genus in East Asia.

Previously, Kowalski and Li (1963) described a new genus and species of large shrew from early Pleistocene cave sediments at Chiachiashan about 300 km west-north-west of Haimao, based on a single mandible with pigmented molars. They designated the mandible as the holotype of a new species, *Peisorex pohaiensis*. Since that time, the holotype has been the only specimen referred to the species.

We compared the holotype with mandibles of *Beremendia* from Haimao, and found that there were no basic morphological differences between them. Thus, we consider that *Peisorex pohaiensis* is conspecific with *Beremendia* from Haimao. In this paper, we provide a revised generic diagnosis of *Beremendia* which includes *Peisorex* as a synonym, and describe the remains of *Beremendia* from Haimao in detail. On the basis of the description, we discuss the systematic position and paleobiogeographic significance of the remains, as well as the taxonomic problems of *Peisorex*.

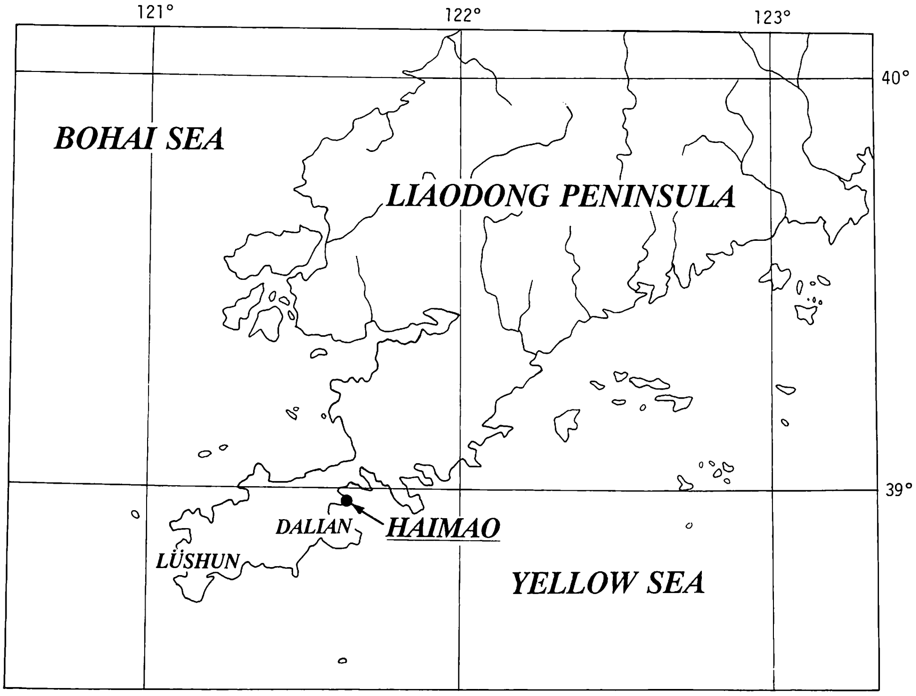

Figure 1. Location of Haimao in Dalian, northeast China.

Geological setting

The quarry is excavated on the southern slope of Beishan (meaning "north hill") at Haimao, near the coast of Dalian Bay. According to Sun *et al.* (1992), the fossiliferous sediments had originally filled a fissure, about 40 to 50 m long in an east-west direction, which formed in Precambrian limestone. Most of the fissure had been already destroyed by limestone quarrying to leave the two pockets of different altitudes before the first excavation began. Yellow clay about 1.5 m thick infilled the upper pocket, the base of which is located about 60.5 m above sea level. Mammalian remains and the ^{14}C age on fossil bone indicate that the clay is late Pleistocene in age. The lower pocket was filled with reddish brown mud of about 0.5 m in thickness. The bottom of the pocket is about 59 m above sea level. This mud yields 28 forms of micro-mammals including the specimens described herein, and is considered to be of early Pleistocene age on the basis of its faunal characteristics (Sun *et al.*, 1992; Xu and Jin, 1992).

Terminology and measuring method

The terminology and measuring method used here are given in Figure 2. The terminology mostly follows that of Reumer (1984) with slight modifications. In the figure, we also add terms generally used for the skull and those used in Kawamura (1992) for the molars (pre-ectoflexus and post-ectoflexus). The following measurements have been taken for the skull and upper tooth row (A and B in Figure 2):

LPL: length from the anterior tip of the premaxilla to the posterior margin of the lacrimal foramen
WR: maximum width of the rostrum measured at A^3
WUI: width across the first upper incisors
LI-A^3: length from the first upper incisor to A^3
LI-M^1: length from the first upper incisor to M^1

Measurement of the mandibles follows that of Reumer (1984) in order to allow comparison with his abundant data. The following parameters are adopted (D and E in Figure 2):

LMH: length from the mental foramen to the uppermost point of the lower margin of the ascending ramus
HC: height of the coronoid process
LUF: length of the upper facet

As regards the lower tooth rows, the following parameter is exclusively measured (C in Figure 2):

LP_4-M_2: length from P_4 to M_2

Measurement of the teeth except A^3 and P_4 also follows that of Reumer (1984) for the same reason. The following parameters are measured (D and F-I in Figure 2):

AW: anterior width
BL: buccal length
H: height of the first upper incisor
L: length
LL: lingual length
LT: length of the talon
PE: length to the posterior emargination
PW: posterior width
TAW: talonid width
TRW: trigonid width
W: width

Among these, BL, LL and PE of M^1 and M^2 are used for calculating the PE-index by the formula, $\{(LL+BL)/2PE\}-1$. This index was introduced by Reumer (1984) to quantify the degree of posterior emargination of these teeth, which is

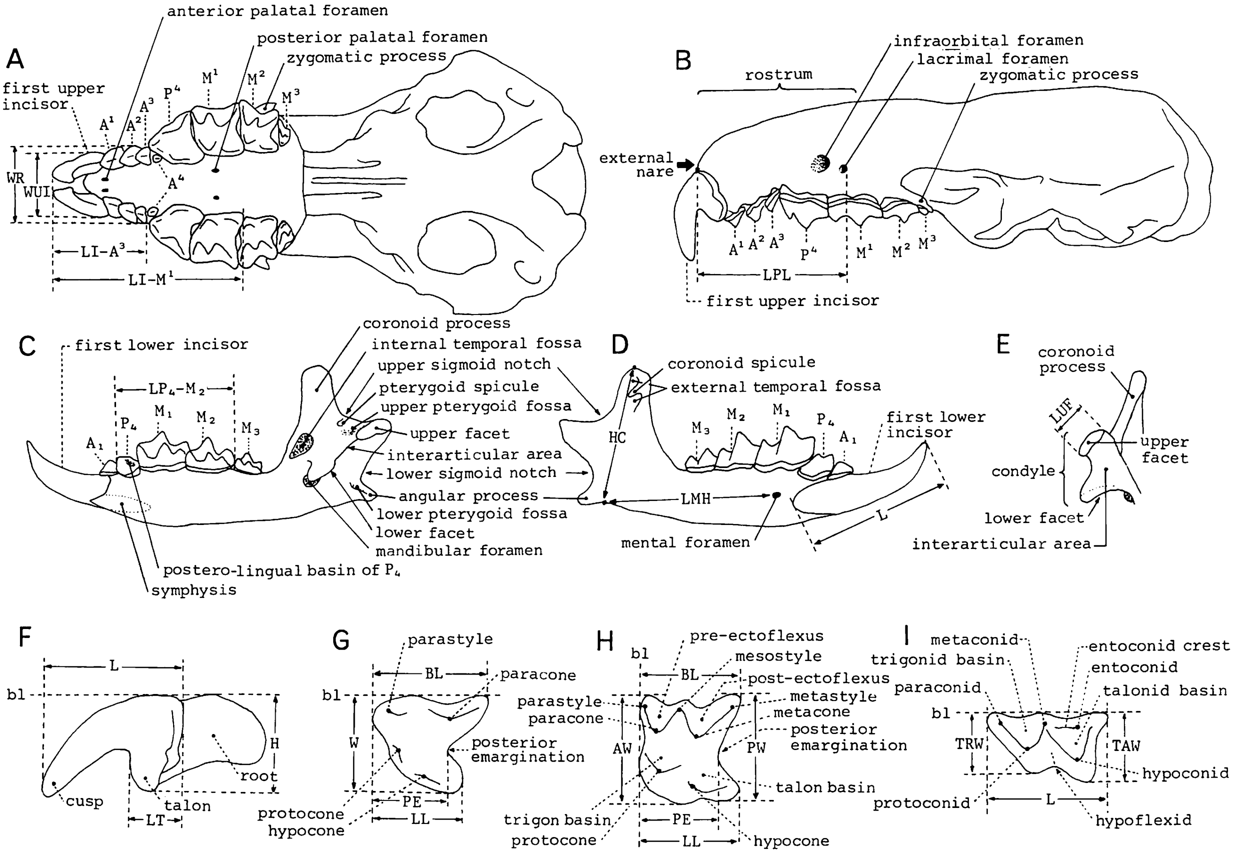

Figure 2. Terminology and measuring method (based mainly on Reumer, 1984). **A** : ventral view of the skull, **B** : lateral view of the skull, **C** : lingual view of the mandible, **D** : buccal view of the mandible, **E** : posterior view of the mandibular ascending ramus, **F** : first upper incisor (labial view), **G** : P^4 (occlusal view), **H** : M^1 (occlusal view), **I** : M_1 (occlusal view). **bl** : base line for measurement; see text for other abbreviations.

often regarded as an important character in soricid classification.

On the other hand, the length (L) and width (W) of A^3 and P_4 are measured in accordance with Kawamura (1993), where each tooth is fixed, with its main cusps being vertical.

The measurements of the Haimao specimens were taken with a measurescope (Nikon : MM-11) with an electric digital counter (Nikon : CM-65), and the holotypes of *Peisorex pohaiensis* and *P. pliocaenicus* were remeasured with a microscope (Wild : TYP 308700 HEERBRUGG).

Systematic paleontology

Order Insectivora Bowdich, 1821
Family Soricidae Gray, 1821
Subfamily Soricinae Fischer von Waldheim, 1817
Tribe Beremendiini Reumer, 1984
Genus ***Beremendia*** Kormos, 1934

Type species.—*Beremendia fissidens* (Petényi, 1864), which was originally named *Crossopus fissidens*.

Diagnosis.—Repenning (1967) and Reumer (1984) described the diagnostic characters of the genus. Adding our observations to them, we provide the following diagnosis : Dental formula 1-4-3/1-2-3 or 1-5-3/1-2-3 ; teeth stained red to almost black ; first upper incisor markedly bifid ; upper antemolars reducing in size from A^1 to A^4, A^4 reduced or lacking, and invisible from the buccal side of the skull ; posterior emargination in P^4 and upper molars moderate ; parastyle of M^1 normal and not strongly developed ; coronoid process leaning anteriorly to varying degree ; upper pterygoid fossa markedly or slightly depressed ; upper facet narrowly elliptic to oval ; interarticular area very broad, and having lingual emargination ; lower facet placed greatly anteriorly, and thus invisible in buccal view ; internal temporal fossa deeply pocketed ; first lower incisor without cusplets on its cutting edge ; its apex markedly bent upward ; P_4 having two cusps and posterolingual basin ; entoconid crest with various degree of development present in lower molars.

Included species.—*B. fissidens* (Petényi, 1864), *B. minor* Rzebik-Kowalska, 1976, and *B. pohaiensis* (Kowalski and Li, 1963). Besides these, *B. ucrainica* (Pidopličko, 1956) was described from several Ukrainian localities, but as already pointed out by Kowalski (1958, 1960), Sulimski (1959) and Rzebik-Kowalska (1976), this species seems to be conspecific with *B. fissidens*.

Geographic and geologic distribution.—Europe (Early Pliocene to middle Pleistocene), west Siberia (early Pleistocene), and north China (middle Pliocene to early Pleistocene).

Discussion.—The holotype of *Peisorex pohaiensis* (V2671) stored in the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, has the mandibular ascending ramus and lower molars which are very similar to those of *Beremendia fissidens*, the type species of the genus, both in morphology and size. We compare the holotype with plastic casts of *B. fissidens* from Austria (Nos. 77/212 and 77/215; collection of the same institute), and the descriptions and illustrations of the same species by Heller (1930), Kormos (1934), Kowalski (1958), Sulimski (1959), Dehm (1962), Repenning (1967), Rzebik-Kowalska (1972, 1976), Meulen (1973), Fejfar and Horáček (1983), and Reumer (1984).

The holotype of *P. pohaiensis* and *B. fissidens* share the following features: coronoid process relatively short and narrow; upper pterygoid fossa clearly depressed; upper facet narrowly elliptic or oval; interarticular area very broad, and having lingual emargination; lower facet placed very anteriorly; internal temporal fossa deeply pocketed; lower molars strongly pigmented and having entoconid crests with the same degree of development.

Additionally, mandibles of *B. fissidens* have wide ranges of morphological variation in such features as the development of the coronoid spicule (absent or inconspicuous in some but marked in others), anterior lean of the coronoid process (very weak to remarkable), size of the mandibular foramen (small to very large), and morphology of the lower part of the condyle (small to large; its apical part narrow and pointed to broad and blunt). In the holotype, the coronoid spicule is inconspicuous, the anterior lean of the coronoid process is slight, the mandibular foramen is very large, and the lower part of the condyle is large and has a broad tip (see A to C in Figure 10). All of these features fall within the variation of *B. fissidens*.

On the other hand, the morphology of the mental foramen is somewhat different between the holotype and *B. fissidens*. In the holotype, the foramen is more anteriorly positioned and larger. Such a difference is, however, not so decisive as to consider that the holotype is generically distinct from *B. fissidens, because the foramen of B. fissidens* is considerably variable in position (but not so anteriorly as in the holotype), and sometimes opens in a large depression below M_1.

It can be concluded that no striking differences indicative of generic distinction are present between the holotype and *B. fissidens*. Thus, *Peisorex pohaiensis* and *B. fissidens* belong to a single genus, although some minor differences, which are specific, are found from observations on the well preserved specimens from Haimao described below. The generic name *Peisorex* (1963) is antedated by *Beremendia* (1934), and thus synonymized with the latter.

Beremendia pohaiensis
(Kowalski and Li, 1963)

Figures 3-12

Peisorex pohaiensis Kowalski and Li, 1963, p. 138, fig. 1.
Beremendia sp. Sun *et al.*, 1992, p. 34, pl. 1, fig. 4a-4d.
Beremendia dalianensis Xu and Jin, 1992, p. 1376 (*nomen nudum*).
Peisorex pliocaenicus Flynn and Wu, 1994, p. 74, fig. 1, pl. 1, fig. 3.

Emended diagnosis.—Size as large as *B. fissidens*, but markedly larger than *B. minor*, A^4 lacking, so that upper antemolars except for P^4 reduced to three in number; mandibular foramen always large and deep, and widely connected with internal temporal fossa; buccal cingula of lower molars remarkably undulated and generally narrower than those of *B. fissidens*.

Referred specimens.—A fragmentary skull with a left first upper incisor and left A^3 to M^2, and with a right first upper incisor and right A^3 (DH8950); a left maxilla with P^4, M^1 and M^2 (DH8952); a right maxilla with P^4, M^1 and M^2 (DH8953); a right maxilla with M^1 and M^2 (DH8954); two left first upper incisors (DH8958, 8959); a fragmentary right first upper incisor (DH8960); a fragment of right M^2 (DH8961); a left mandible with a first lower incisor, M_1 and M_2 (DH8955); a left mandibular fragment (DH8956); a right mandible with a first lower incisor and P_4 to M_2 (DH8951); a right mandible with M_1 to M_3 (DH8957); a fragment of right M_1 (DH8962).

Storage.—All the specimens are tentatively stored in the Dalian Natural History Museum (DH: prefix for provisional specimen numbers of this museum), but will be transferred to the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica.

Description.—

Skull: The external naris is a large opening with a trapezoidal shape in dorsal view. The posterior margin of the naris slightly protrudes to the front at its medial part, and is situated above A^2. The rostrum is relatively broad and stout. An elliptical depression with an oblique axis is observed on the lateral wall of the rostrum above A^1. The infraorbital foramen opens above the parastyle of M^1. It forms a broad depression which diverges toward the front and reaches above the parastyle of P^4. The lacrimal foramen with a round outline opens just behind the infraorbital foramen, above the anterior part of M^1. An oval depression is present between the lacrimal foramen and the alveolar margin of M^1. The zygomatic process is broad but indistinct. The anterior palatal foramina are situated between left and right A^1s, and open very closely to each other in a single shallow depression. The medial part of the bony palate is relatively flattened, and from this level, its lateral parts rise slightly to form the alveoli of the upper teeth. The alveoli of A^1 and A^2 are present between the first upper incisor and A^3, whereas no alveolus is observed between A^3 and P^4, indicating a complete absence of A^4 (Figure 3B). The posterior palatal foramen is placed medial to the middle of M^1.

First upper incisor: The cusp is distinctly bifid, namely having a supplementary cusplet on the medial face (Figure 5). The apical part of the cusp including the cusplet is stained red to almost black. The talon is not pigmented. It

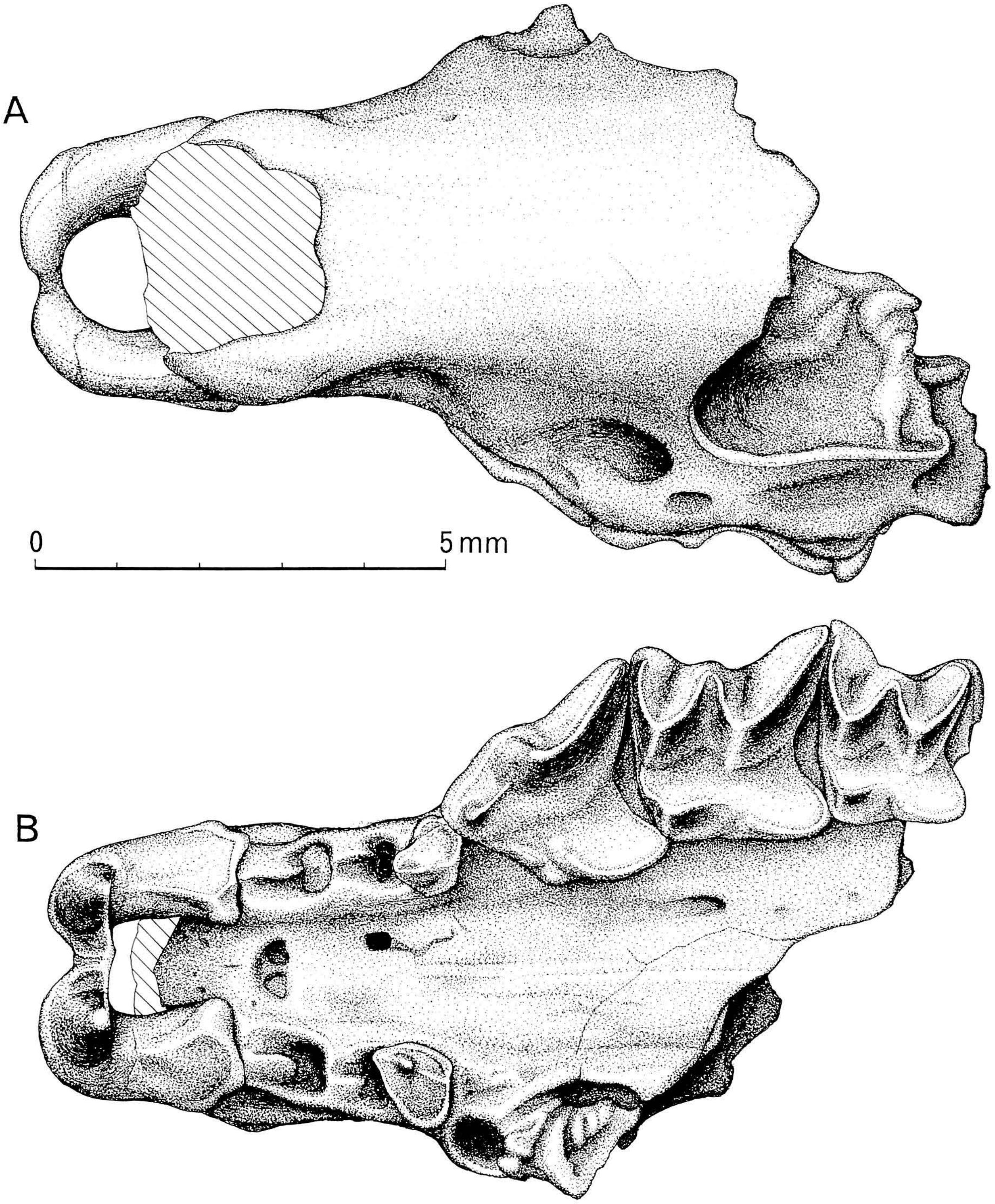

Figure 3. Fragmentary skull with incomplete upper dentition of *Beremendia pohaiensis* from Haimao (DH8950). **A**: dorsal view, B: palatal view (anterior part of left A^3 damaged).

is broad mesiodistally, and is trapezoidal to squarish in shape in lateral view, which seems to correspond to the "spade-shaped" morphotype of Rzebik-Kowalska (1976). The lateral root-crown junction line is nearly perpendicular to the base line of the tooth (bl in Figure 2F), or slightly inclines to the front. This junction line is straight (in DH8958), or slightly undulated (in DH8950; Figure 4). An indistinct cingulum is observed along the junction line. The root is robust, with a longitudinal deep groove on the lower part of the lateral face. The posterior part of the root is remarkably bent ventrally.

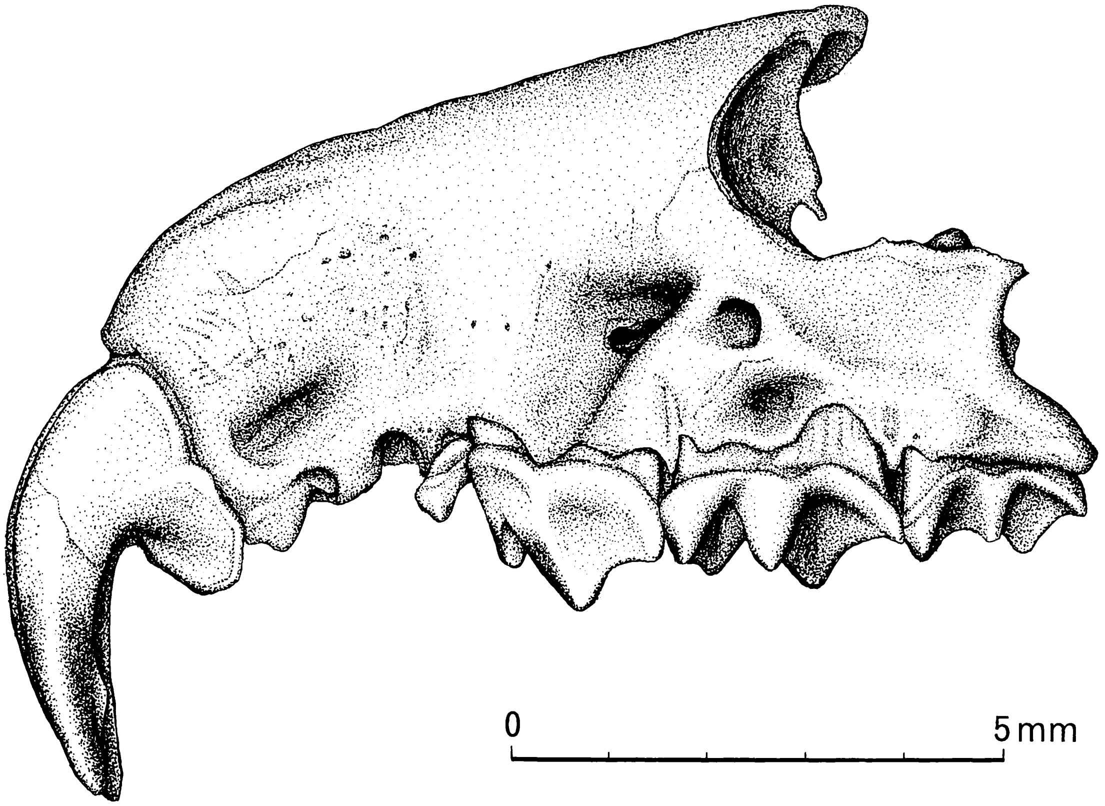

Figure 4. Fragmentary skull with incomplete dentition of *Beremendia pohaiensis* from Haimao (DH8950). Left lateral view.

A^3 : This tooth is unicuspid, with a rounded triangular outline in occlusal view. The cusp is biased anteriorly, and the red pigmentation of its apical part is much lighter than in other teeth. From the cusp, a short ridge runs to the anterior tip of the crown, and another ridge extends to the posterior margin of the crown. The posterior part of the latter ridge rises slightly, possibly representing a vestige of a cusp. These ridges form a straight line which is oblique to the median line of the skull in occlusal view. The basal part of the crown is surrounded by a cingulum, which is thickest in the posterobuccal part where the crown protrudes dorsally.

P^4 : The occlusal outline is a rounded triangle, which is broader than the "tongue-shaped" type illustrated by Rzebik-Kowalska (1976, fig. 4). The parastyle is a high conical cusp at the anterior tip of the crown, and its apical part is stained red. A weak cingulum surrounds the parastyle. A ridge with weak pigmentation (in DH8950) or without pigmentation (in DH8952 and 8953) extends from the parastyle to the anterior face of the paracone. The paracone, the highest cusp, is placed somewhat anterior to the middle of the buccal part of the crown. It is stained red to dark red. A high sharp ridge with strong red pigmentation runs from the paracone to the posterobuccal corner of the crown. The lingual part of the crown including the protocone and hypocone is very low and never pigmented. The protocone is a small indistinct cusp, which is placed on the anterolingual margin of the crown near the lingual base of the parastyle. A small supplementary cusp adjoins the posterolingual side of the protocone. An indistinct valley separates these two cusps from the hypocone which is much higher than those cusps. A low blunt ridge extends from the hypocone to the posterolingual corner of the crown, where it is slightly elevated. The posterior margin of the crown is moderately emarginated (in DH8950 and 8952) or strongly emarginated (in DH8953).

M^1 : The occlusal outline is roughly a square with rounded corners. The W-shaped ectoloph is a high sharp ridge, and is strongly stained red to dark red. The parastyle is poorly developed as in many soricid genera including *Sorex*, and much weaker than in *Amblycoptus* and *Anourosorex*. The paracone is situated very near the anterior margin of the crown. The metacone is the highest cusp of the crown. The metastyle is a ridge-like elongate cusp, which protrudes posterobuccally beyond the level of the parastyle and mesostyle, so that the post-ectoflexus is much larger than the pre-ectoflexus. No cingulum is observed on the buccal face of the crown. The lingual part of the crown except for the protocone shows no pigmentation. The protocone is a distinct cusp with red pigmentation, but it is much lower than the ectoloph. From the protocone, a low ridge extends along the anterior margin of the crown to the lingual base of the paracone, and another ridge extends posteriorly. The latter ridge becomes indistinct or extinguished at the central part of the crown. A shallow broad valley separates this

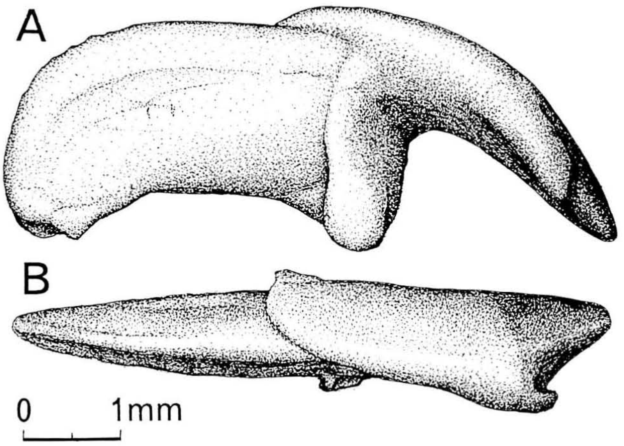

Figure 5. Left first upper incisor of *Beremendia pohaiensis* from Haimao (DH8959). **A**: medial view, **B**: dorsal view.

ridge from the hypocone which is situated at the middle of the lingual margin of the crown. The hypocone is much lower and less developed than the protocone. A low ridge runs from the hypocone to the posterolingual corner of the crown. This corner protrudes greatly posteriorly, so that the talon basin is much larger than the trigon basin. The posterior emargination is moderate (PE-index: 0.23-0.27).

M^2: The basic construction, pigmented area and the degree of pigmentation on the crown are the same as those in M^1, but the following features differ from those of M^1. The parastyle is better developed than in M^1, and protrudes buccally beyond the level of the metastyle, whereas the metastyle is much less developed than in M^1. The posterior protrusion of the posterolingual corner of the crown is weaker than in M^1, and the posterior emargination is moderate but somewhat less than in M^1 (PE-index: 0.18-0.22).

Mandible: The horizontal ramus is stoutly built relative to that of *Sorex*, and attains its maximum height at the posterior root of M_1. The mental foramen opens below the hypoflexid of M_1. The symphysis comprises a pair of ridges elongated anteroposteriorly and a broad groove between them. It terminates below the posterior root of M_1. The ascending ramus is broad anteroposteriorly, and leans markedly toward the buccal side (Figure 7). The coronoid process is narrow and short relative to those of *Sorex, Petenyia* and *Blarinella*. This process leans forward in lateral view. The tip of the process is rounded and thickened. The coronoid spicule and external temporal fossa are inconspicuous (in DH8951 and 8956) or absent (in DH8957). The upper sigmoid notch is high in position, and is not emarginated ventrally, so that its posterior part is nearly horizontal or slightly sloping backward in lateral view. The pterygoid spicule forms a small boss in DH8956 and 8957, but is inconspicuous in DH8951 (Figures 10 and 11). The upper pterygoid fossa is a relatively large depression with a circular outline on the dorsolingual face of the condyle. The upper facet is transversely narrowly elliptic. Its long axis is set obliquely to that of the mandible in dorsal view (Figure 11). The interarticular area is very broad and diverges toward the lower facet (Figures 7 and 12). Its lingual margin is emarginated, whereas its buccal margin is almost straight (Figure 12). The lower part of the condyle with the lower facet on its ventral side is shifted farther forward and strongly protrudes linguoventrally (Figures 6B, 7, 10 and 11). Its anterior margin is placed on the same straight line as the posterior margin of the internal temporal fossa in lingual view. Owing to its anterior position, the lower facet is invisible in buccal view (Figures 6A and 9). The posterior margin of the lower facet is strongly emarginated in ventral view (Figure 12). The internal temporal fossa is a very large, deep depression with a triangular outline in DH8957 (Figure 10). In DH8951 and 8956, however, it is divided into a very deep oval depression in its lower part and a relatively shallow oval depression in its upper part. The latter is continuous to a depression just below the tip of the coronoid process in DH8951 (Figure 6B). The mandibular foramen is very large and broadly elliptic. This foramen continues to the internal temporal fossa inside the bony bridge which separates them superficially. The lower sigmoid notch is not greatly emarginated, and forms a nearly straight line extending diagonally from the upper facet to the base of the angular process in lateral view. The lower pterygoid fossa is represented by a shallow horizontal groove, which runs from the mandibular foramen to the base of the angular process. It is accompanied by a ridge along its lower side. This ridge is continuous to the central ridge of the angular process. The area below these ridges is remarkably excavated.

First lower incisor: This tooth extends straight forward in dorsal view (Figure 8). The apical part with red to almost black pigmentation is strongly bent upward (Figure 6). The cutting edge is smoothed with no cusplets, which corresponds to the "acuspulate" condition of Reumer (1984, fig. 3). No cingulum is present along the posterior margin of the crown. On the lingual face of the crown, a narrow but marked groove runs from the tip to the root-crown junction. Another indistinct short groove is observed below the posterior part of the marked groove. The crown reaches below the posterior margin of P_4 on the buccal face.

P_4: The occlusal outline is roughly triangular. Two main cusps are present on the crown. The anterior one is higher, and biased lingually in occlusal view (Figure 8) The two cusps are connected by a high sharp ridge which encloses a posterolingual basin on its lingual side. This basin is shallow and drains steeply posterolingually. The cusps and ridge are stained red to dark red. A very thick cingulum is observed on the buccal base of the crown, where the crown hangs over the root. This overhang is weaker than in *Blarinoides*. Another cingulum on the lingual base of the crown is also well developed, and ascends along the posterior margin of the crown to form a small cusplet on the margin.

M_1 and M_2: The occlusal outline is trapezoidal. The ectolophid with W-shaped occlusal pattern is stained red to dark red. Of the ridges forming the ectolophid, a ridge connecting the protoconid with the paraconid is much longer than that connecting the protoconid with the metaconid. Each ridge has a notch at its middle part. The protoconid is the highest cusp of the crown, and situated anterobuccal

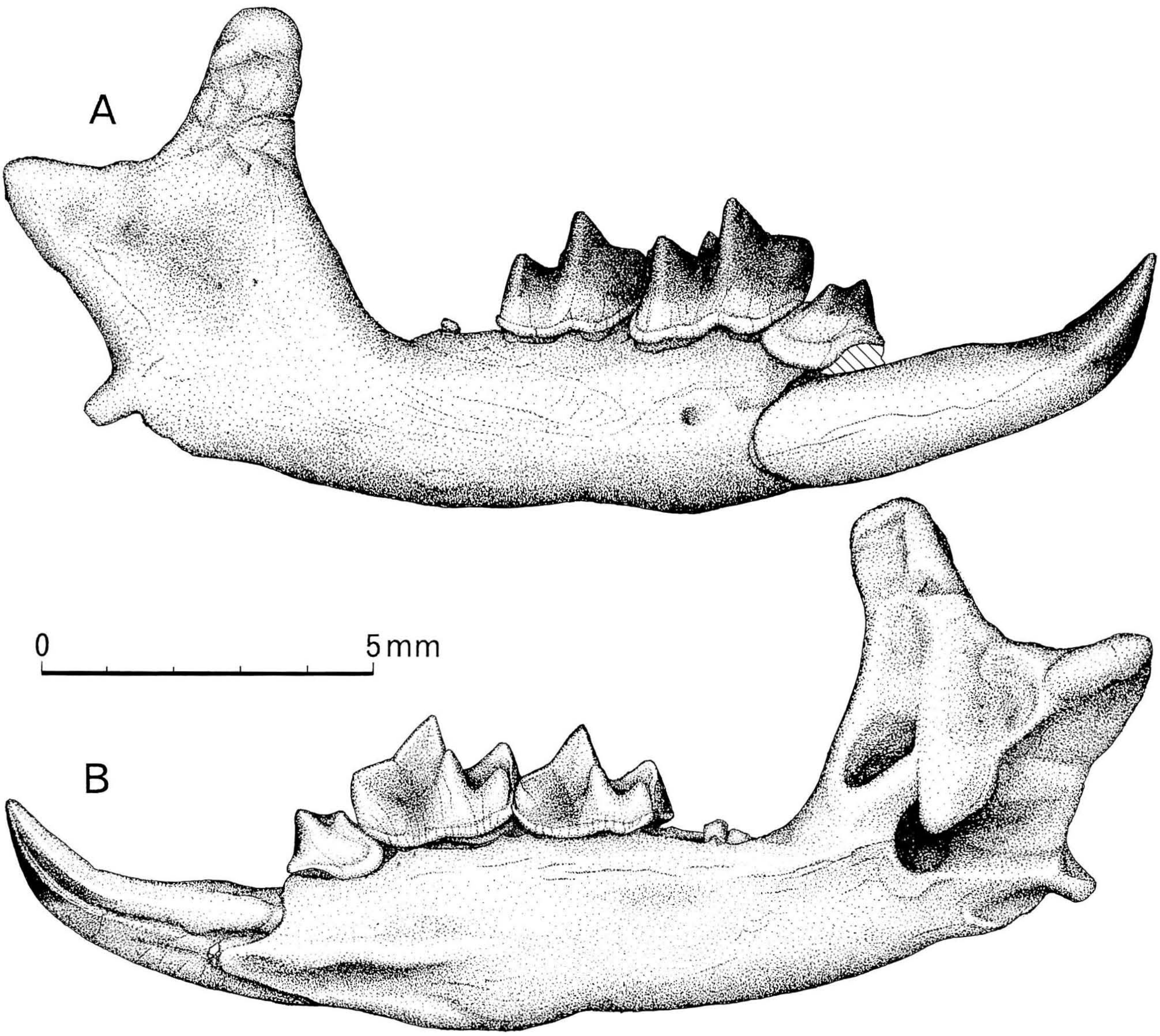

Figure 6. Right mandible with first lower incisor, P_4, M_1 and M_2 of *Beremendia pohaiensis* from Haimao (DH8951). **A** : buccal view, **B** : lingual view.

to the metaconid. The hypoflexid steeply descends buccally and reaches the buccal cingulum. A ridge extending anterolingually from the hypoconid descends toward the protoconid, and attaches to its posterior face. Another ridge extends lingually from the hypoconid, and forms an indistinct cusplet at its lingual end. This ridge is separated from the entoconid by a marked valley. Differing from the other main cusps, the entoconid is a conical isolated cusp without pigmentation. The entoconid crest connecting the anterior base of the entoconid with the posterior base of the metaconid is low and short in M_1 (Figures 6B and 8). In M_2, however, it is somewhat higher and longer. The trigonid basin is larger than the talonid basin. The cingulum surrounding the base of the crown is well developed, but much thinner than that of P_4. It is remarkably undulated on the buccal face (Figure 6A).

M_3 : The occlusal outline is roughly semicircular. The trigonid is basically similar to those of M_1 and M_2 in morphology, but is smaller. On the other hand, the talonid is strongly reduced, so that the talonid basin is much smaller and shallower than the trigonid basin. A ridge extends backward from the posterior face of the protoconid, and then curves lingually to form a small cusp at its lingual end (Figure 8A). This cusp adjoins the entoconid, which is also small and feeble. The entoconid crest is lacking, so that the talonid basin opens lingually between the entoconid and metaconid. The cingulum on the buccal base of the crown is well developed, while that on the lingual base is weaker, and interrupted below the metaconid.

Measurement.—The measurements of the skull, mandibles

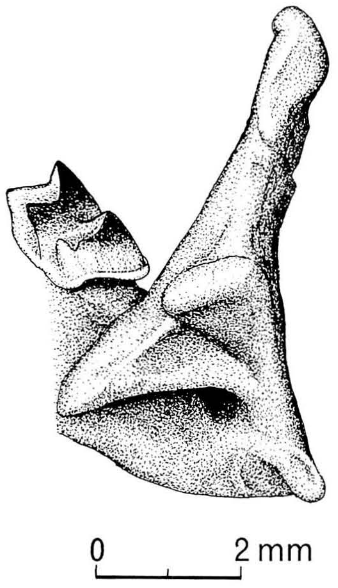

Figure 7. Posterior view of the right mandible of *Beremendia pohaiensis* from Haimao (DH8951).

Table 1. Measurements (in mm) of the skull and upper dentition of *Beremendia pohaiensis* from Haimao.

Element	Parameter	DH8950	DH8952	DH8953	DH8954	DH8958	DH8959
Skull	LPL	7.28	–	–	–	–	–
	WR	3.74	–	–	–	–	–
	WUI	3.40	–	–	–	–	–
Upper tooth row	LI-A^3	5.27	–	–	–	–	–
	LI-M^1	9.62	–	–	–	–	–
Left first upper incisor	L	2.78	–	–	–	3.42	3.53
	H	2.51	–	–	–	2.38	2.41
	LT	1.28	–	–	–	1.53	1.52
Right first upper incisor	L	2.70	–	–	–	–	–
	H	2.57	–	–	–	–	–
	LT	1.28	–	–	–	–	–
Left A^3	W	0.94	–	–	–	–	–
Right A^3	L	1.23	–	–	–	–	–
	W	0.91	–	–	–	–	–
P^4	BL	2.67	2.51	2.71	–	–	–
	LL	2.03	2.19	1.98	–	–	–
	PE	1.91	1.95	1.72	–	–	–
	W	2.42	2.48	2.41	–	–	–
M^1	BL	2.45	2.59	2.50	2.52	–	–
	LL	2.35	2.56	2.39	2.43	–	–
	PE	1.95	2.07	1.95	1.94	–	–
	AW	2.53	2.53	2.57	2.57	–	–
	PW	2.57	2.61	2.46	2.55	–	–
M^2	BL	1.81	2.01	1.82	1.93	–	–
	LL	1.80	1.81	1.83	1.80	–	–
	PE	1.51	1.57	1.53	1.58	–	–
	AW	2.49	2.46	2.41	2.42	–	–
	PW	1.93	1.90	2.01	1.89	–	–

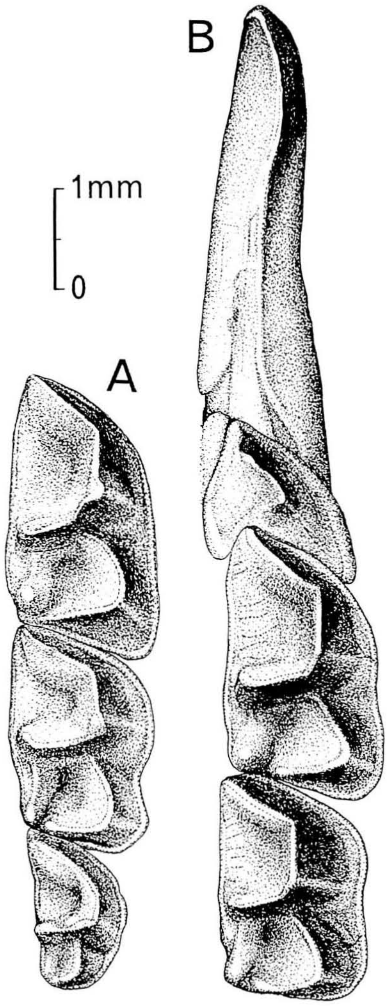

Figure 8. Right lower dentition of *Beremendia pohaiensis* from Haimao. Occlusal view. **A**: M_1-M_3 (DH8957), **B**: first lower incisor, P_4, M_1 and M_2 (DH8951).

and dentition are given in Tables 1 and 2.

Systematic position and comparison.—The specimens undoubtedly belong to the subfamily Soricinae, because the internal temporal fossa is deeply pocketed, the interarticular area of the mandibular condyle is emarginated lingually, and P_4 has a posterolingual basin. On the basis of the key given by Reumer (1984), characters such as the presence of the entoconid crest, very broad interarticular area of the condyle, strong anterior shift of the lower facet and fissident first upper incisor indicate that the specimens are referable to the tribe Beremendiini which comprises a single genus, *Beremendia*. In addition to these characters, we can observe the following characters in the present specimens, which are diagnostic of *Beremendia*: teeth pigmented; posterior emargination of P^4 and upper molars moderate; coronoid process leaning anteriorly; upper pterygoid fossa distinct; upper articular facet narrowly elliptical; first lower incisor acuspulate and with the apical part strongly bent upward. Thus, the specimens are safely allocated to *Beremendia*.

Table 2. Measurements (in mm) of the mandibles and lower dentition of *Beremendia pohaiensis* from Haimao.

Element	Parameter	DH8951	DH8956	DH8957	DH8955
Mandible	LMH	7.18	–	–	–
	HC	6.46	6.05±	5.93	–
	LUF	1.86	1.59	1.69	–
Lower tooth row	LP_4 -M_2	5.80	–	–	–
First lower incisor	L	6.69	–	–	6.19
P_4	L	1.85	–	–	–
	W	1.45	–	–	–
M_1	L	2.71	–	2.82	2.76
	TRW	1.61	–	1.46	1.50
	TAW	1.69	–	1.54	1.63
M_2	L	2.34	–	2.34	2.15
	TRW	1.42	–	1.40	1.33
	TAW	1.41	–	1.31	1.27
M_3	L	–	–	1.58	–
	TRW	–	–	0.90	–

Table 3. Remeasurements (in mm) of the holotypes of "*Peisorex pohaiensis*" (V2671) and "*P. pliocaenicus*" (V8900).

Element	Parameter	*P. pohaiensis* (V2671)	*P. pliocaenicus* (V8900)
M_1	L	2.75	2.71
	TRW	1.70	1.46
	TAW	1.81	1.57
M_2	L	2.45	2.27
	TRW	1.54	1.54
	TAW	1.30	1.33
M_3	L	1.70	1.65
	TRW	0.97	0.99

We first compare the present specimens with the holotype of "*Peisorex pohaiensis*" here called *Beremendia pohaiensis*. The holotype is very similar to the present specimens in the morphology of the ascending ramus (Figures 9-12), and there are no basic differences between them, although the mandibular bone of the holotype is somewhat larger and stouter than those of the present specimens. The lower molars of the holotype are also very similar to those of the present specimens both in morphology and size (Tables 2 and 3). The present specimens are, therefore, identifiable with *Beremendia pohaiensis*.

We secondly compare the present specimens with the holotype of "*Peisorex pliocaenicus*" (V8900 stored in the Vertebrate Paleontology and Paleoanthropology, Academia Sinica) which was recently described from the middle Pliocene in the Yushe Basin by Flynn and Wu (1994). The holotype, the only specimen of the species, is a right mandible with M_1, M_2 and M_3. The morphological characters of the holotype are well coincident with those of the present specimens, namely, the position of the mental foramen, shape of the condyle and upper pterygoid fossa, position of the lower facet, size of each mandibular and dental element (Tables 2 and 3), and other minor characters.

Such morphological congruences indicate that the present specimens are conspecific with "*P. pliocaenicus*". Moreover, we directly compared the holotype of "*P. pliocaenicus*" with that of *B. pohaiensis*, and remeasured their lower molars (Table 3). Comparison and remeasurement reveal that morphological and size differences between them are very slight, and the diagnostic characters of "*P. pliocaenicus*" mentioned by Flynn and Wu (1994) are not decisive for specific distinction, when we take the Haimao specimens into consideration. In conclusion, "*P. pliocaenicus*" is synonymous with *B. pohaiensis*.

The Haimao specimens provide us much knowledge on the morphology of the skull, upper teeth, anterior part of mandible, first lower incisor and P_4 of *B. pohaiensis* as well as the morphological variation of its mandible, all of which were hitherto unknown. On the basis of such knowledge,

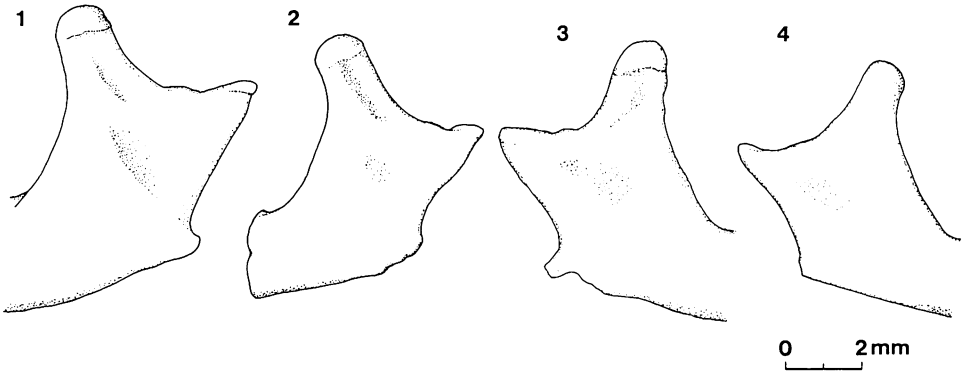

Figure 9. Simplified sketch of the mandibular ascending rami of *Beremendia pohaiensis* in buccal view, comparing the holotype of "*Peisorex pohaiensis*" (**1**) with the specimens from Haimao (**2**-**4**). **1** : V2671, **2** : DH8956, **3** : DH8951, **4** : DH8957.

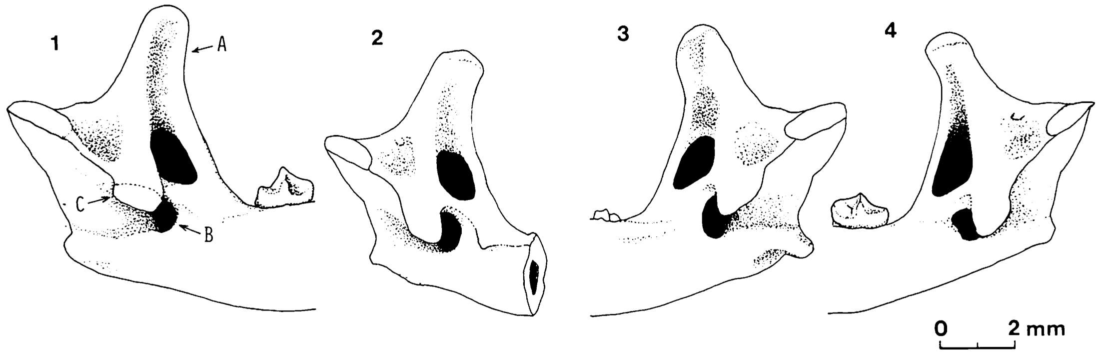

Figure 10. Simplified sketch of the mandibular ascending rami of *Beremendia pohaiensis* in lingual view, comparing the holotype of "*Peisorex pohaiensis*" (**1**) with the specimens from Haimao (**2**-**4**), and showing the characteristic parts (A-C). **1** : V2671, **2** : DH8956, **3** : DH8951, **4** : DH8957. **A** : anterior lean of the coronoid process, **B** : size of the mandibular foramen, **C** : shape of the lower part of the condyle.

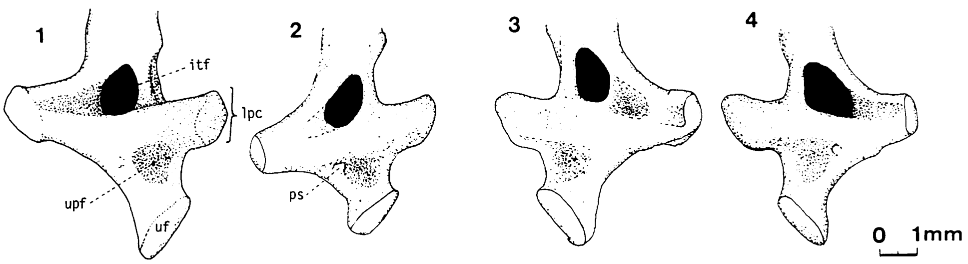

Figure 11. Simplified sketch of the mandibular ascending rami of *Beremendia pohaiensis* in dorsal view, comparing the holotype of "*Peisorex pohaiensis*" (**1**) with the specimens from Haimao (**2**-**4**). **1** : V2671, **2** : DH8956, **3** : DH8951, **4** : DH8957. **itf** : internal temporal fossa, **lpc** : lower part of the condyle, **ps** : pterygoid spicule, **uf** : upper facet, **upf** : upper pterygoid fossa.

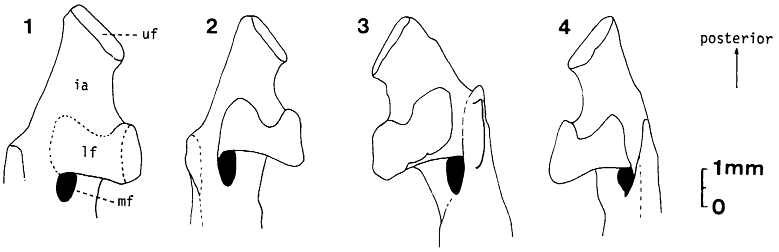

Figure 12. Simplified sketch of the mandibular condyles of *Beremendia pohaiensis* in ventral view, comparing the holotype of "*Peisorex pohaiensis*" (**1**) with the specimens from Haimao (**2**-**4**). **1** : V2671, **2** : DH8956, **3** : DH8951, **4** : DH8957. **ia** : interarticular area, **lf** : lower facet, **mf** : mandibular foramen, **uf** : upper facet.

we compare *B. pohaiensis* with the species of *Beremendia* hitherto described.

Reumer (1984) listed the four species as members of the genus : *B. fissidens*, "*B. sinensis*", *B. ucrainica* and *B. minor*. *B. ucrainica* is probably conspecific with *B. fissidens* as already mentioned, and "*B. sinensis*" cannot be included in the genus as discussed below. Thus, *B. fissidens* and *B. minor* are important for comparison to *B. pohaiensis*. *B. fissidens* is generally similar to *B. pohaiensis* in the morphology of the skull, mandible and dentition, but the following differences are also observed ; in *B. fissidens*, the external naris is more slender (Sulimski, 1959 ; fig. 4), the depression behind the first upper incisor terminates more posteriorly on the lateral wall of the rostrum (Sulimski, 1959 ; Rzebik-Kowalska, 1976), A^4 is always present, the buccal cingula of the lower molars are generally thicker and less undulated, and the mandibular foramen is more variable is size. We cannot evaluate wheather the first and second differences represent species level or individual variation, because the specimens described in the above-mentioned literature are few. On the other hand, the third difference is more decisive because in *B. pohaiensis* A^4 is completely lacking, while the literature has shown the presence of A^4 in *B. fissidens* on the basis of sufficient numbers of specimens. We consider that other differences are also specific, although they are subject to individual variation.

As regards size, *B. fissidens* shows a wide range of variation (Sulimski, 1962; Rzebik-Kowalska, 1976; Reumer, 1984). The measurements of *B. pohaiensis* are plotted well within the range of *B. fissidens*, toward the larger end of the range.

As described by Rzebik-Kowalska (1976) and Reumer

Figure 13. Geographic distribution of *Beremendia*. ● = representative fossil locality, ○ = questionable record in East Asia.

1: Sugworth (Stuart, 1980), **2**: Courterolles (Brochet *et al*., 1983), **3**: Valerots (Chaline, 1972a, b), **4**: Saint-Sauveur (Crochet and Michaux, 1981), **5**: Mas Rambault (Chaline, 1972b), **6**: Brielle (Meulen and Zagwijn, 1974), **7**: Tegelen (Reumer, 1984), **8**: Hohensülzen (Heller, 1962; Storch *et al*., 1973), **9**: Upper Terrace of the River Werra (Heinrich, 1982), **10**: Sackdillinger Höhle (Heller, 1930) and Deinsdorf (Heller, 1963), **11**: Weißenburg 7 (Koenigswald, 1971) and Schernfeld (Dehm,1962), **12**: Arondelli (Berzi *et al*., 1970), **13**: Soave (Maul, 1990), **14**: Monte Peglia (Meulen, 1973), **15**: Podumci 1 (Maul, 1990), **16**: Chlum (Fejfar and Horáček, 1983), **17**: Stránská skála (Rzebik-Kowalska, 1972), Holštejn (Musil, 1966; Fejfar and Horáček, 1983) and Mokrá (Fejfar and Horáček, 1983), **18**: Ivanovce (Fejfar, 1966) and Skalka (Maul, 1990), **19**: Koliňany (Fejfar and Horáček, 1983), **20**: Hajnáčka (Fejfar, 1964), **21**: Plešivec (Fejfar and Horáček, 1983), Gombasek (Maul, 1990) and Včeláre (Fejfar and Horáček, 1983; Horáček, 1985), **22**: Deutsch-Altenburg (Mais and Rabeder, 1977), **23**: Dunaalmás (Jánossy, 1986), **24**: Villány (Kormos, 1934; Kretzoi, 1956; Reumer, 1984; Jánossy, 1986), Beremend (Kretzoi, 1956; Jánossy, 1986), Nagyharsányhegy (Kretzoi, 1956), Csarnóta (Kretzoi, 1956, 1959; Reumer, 1984) and Somssich Hill (Jánossy, 1986), **25**: Tarkő (Jánossy, 1962, 1969, 1986), **26**: Osztramos (Jánossy and Kordos, 1977; Reumer, 1984; Jánossy, 1986), **27**: Betfia (Terzea and Jurcsák, 1968; Terzea, 1973), **28**: Chişcău (Maul, 1990), **29**: Węże, Rębielice Królewskie and Zalesiaki (Rzebik-Kowalska, 1976), **30**: Kamyk (Kowalski, 1960), **31**: Kielniki and Zamkowa Dolna (Rzebik-Kowalska, 1976), **32**: Kadzielnia (Kowalski, 1958; Rzebik-Kowalska, 1976) and Kozi Grzbiet (Rzebik-Kowalska, 1976), **33**: Żabia Cave (Bosák *et al*., 1982), **34**: Chertkov (Pidopličko, 1956) and Gorishnya Vygnanka (Maul, 1990), **35**: Uryv (Agadjanian, 1977), **36**: Razdol'e (Zazhigin, 1980), **37**: Yushe Basin (Flynn and Wu, 1994; this paper), **38**: Chiachiashan (Kowalski and Li, 1963; this paper), **39**: Haimao (this paper), **40**: Beregovaya (Erbajeva; per. comm.), **41**: Bilike (Qiu and Qiu, 1995), **42**: Nihewan (Cai, 1987), **43**: Zhoukoudian (Kretzoi, 1956)

(1984), the morphology of *B. minor* is identical with that of *B. fissidens*, but *B. minor* is decidedly smaller than *B. fissidens*. The metrical data given by these authors clearly indicate that *B. minor* is much smaller than *B. pohaiensis*.

Discussion.—Fossil localities of *Beremendia*, hitherto known, are concentrated in Europe (Figure 13). In East Asia, however, only three records are present in the literature. They are from the Middle Pleistocene at Locality 1 of Zhoukoudian (=Choukoutien), from the Late Pliocene in the Nihewan Basin and from the Early Pliocene of Bilike. The first one is represented by only one mandible described by Zdansky (1928) as a new species of *Neomys*, "*N. sinensis*". Subsequently, Kretzoi (1956) transferred this to *Beremendia*, and this opinion was followed by Sulimski (1959) and Repenning (1967). On the other hand, Kowalski and Li (1963) provided the different view that "*N. sinensis*" did not belong to *Neomys* and also differed from *Beremendia*. On the basis of the description and figures given by Zdansky (1928), the latter view is more reasonable, because "*N. sinensis*" is distinct from *Beremendia* in having the teeth unpigmented, the mental foramen more anteriorly placed, the lower part of the mandibular condyle more posteriorly placed, and in having very weak cingula on the lower molars. Thus, we believe that "*N. sinensis*" belongs to a different genus from *Beremendia*. Moreover, the occurrence of "*N. sinensis*" from Locality 1 of Zhoukoudian is questionable, as already mentioned by Young (1934) who subsequently examined abundant material from the same locality. He stated that no further trace of "*N. sinensis*" had been obtained there and "Either, the species is exceptionally rare in Choukoutien ; or some confusion has been made by Zdansky in the locality." Additionally, as regards soricid remains from Zhoukoudian, Kowalski (1958) mentioned that *Neomys bohlini* described by Young (1934) was nearer to *Beremendia* than to *Neomys*. This opinion is, however, untenable, because *N. bohlini* is much smaller and is considerably different from *Beremendia* in the shape of the mandible. This species was subsequently included in *Chodsigoa* by Repenning (1967).

The second one from the Nihewan Basin is represented by only three isolated molars which were assigned to "? *Beremendia* sp." by Cai (1987). His description does not allow one to judge whether these molars are referable to *Beremendia* or other soricid genera.

The third one is the record of *Beremendia* very recently mentioned by Qiu and Qiu (1995). Unfortunately, they gave neither specific determination nor description of the specimens allocated to *Beremendia*. Thus, we cannot judge whether their allocation is correct or not.

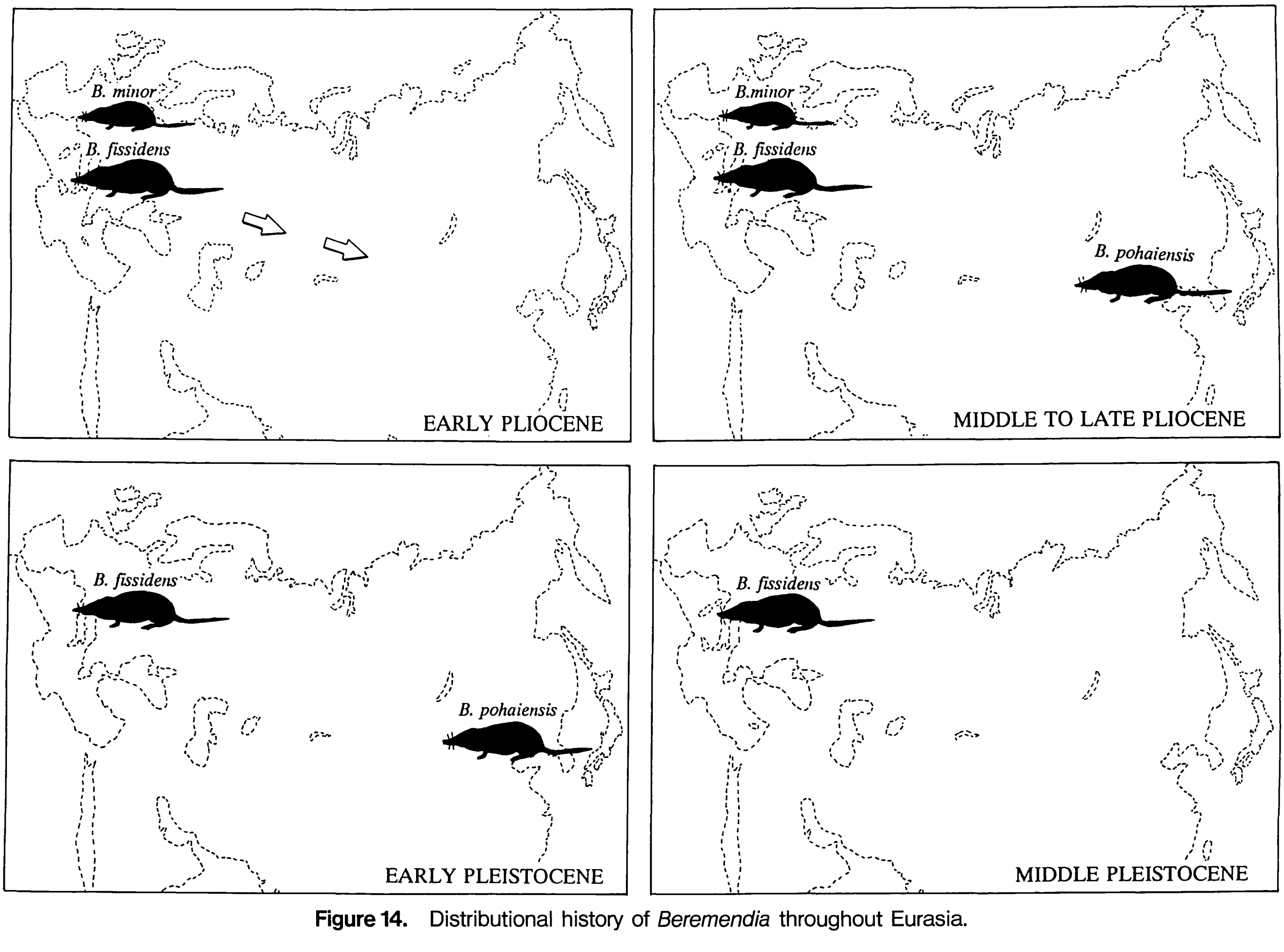

Figure 14. Distributional history of *Beremendia* throughout Eurasia.

Besides these records, the possibility of the occurrence of *Beremendia* from Transbaikalia is suggested by M.A. Erbajeva (personal communication). According to her, however, the occurrence is quite controversial. At any rate, the well preserved specimens from Haimao, as well as the two mandibles originally assigned to *Peisorex*, first demonstrate the distribution of the genus in East Asia (Figure 13).

Between Europe and East Asia, *Beremendia* was recorded from the early Pleistocene of Razdol'e, western Siberia (Zazhigin, 1980). He regarded it as a new species, but unfortunately, he gave no description of the species in the article.

Beremendia first appeared in the early Pliocene of Europe, and at that time, it was already represented by two species, *B. fissidens* and *B. minor*, which coexisted until the latest Pliocene or earliest Pleistocene (Reumer, 1984). In the early Pleistocene, *B. fissidens* became the only representative of the genus in Europe, and survived until the middle Pleistocene there. On the other hand, *B. pohaiensis* from the Yushe Basin indicates that *Beremendia* already inhabited north China at least in the middle Pliocene. This possibly resulted from its eastward migration from Europe by that time, because its remains are more abundant and diversified in the early and middle Pliocene of Europe. A scenario of its distributional history throughout Eurasia is shown in Figure 14.

Conclusions

The well preserved large shrew remains obtained from early Pleistocene fissure sediments at Haimao are allocated to the genus *Beremendia*, because they have the following diagnostic characters: the teeth are heavily pigmented; the first upper incisor is markedly bifid; the posterior margins of P^4 and upper molars are moderately emarginated; the coronoid process of the mandible leans anteriorly, and the upper pterygoid fossa is distinct; the interarticular area is very broad, and has lingual emargination; the lower facet is placed very anteriorly; the internal temporal fossa is deeply pocketed; the first lower incisor has no cusplets on its cutting edge, and its apical part is strongly bent upward; the posterolingual basin and entoconid crest are present on P_4, and on M_1 and M_2, respectively.

On the other hand, the holotype of *Peisorex pohaiensis*, the only specimen of the type species of the genus *Peisorex*, is re-examined and compared with *Beremendia fissidens*, the type species of *Beremendia*. The comparison reveals that there are no basic morphological differences indicative of generic distinction between them. *Peisorex* is, therefore, synonymous with *Beremendia*, and is preoccupied by the latter. The species name, *Peisorex pohaiensis*, should be replaced by *Beremendia pohaiensis*.

In comparison with the holotype of *B. pohaiensis*, the Haimao remains well coincide with the holotype in morphology and size. Thus, they are identified as *B. pohaiensis*. Furthermore the holotype of "*Peisorex pliocaenicus*" recently described is compared with the Haimao remains and the holotype of *B. pohaiensis*. The comparison reveals that all of them are conspecific, and "*P. pliocaenicus*" is synonymized with *B. pohaiensis*.

The Haimao remains provide us much knowledge on hitherto unknown osteological and dental features of *B. pohaiensis*. Armed with this knowledge, we can distinguish *B. pohaienis* from the known species of the genus in the lack of A^4, and in having the mandibular foramen always large and deep, and the buccal cingula of the lower molars thinner and remarkably undulated.

Fossil records of *Beremendia* were hitherto concentrated in Europe. Only three records of the genus were previously known in East Asia, but they were insufficiently described. The identification of the Haimao remains as *Beremendia*, as well as the new allocation of "*Peisorex pohaiensis*" and "*P. pliocaenicus*" to the same genus, verifies the first reliable record of *Beremendia* in East Asia.

Its occurrence in north China indicates that it was distributed in both eastern and western Eurasia from the middle Pliocene to the early Pleistocene. We can construct a scenario with *Beremendia* first appearing in the early Pliocene of Europe, and then expanding eastward to East Asia by the middle Pliocene, where it became extinct by the end of the early Pleistocene, while it survived until the middle Pleistocene in Europe (Figure 14).

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1011 Stable isotope records of the Pliocene fossil *Akebiconcha kawamurai* (Bivalvia : Vesicomyidae) from the Tamari Formation, Central Japan : Indication of chemoautotrophic symbiosis

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Abstract. **Stable oxygen and carbon isotope profiles of the Early Pliocene fossil *Akebiconcha kawamurai* from the Tamari Formation, Central Japan, are constructed to obtain environmental and physiological information using a series of samples from the shell surface for a high-resolution record. The $\delta^{18}O$ profile indicates that hydrographic conditions were stable and similar to those of modern bathyal depths. The isotopic temperature was estimated to be around 6 to 8°C with a little seasonal variation. The $\delta^{13}C$ profile shows an apparently progressive by increasing trend during shell growth, a feature which has been identified from some live mollusks containing symbiotic bacteria. Therefore, the stable isotopic geochemical profiles are regarded as potential indicators of the paleoecological habitat and symbiosis with chemoautotrophic bacteria of fossil mollusks.**

Key words : Pliocene, chemoautotrophic symbiosis, stable isotopic record, chemoautotrophic bivalve, Tamari Formation, Shizuoka, Japan

Introduction

Nobuhara and Tanaka (1993) described the molluscan assemblage dominated by *Akebiconcha kawamurai* from several shell beds intercalated in massive silt of the Early Pliocene Tamari Formation, Central Japan (Figures 1A, B). The *A. kawamurai* assemblage is commonly associated with *Solemya johnsoni, Lucinoma* aff. *acutilineata*, and *Conchocele bisecta*. The Japanese vesicomyid clam *A. kawamurai* lives at bathyal depths on the Pacific side of Central Japan (Kuroda, 1943) and is taxonomically closely related to *Calyptogena* species that have been observed in various reducing environments (Arp *et al*., 1984 ; Kennicutt II *et al*., 1985 ; Okutani and Egawa, 1985). Many living species of *Calyptogena, Lucinoma*, and *Solemya* are known to prefer reducing environments and possess endosymbiotic chemoautotrophic bacteria which provide energy to the host (Felbeck *et al*., 1981 ; Cavanaugh, 1983). On the basis of the species composition and its extraordinarily large biomass compared with the oxic-environment molluscan assemblage between the shell beds, Nobuhara and Tanaka (1993) presumed that *A. kawamurai* might be sustained by a sulphide-energy-based metabolism with chemoautotrophic symbionts.

It is generally recognized that the $\delta^{13}C$ of soft parts in live chemosymbiotic mollusks indicates the source of the carbon, since from an identical CO_2 source the carbon fixed by sulphide-oxidizing bacteria is more ^{13}C-depleted than that fixed by phytoplankton (Spiro *et al*., 1986). However, the identification of a symbiotic relationship in the fossil record is more problematic because the viscera and symbionts are not preserved, nor do the latter produce identifiable structures in the hard parts or skeleton of the host. Recent studies have reported stable isotope profiles from the shells of live chemoautotrophic symbiont-bearing mollusks (Rio *et al*., 1992 ; Oba and Hattori, 1995). Presented here are shell oxygen and carbon isotope profiles from a specimen of the bivalve mollusk *Akebiconcha kawamurai* obtained from the Early Pliocene Tamari Formation. The shell isotopic composition of this specimen by comparison with living mollusks is used to infer a symbiotic association with chemoautotrophic bacteria in a paleoecological setting.

Geologic setting and fossil collection site

The Late Miocene and Early Pliocene Tamari Formation is one of the late Neogene marine sedimentary units exposed in the Kakegawa area, Central Japan (Figure 1A). More than

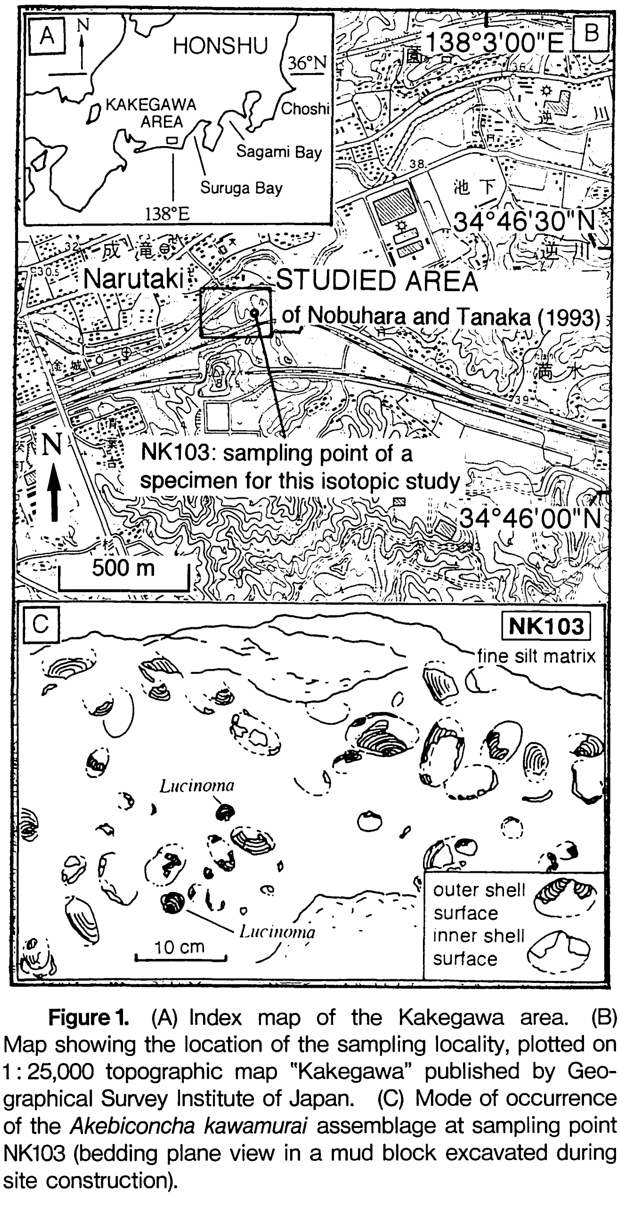

Figure 1. (A) Index map of the Kakegawa area. (B) Map showing the location of the sampling locality, plotted on 1 : 25,000 topographic map "Kakegawa" published by Geographical Survey Institute of Japan. (C) Mode of occurrence of the *Akebiconcha kawamurai* assemblage at sampling point NK103 (bedding plane view in a mud block excavated during site construction).

200 meters of massive grayish fine-grained silts were deposited in a deep-marine setting (Ishibashi, 1989). The Tamari Formation is exposed as an inlier surrounded by turbiditic alternations of sand and silt of the Pliocene Horinouchi Formation. Sedimentary facies analyses have shown that the Tamari Formation was deposited on the slope of a fore-arc basin similar to the present western part of Suruga Bay (Ishibashi, 1989 ; Tsukawaki, 1994).

The horizon from which specimens were collected by Nobuhara and Tanaka (1993) is situated by Ibaraki (1986) between Datum 11 (3.7 Ma) and Datum 18 (3.0 Ma) based on the planktonic foraminiferal biostratigraphy. Abundant large and small shells of mollusks inhabiting reducing environments are closely or sporadically spaced within the shell beds and supported by a silt matrix (Figure 1C). Most of the shells lie with their commissure planes parallel to the bedding. The mode of occurrence, however, implies that the sampling point NK103 was close to the original habitat (Nobuhara and Tanaka, 1993).

Materials and analytical method

The right valve of an articulated specimen of *Akebiconcha kawamurai* from the sampling point NK103 was used for this isotopic study. The shell is more than 49.9 mm in length (the posterior and anterior ends are lost) and 39.9 mm in height (Figure 2A). It was collected from a fresh outcrop of massive silt at a golf driving range under construction.

This study incorporates a serial shell-sampling method to provide a detailed stable isotope record encompassing the life of the mollusk : this method has previously been employed successfully to assess intra-shell isotopic variability (Arthur *et al*., 1983 ; Krantz *et al*., 1987 ; Cornu *et al*., 1993 ; Weidman *et al*., 1994). Twenty-eight carbonate powder samples were obtained from the outer shell layer along the axis of maximum growth using a dental drill with a 0.3 mm bur (Figure 2A). Careful sample drilling avoided penetrating the inner shell layer. Prior to drilling, the shell exterior was ground lightly to remove fouling organisms and any surficially attached materials. Approximately 0.5 mg of each carbonate powder sample was reacted with purified phosphoric acid at 90°C to produce carbon dioxide gas which was subsequently analyzed on a VG PRISM mass spectrometer. All isotope values are reported in δ notation relative to the PDB standard as below (Craig, 1965).

$$\delta^{18}\mathrm{O}\ (‰)=\left[\frac{(^{18}\mathrm{O}/^{16}\mathrm{O})_{\mathrm{SAMPLE}}-(^{18}\mathrm{O}/^{16}\mathrm{O})_{\mathrm{STANDARD}}}{(^{18}\mathrm{O}/^{16}\mathrm{O})_{\mathrm{STANDARD}}}\right]\times 1000$$

$$\delta^{13}\mathrm{C}\ (‰)=\left[\frac{(^{13}\mathrm{C}/^{12}\mathrm{C})_{\mathrm{SAMPLE}}-(^{13}\mathrm{C}/^{12}\mathrm{C})_{\mathrm{STANDARD}}}{(^{13}\mathrm{C}/^{12}\mathrm{C})_{\mathrm{STANDARD}}}\right]\times 1000$$

On the basis of the reproducibility of standards and replicate analyses of samples, precision is $\pm 0.1‰$ for both δ^{18}O and δ^{13}C.

Results and discussion

Stable oxygen and carbon isotope profiles of fossil shells provide important paleoenvironmental information such as annual temperature range, seasonal salinity variations, extent of primary productivity and food sources (Chinzei and Aoshima, 1976 ; Krantz, 1990 ; Cornu *et al*., 1993). However, the isotopic composition of shell carbonate may also be influenced by internal biological effects such as the metabolic activity of symbionts (Romanek *et al*., 1987).

δ^{18}O profile : The δ^{18}O profile across the shell expresses no significant variation (Figure 2B). This suggests that the shell carbonate was secreted under relatively uniform temperature conditions. The paleotemperature is calculated by using the aragonite isotope temperature equation of Horibe and Oba (unpublished) as follows.

$$T=18.5-4.72\ (\delta_s^{+}-\delta_{sw}^{+})+0.12\ (\delta_s^{+}-\delta_{sw}^{+})^2$$

The estimated temperature is around 6 to 8°C with a little seasonal temperature variation. This assumes the same isotopic composition as present seawater, because the

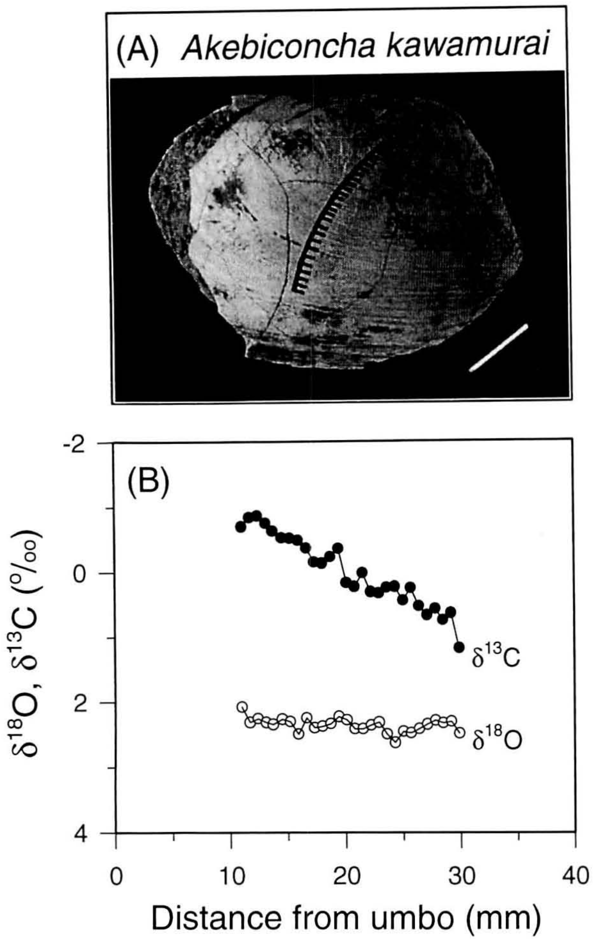

Figure 2. (A) Sampling positions of carbonate powders for isotopic analyses from the fossil *Akebiconcha kawamurai* specimen. Scale=1 cm. (B) Oxygen and carbon isotope profiles of the *A. kawamurai* specimen. The lack of distinct seasonality in the δ^{18}O profile suggests stable hydrographic conditions during growth. The δ^{13}C profile also displays no apparent seasonality, but becomes progressively more positive during growth.

mean oxygen isotopic value of benthic foraminifera at ODP site 659 between 3.0 and 3.7 Ma is nearly the same as the Holocene level (Tiedemann *et al*., 1994). This interpretation of the δ^{18}O profile implies that *A. kawamurai* lived below the depth of the thermocline. The uniform hydrographic conditions were similar at depths greater than 400 m in present-day Sagami Bay as observed by Kawabe and Yoneno (1987).

The paleoenvironment inferred from the isotope results is consistent with the interpretation from the fossil assemblages at the sampling locality NK103. Nobuhara (1992) reported that the species compositions of the fossil molluscan assemblages are similar to the fauna living at intermediate water depths (600-800 m) in Sagami Bay because both contain some cold-water species such as *Neptunea constricta* and *Solemya johnsoni*. In addition, the benthic foraminiferal assemblage obtained from the sampling point NK103 includes many species which indicate a paleodepth of about 1000 m : *Bulimina aculeata, B. striata, Sphaeroidina bulloides, Globobulimina auriculata, Oridorsalis umbonatus, Bolivinita quadrilatera*, and *Osangularia bengalensis* (Prof. Kitazato, personal communication).

δ^{13}C profile : The interpretation of carbon isotope profiles may be more problematic than for oxygen isotope profiles because of a variety of environmental and biological influences (Grossman and Ku, 1986 ; Romanek *et al*., 1987). The δ^{13}C profile of the *Akebiconcha* specimen shows a range of variation between −0.86 and +1.18‰, but displays no obvious seasonality (Figure 2B). These values fall within the range of normal seawater isotopic composition. However, δ^{13}C values become increasingly more positive through growth, which suggests that biological processes may be affecting the δ^{13}C values for this shell. If the primary carbon source of the *Akebiconcha* shell is the dissolved inorganic carbon (DIC) of ambient seawater, the lack of seasonality in the δ^{13}C profile in part reflects that $\delta^{13}C_{DIC}$ of seawater was almost uniform during growth. In contrast, δ^{13}C profiles of non-symbiotic mollusks living in shallow seas generally show an apparent seasonality related to the intensity of primary productivity in the water column (Arthur *et al*., 1983 ; Krantz *et al*., 1987). Therefore, the habitat of *Akebiconcha kawamurai* may have been somewhere beyond the seasonal influence of phytoplankton blooms in surface water, as would be also expected from the δ^{18}O profile.

Figure 3A summarizes previously published stable oxygen and carbon isotope values from several chemosynthetic bivalves. The relatively narrow range of δ^{18}O values should be largely dependent on the ambient water temperature at the time of carbonate secretion on the basis of oxygen isotopic equilibrium (Epstein *et al*., 1953). In contrast, the range of δ^{13}C values is large. Anomalously lighter carbon isotope values for fossil *Calyptogena* collected from Pliocene strata on the Miura Peninsula, Central Japan, were caused by isotopically extremely light CO_2 gas derived from respiration (Niitsuma *et al*., 1989). On the other hand, Kulm *et al*. (1986) noted that the cold-seep bivalve *Calyptogena* from off the coast of Oregon incorporates most of its carbon from the seawater bicarbonate reservoir. The δ^{13}C values of this study are similar to those observed by Kulm *et al*. (1986) and Oba and Hattori (1995). Biological effects of chemosymbionts on the isotope values are not clearly characterized as shown in Figure 3A. However, a progressive trend of increasingly more positive δ^{13}C values similar to our results has been reported from some live chemosymbiotic molluscan shells (Figure 3B). Rio *et al*. (1992) showed a gradual rise of the mean δ^{13}C from both *Bathymodiolus thermophilus* living in the hydrothermal vent of the East Pacific Rise and *Codakia orbicularis* in shallow-water reducing muds of the Great Bahama Bank. In addition, *Calyptogena soyoae* living in a cold-seep region of Sagami Bay also exhibits a progressive increase of δ^{13}C values during ontogeny (Oba and Hattori, 1995).

There has been no clear explanation for this progressive increase of δ^{13}C values during shell growth. Rio *et al*. (1992) noted that the carbon source in the extrapallial fluid of a chemosymbiotic mollusk is a mixture of seawater bicarbon-

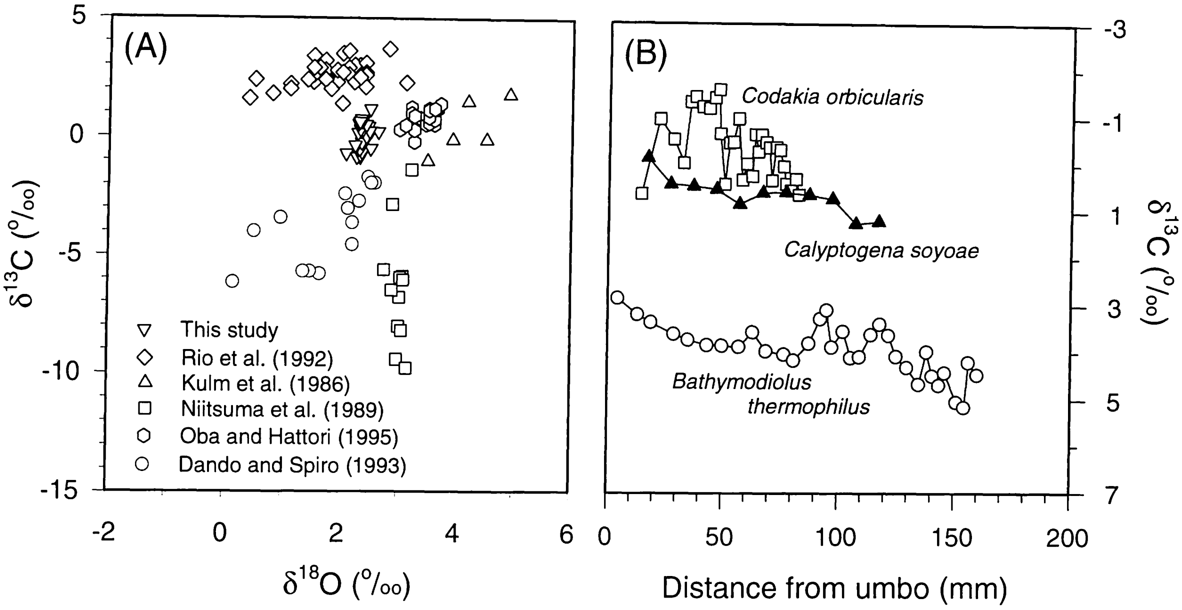

Figure 3. (A) Scatter plots of $\delta^{18}O$ vs $\delta^{13}C$ values previously reported for chemosynthetic mollusks. There is no clear characterization between $\delta^{18}O$ and $\delta^{13}C$ on the biological effects of chemosymbionts. (B) Carbon isotope profiles of chemosymbiotic shells, *Bathymodiolus thermophilus* sampled in the vicinity of a hydrothermal vent, *Codakia orbicularis* from the Great Bahama Bank (Rio *et al.*, 1992) and *Calyptogena soyoae* from Sagami Bay (Oba and Hattori, 1995). Note the progressive increase of $\delta^{13}C$ during the growth of mollusks.

ate, which can migrate through the mantle or pallial edge, and respiratory CO_2 from the chemosynthetic bacteria and the bivalve itself. The respiratory CO_2 has much lighter $\delta^{13}C$ values than ambient seawater (Tanaka *et al.*, 1986 ; Niitsuma *et al.*, 1989). Several authors have documented that an ontogenetic depletion in $\delta^{13}C$ values was due largely to changes in metabolism with age (Krantz *et al.*, 1987 ; Romanek *et al.*, 1987). If a significant part of the metabolic CO_2 is incorporated into the shell during formation, the isotopic composition of the shell carbonate would be lighter than equilibrium values. However, in this study the $\delta^{13}C$ profile of *Akebiconcha kawamurai* shows an inverse pattern with increasing $\delta^{13}C$ values through ontogeny (Figure 2B). For an explanation of this positive trend in the $\delta^{13}C$ profile, Rio *et al.* (1992) proposed the following hypothesis. The sulphide-oxidizing bacteria take up a portion of the dissolved inorganic carbon from the extrapallial liquid for their biosynthesis. A large isotopic fractionation arises in this metabolic uptake process. The chemosynthetic bacteria selectively extract light carbon (^{12}C) leading to high concentrations of ^{13}C in the extrapallial liquid, which is subsequently used in shell formation. The progressive $\delta^{13}C$ increase may be controlled by the following factors : (1) metabolic activity (extraction) of the symbiotic bacteria gradually increased during the shell growth ; and (2) shell carbonate secretion decreased in later growth stages relative to the rate of bacterial metabolic extraction.

Another interpretation is based on the measurement of different isotopic ratios from different parts of the same shell surface (Niitsuma *et al.*, 1989 ; Oba and Hattori, 1995). Oba and Hattori (1995) reported that carbon isotope values of the ventral part of a cold-seep bivalve, *Calyptogena soyoae*, differ by ca 2 ‰ from portions of the shell below and above the sediment surface. *C. soyoae* changes its life position from infaunal to semi-epifaunal during shell growth (Horikoshi and Hashimoto, 1993). Such a change of habitat could result in the isotopic change. The life position of *Akebiconcha kawamurai* has not been directly observed. More data from isotope profiles and more information on life position are necessary to confirm this hypothesis.

The stable isotope profiles constructed from *Akebiconcha kawamurai* are consistent with the paleoecology interpreted by Nobuhara and Tanaka (1993). *A. kawamurai* is inferred to have lived in a stable bathyal habitat and possessed endosymbiotic sulphide-oxidizing bacteria. However, the cause of reducing conditions in the ecosystem of the *Akebiconcha* community is unclear ; cold seeps or a hypoxic water mass caused by restricted circulation are both probable. Nobuhara and Tanaka (1993) inferred that the occurrence of a reducing environment was related to a dissolved-oxygen minimum at bathyal depths. Alternatively, Kanie *et al.* (1992) reported calcareous siltstones and lenticular-shelly limestone from the same studied area. They suggested that calcification was dominantly controlled by methane seepage. Therefore, further studies on the isotopic composition of authigenic carbonate are needed to determine the environmental settings of these reducing environments.

Conclusions

Stable oxygen and carbon isotope profiles of the Early Pliocene fossil *Akebiconcha kawamurai* from the Tamari

Formation, Central Japan, provide the following paleoenvironmental and paleoecological information.

(1) Both oxygen and carbon isotope profiles show no apparent seasonality. The estimated isotopic temperature from $\delta^{18}O$ values and small seasonal variations imply that *A. kawamurai* lived in a stable bathyal habitat below the depth of the thermocline. An analogous setting would be at intermediate water depth of the present Sagami Bay.

(2) The $\delta^{13}C$ profile exhibits a trend towards progressively more positive values during shell growth. The same characteristic has been identified from some live mollusks containing chemosymbiotic bacteria. According to Rio *et al.* (1992), this isotopic feature reflects the role of symbiotic sulphide-oxidizing bacteria which preferentially extract light carbon from the extrapallial liquid for biosynthesis.

Acknowledgments

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1012 Laboratory observations of sexual and asexual reproduction of *Trochammina hadai* Uchio

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Abstract. ***Trochammina hadai*** **Uchio is abundant in brackish water bays around the Japanese Islands and exhibits a biphasic life cycle in natural environments. In the laboratory sexual reproduction, characterized by the release of thousands of gametes, occurred in spring. The release of gametes continued for 1.5 hours. After gametogenesis, parts of the cytoplasm still remained in the mother test. Asexual reproduction took place in the laboratory during autumn and continued for 6 hours. The mother test was not destroyed during asexual reproduction. The geographical distribution of *T. hadai* in Hamana Lake differs from season to season. This may be explained by the differential dispersal of juveniles during the sexual and asexual phases, which take place at different times of the year.**

Key words : Reproduction, biphasic life cycle, microspheric and megalospheric generations, geographic distribution, *Trochammina hadai*

Introduction

Recently, agglutinated foraminifers have become one of the important groups in the study of extreme environments such as the deep sea and brackish waters (Hessler and Jumars, 1974 ; Bernstein *et al*., 1978 ; Bernstein and Meador, 1979 ; Gooday, 1986, 1988, 1990 ; Gooday and Lambshead, 1989 ; Schroeder *et al*., 1988). Foraminiferal biomass may be significant in such environments, e.g., accounting for up to 50% of the total biomass in the deep sea (Snider *et al*., 1984). Foraminifers also may act as an important factor in the deep-sea carbon budget (Gooday *et al*., 1992). The foraminiferal fauna below the calcite compensation depth (CCD) is composed entirely of agglutinated species. Thus, biological information about agglutinated foraminifers is required for understanding deep-sea biology, ecology and biogeochemical cycles.

Agglutinated foraminifers are also widely distributed in coastal regions. They are good indicators for monitoring polluted environments (Alve, 1991). In this case as well, study of the biology of agglutinated foraminifers is important for an understanding of modern ecological processes. However, investigations of the biology and ecology of agglutinated foraminifers are scarce even for shallow marine environments in comparison to calcareous foraminifera (Boltovskoy, 1966 ; Matera and Lee, 1972 ; Salami, 1976 ; Sliter, 1968 ; Angell, 1980, 1990).

Trochammina hadai Uchio is an agglutinated foraminifer that is abundant in brackish waters of Japan (Ishiwada, 1958 ; Uchio, 1962a, b ; Ikeya, 1970, 1977 ; Matoba, 1970). This species, together with *Ammonia beccarii* (Linné), accounts for the greater portion of the foraminiferal population in brackish waters.

To understand the life history of *T. hadai,* we observed almost continually the seasonal changes of populations at a fixed station in Hamana Lake, Central Japan, from 1988 through 1990. The biphasic life cycle was inferred from the seasonal occurrences of the natural populations (Matsushita and Kitazato, 1990). To examine our investigations under natural conditions we cultured *T. hadai* in the laboratory. During the course of this culture experiment, both sexual and asexual reproduction were observed. Here, we describe the reproductive processes of *T. hadai* in detail.

Method of study

Culture studies were carried out at the Fisheries Laboratory of the Faculty of Agriculture, University of Tokyo at Maisaka, which faces Hamana Lake in Shizuoka Prefecture, Japan. Sediment samples for culture were collected by SCUBA diving from a fixed station in the Shonai Inlet of Hamana Lake, where we observed almost continually the seasonal occurrences of natural populations of *T. hadai* (Matsushita and Kitazato, 1990). Sediments were transported with ambient sea water to the laboratory. Living individuals were picked from the sediments and transferred to a petri dish

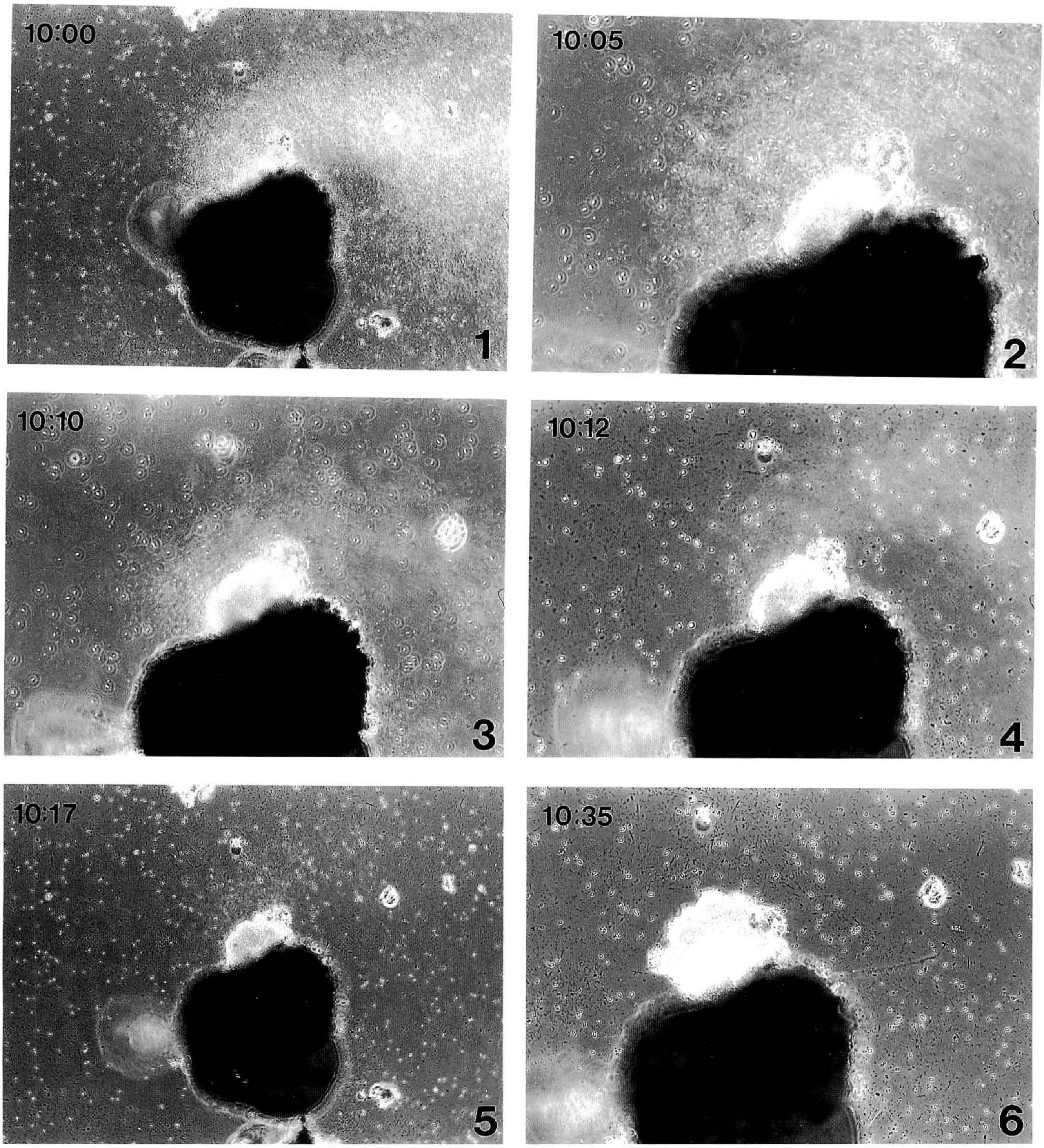

Figure 1. Successive photographs of sexual reproduction. Time of photographic exposure is given in the upper left corner of each photograph. All photographs were taken on March 20, 1990. 1. Release of gametes. ×25.4. 2. Clusters of gametes rising up from aperture. ×50.8. 3. Clusters of gametes. ×38.1. 4. Clusters of gametes. ×38.1. 5. Clusters of gametes. ×25.4. 6. Clusters of gametes. ×38.1

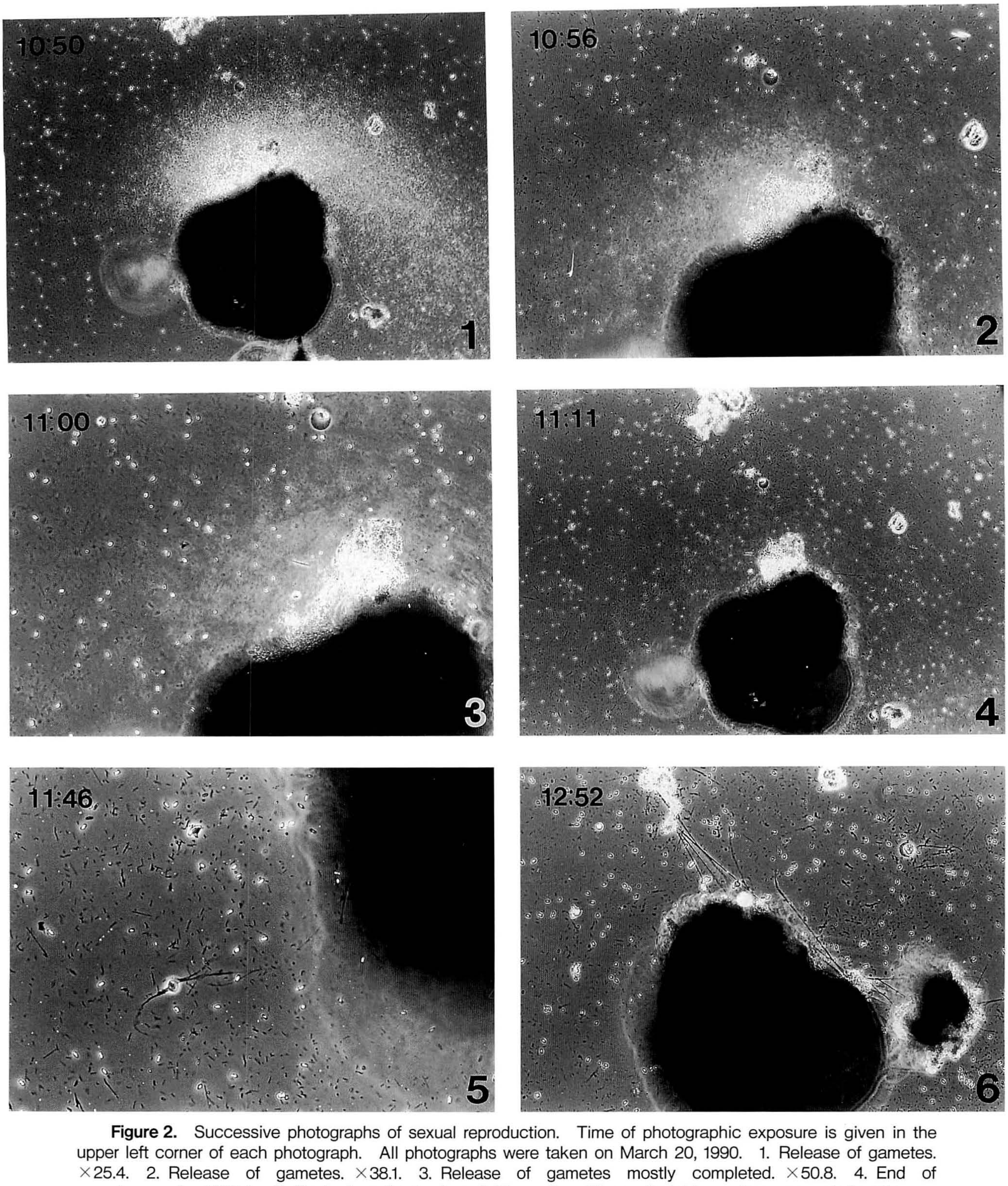

Figure 2. Successive photographs of sexual reproduction. Time of photographic exposure is given in the upper left corner of each photograph. All photographs were taken on March 20, 1990. 1. Release of gametes. ×25.4. 2. Release of gametes. ×38.1. 3. Release of gametes mostly completed. ×50.8. 4. End of gametogenesis. ×25.4. 5. Beginning of extrusion of rhizopodia. The end of rhizopodia are rounded and creep shaped. ×76.2. 6. Extrusion of many rhizopodia and movement of foraminifer. ×38.1

using a pipette. Individuals were cleaned with filtered sea water by transferring from one dish to another repeatedly. Each individual was put in a petri dish for culture. Both dried green algae of the genus *Chlorella* and living diatoms of the genus *Navicula* served as foods. Diatoms were supplied by the fisheries laboratory. Small amounts of carborundum particles were added to a petri dish instead of using natural sediments. All petri dishes were placed in a laboratory at room temperature (15-18°C) and were exposed to natural light through laboratory windows. Bottom waters (salinity: 28‰) collected at the fixed station was used for culture. Cultures for observing sexual reproduction were carried out from March 14 through 24, 1990. Cultures for asexual reproduction were performed during the period from October 26 to November 9, 1990. The periods for observations were determined from the population dynamics data of natural populations of *T. hadai*, which were continually monitored at a fixed station in the Shonai Inlet (Matsushita and Kitazato, 1990).

The reproductive processes were observed with a phase contrast apparatus attached to an inverted microscope (Nikon Diaphoto TMD and Olympus IMT-2). Both gamogony and agamogony were recorded on Kodak Plus-X film and video tapes respectively.

Reproductive process

Sexual reproduction: Sexual reproduction occurred only in spring. Seven of the 30 adult individuals reproduced sexually in March. One individual reproduced in May. Sexual reproduction took place around half moon in March, and just one day after full moon in May. No asexual reproduction occurred in culture during the spring season.

Sexual reproduction progressed as follows (Figures 1 and 2).

1) Prior to reproduction, mature individuals that exhibited dark orange cytoplasm withdrew their rhizopodia except for rhizopodia needed to anchor the test at the bottom. During sexual reproduction no reproductive cyst was constructed around the mother tests.

2) Release of gametes took place twice. At first, gametes were released from the aperture (Figures 1-1 and -2). Then, several clusters of gametes were extruded (Figures 1-5 and -6), and the second release of gametes occurred explosively 15 minutes later (Figure 2-1). The morphology of each gamete is droplet-like in outline and consists of two flagellae, based on light microscope observations. A sketch of gametes is drawn in Figure 8. However, morphologic details of the gamete have not yet been elucidated under an electron microscope.

3) Release of gametes continued for 1.5 hours. The mother test did not move during reproduction and the gametes dispersed quickly. We did not observe zygote formation.

4) After the release of gametes a part of the cytoplasm still remained within the mother test and slowly rhizopodia

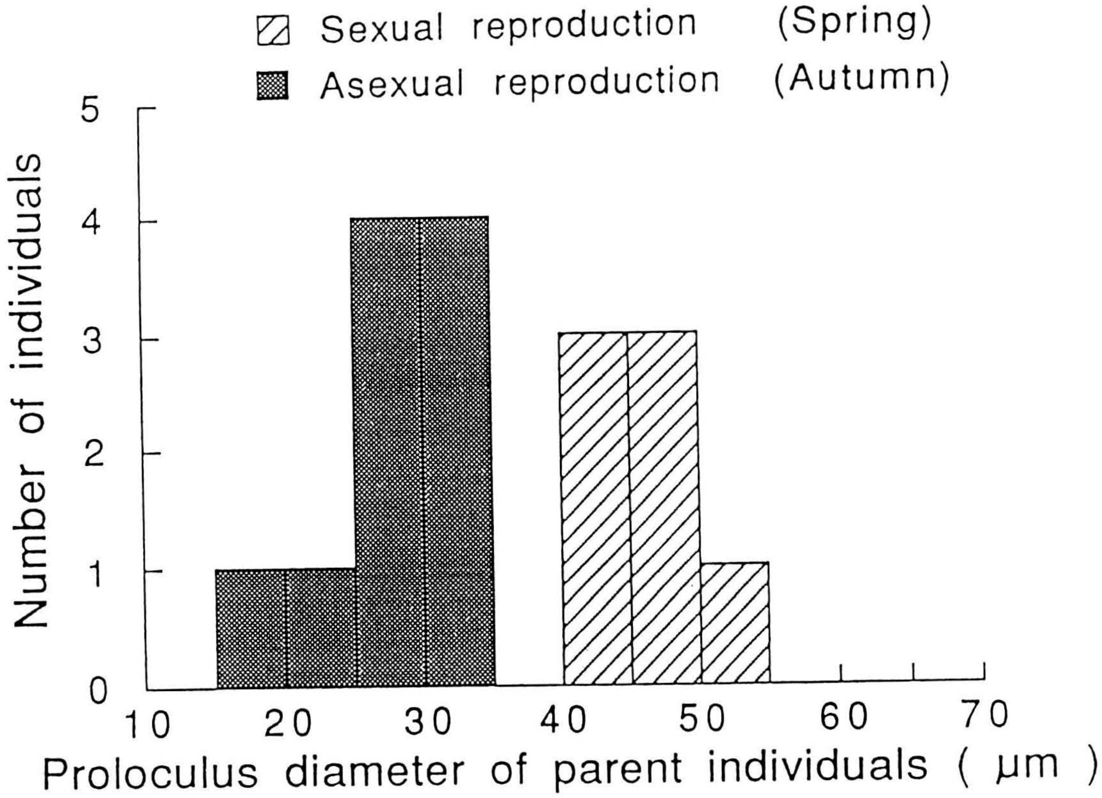

Figure 3. Proloculus diameters of mother tests that reproduced in laboratory cultures.

extruded again from the aperture, and the test moved away (Figure 2-6).

All individuals that released gametes had a large proloculus, ranging from 40 to 55 μm in diameter (Figure 3). Test diameters of mother individuals ranged from 383 to 540 μm (Table 1a).

In order to obtain zygotes we mixed gametes of two different mother individuals. However, they did not form a zygote within the culture. The gametes were very difficult to maintain under culture conditions, as they died within a day.

Asexual reproduction : Asexual reproduction took place in autumn. Eleven individuals among 30 adults reproduced asexually within our culture. Reproduction took place within three days after full moon. No sexual reproduction was observed in autumn.

The reproductive process progressed as follows.

1) Reproductive cyst formation : A reproductive cyst, formed from chlorella cells and/or diatom frustules, was constructed around the mother test, leaving vacant spaces (Figure 4). During construction of the cyst, the individuals extruded radially many rhizopodia along the bottom of the petri dishes to collect material to form the cyst. This rhizopodial pattern used during construction of the cyst is different from the usual pattern. Usually, *T. hadai* extrudes rhizopodia mainly in front of (i.e., in the direction of movement) and behind the test (Figure 5).

2) Cytoplasm invades the reproductive cyst : One or two hours after the reproductive cyst was constructed, the cytoplasm spread slowly into the cyst and the space was filled with cytoplasm.

3) Multiple division : Multiple division occurred synchronously within the cyst cavity and within the mother test (Figure 6-1). First, the velocity of cytoplasmic streaming

Table 1. Test diameters and proloculus diameters of mother tests with regard to sexual and asexual reproduction. 1a. Individuals participating in sexual reproduction. 1b. Individuals participating in asexual reproduction.

Table 1a. Individuals participating in sexual reproduction

Specimen no.	Test diameter (μm)	Proloculus diameter (μm)
1	478	41
2	420	46
3	447	46
4	383	42
5	505	48
6	435	42
7	457	?
8	540	55

Table 1b. Individuals participating in asexual reproduction

Specimen no.	Test diameter (μm)	Proloculus diameter (μm)
1	407	28
2	459	33
3	425	31
4	507	32
5	489	26
6	533	25
7	451	32
8	422	?
9	486	26
10	441	20
11	425	30

Figure 4. Reproductive cysts were constructed around a mother test during asexual reproduction. The photograph was taken on November 3, 1990. ×25.4.

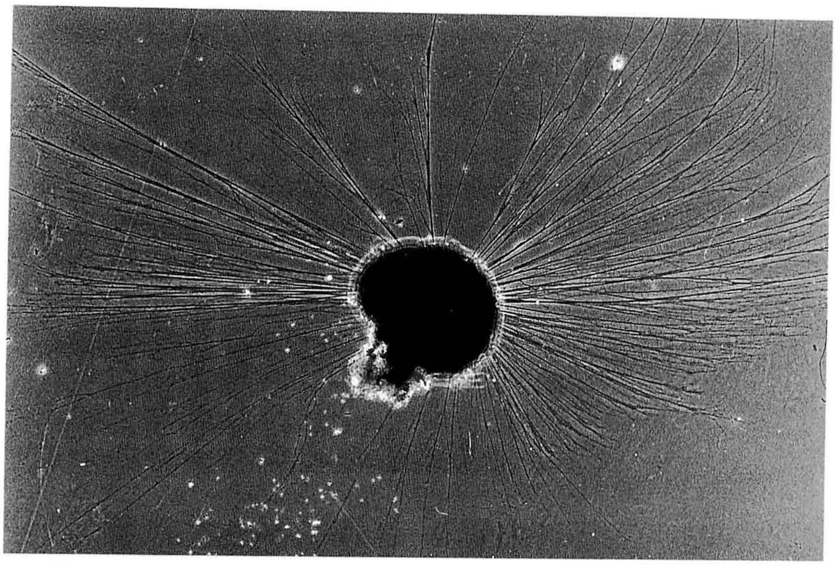

Figure 5. Usual rhizopodial extrusion of *Trochammina hadai*. Rhizopodia were extruded in two directions. The photograph was taken on October 27, 1990.

accelerated and then multiple division occurred within a few minutes. Fifty to one hundred gamont juveniles were visible both in the reproductive cyst and in the mother test 15 minutes after the division.

4) Spreading of juvenile individuals: Mostly one or two hours after multiple division, juvenile gamonts started to leave the mother test (Figure 6-2, -3 and -4). Juvenile individuals are spherical without an arenaceous wall (Figure 6-5 and -6). The diameters of juvenile gamonts ranged from 45 to 65 μm. This is the same as the proloculus diameters of megalospheric adults (Figure 3). Immediately after juveniles left the mother test, they started to collect both *Chlorella* cells and diatom frustules.

5) Formation of an agglutinated test: One or two hours after juveniles had left the mother test, most individuals started to collect carborundum grains to form an arenaceous wall. At first, the individuals gathered any particles around the cell and fixed them on the first chamber wall (proloculus wall), after which the foraminifers grabbed selectively carborundum grains that had been placed to one side. This shows that *Trochammina hadai* definitely discriminates carborundum grains from other biogenic particles. Carborundum grains were cemented first on one side of the cell and then their use gradually extended around to the other side (Figure 7). This means that the test formation of agglutinated foraminifera probably starts from one point. This observation of the initiation of chamber formation is similar to the description by Bender (1992) for *Textularia candeiana* d'Orbigny. Nearly the same chamber formation process was described by Angell (1990) for *Trochammina inflata.*

Asexual reproduction continued for approximately 6 hours. The mother test was not destroyed during asexual reproduction, as observed by Salami (1976) for *T.* cf. *T. quadriloba* Hoeglund. However, the mother test was weakened and fragile after reproduction.

The proloculus diameters of mother tests that released gamonts were smaller than those of the gamonts. They ranged from 20 to 33 μm (Figure 3). Test diameters of the mother tests ranged from 407 to 533 μm (Table 1b).

Discussion

Both sexual and asexual reproduction took place during specific seasons (Figure 8). Sexual reproduction occurred only in spring and asexual reproduction during autumn. No exceptions have been observed. The observations support well our previous observations that the life cycle of *T. hadai* is biphasic and annual (Matsushita and Kitazato, 1990).

What fundamental factors control seasonal timing of reproduction? Dissolved oxygen and temperature of Hamana Lake bottom waters are roughly the same in spring and autumn during the two types of reproduction, suggesting there may be some connection between these variables and physiological cues or limits to reproduction. Water temperature at Hamana Lake fluctuates seasonally between about 6 and 27°C, but the spring and autumn periods of reproduction both fall within the limited temperature range of 13-18°C (Figure 9). The dissolved oxygen content of the bottom water both in spring and autumn is about 5-8 ml/l, restricted compared with the annual range of <2 to >10 ml/l. Thus, reproduction may take place under conditions of approximately 15°C and 6 ml/l in dissolved oxygen. We could not find a direct relationship between water salinity and reproductive season, as seasonal salinity changes can fluctuate from year to year, largely due to variable precipitation rates.

Nutrient conditions also do not seem to be one of the controlling factors of reproduction. Seasonal chlorophyll-*a* concentration in the Shonai Inlet shows that phytoplankton production was high throughout the year, although activity was slightly lower in spring and autumn (Anil *et al.*, 1990).

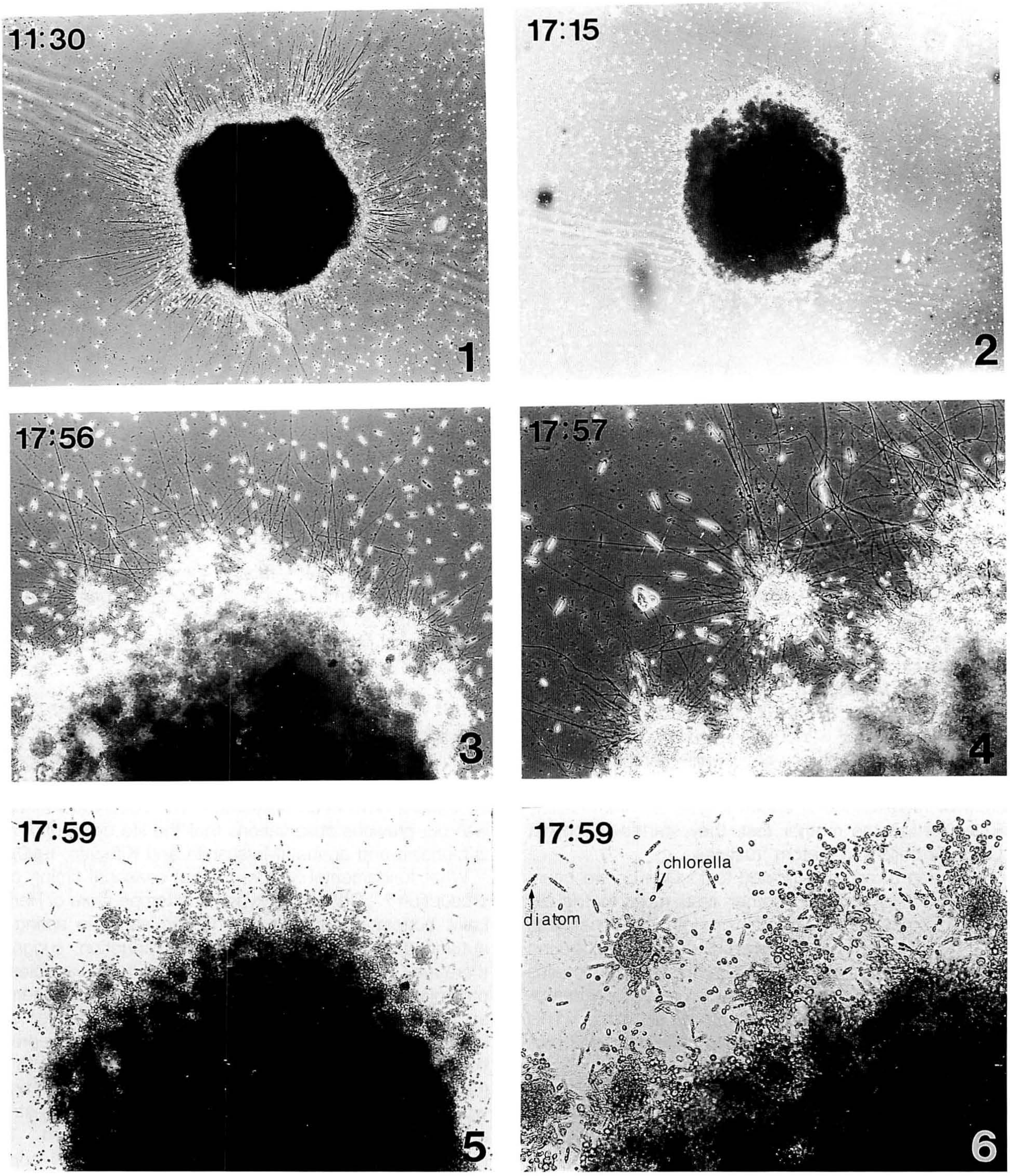

Figure 6. Successive photographs of asexual reproduction. Time of photographic exposure is given in the upper left corner of each photograph. All photographs were taken on November 4, 1990.

1. Construction of blood cyst. ×32. 2. Gamont individuals. ×20. 3. Gamonts depart from cyst under phase contrast. ×50. 4. Enlargement of gamonts showing rhizopodia extruding from each gamont under phase contrast. ×90. 5. Gamonts depart from cyst. ×50. 6. Gamont collecting *Chlorella* cells and diatom frustules for food. ×96.

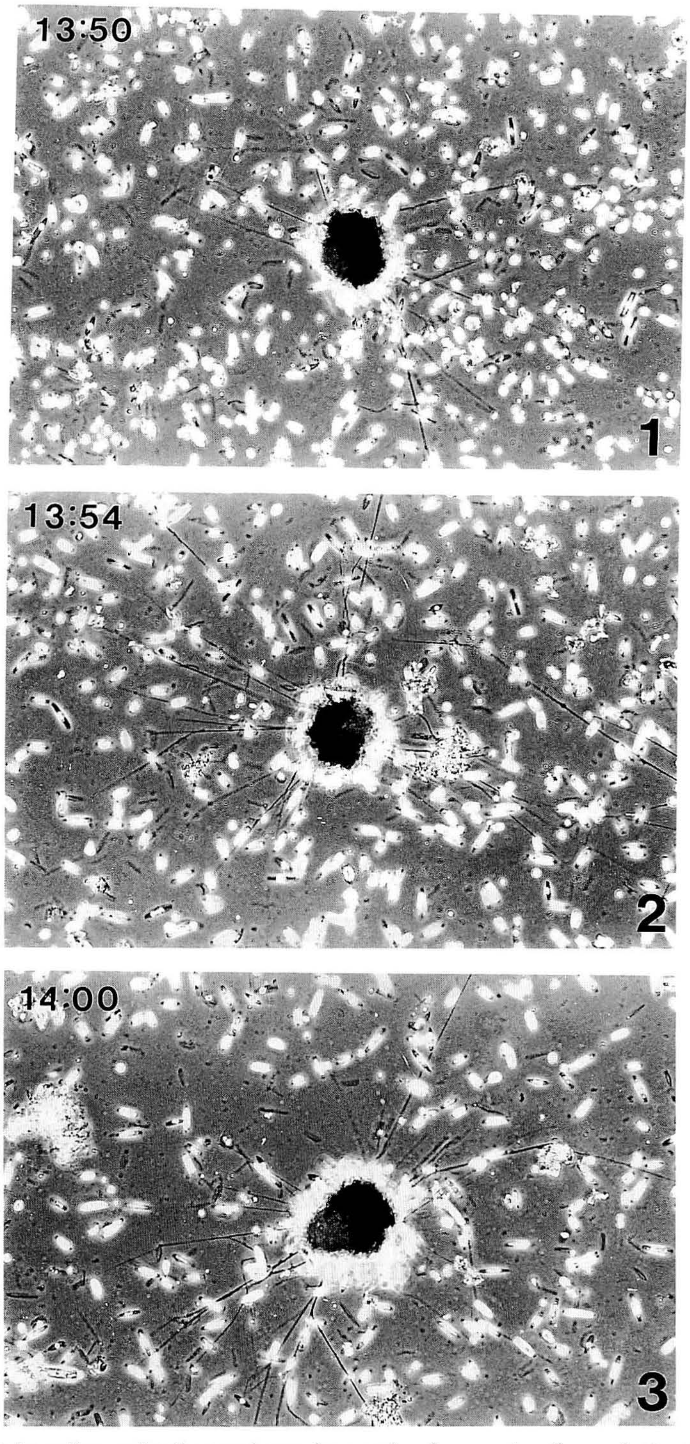

Figure 7. Gamont juveniles collecting carborundum grains for constructing a test wall. The upper hemisphere of each cell is covered by carborundum grains. Time of photographic exposure is given in the upper left corner of each photograph. Prior to this stage, multiple division had occurred at 9 : 30 on November 5, 1990.

Nutrient levels are thus likely sufficient at all times.

In some organisms there is a temporal relationship between reproduction dates and the lunar cycle. Sexual reproduction mainly took place around half moon. Asexual reproduction occurred within three days after full moon, which may be comparable to the reproduction cycle of some planktonic foraminifers (Spindler *et al*., 1979 ; Bjima *et al*., 1990). Further research is needed, including experimental

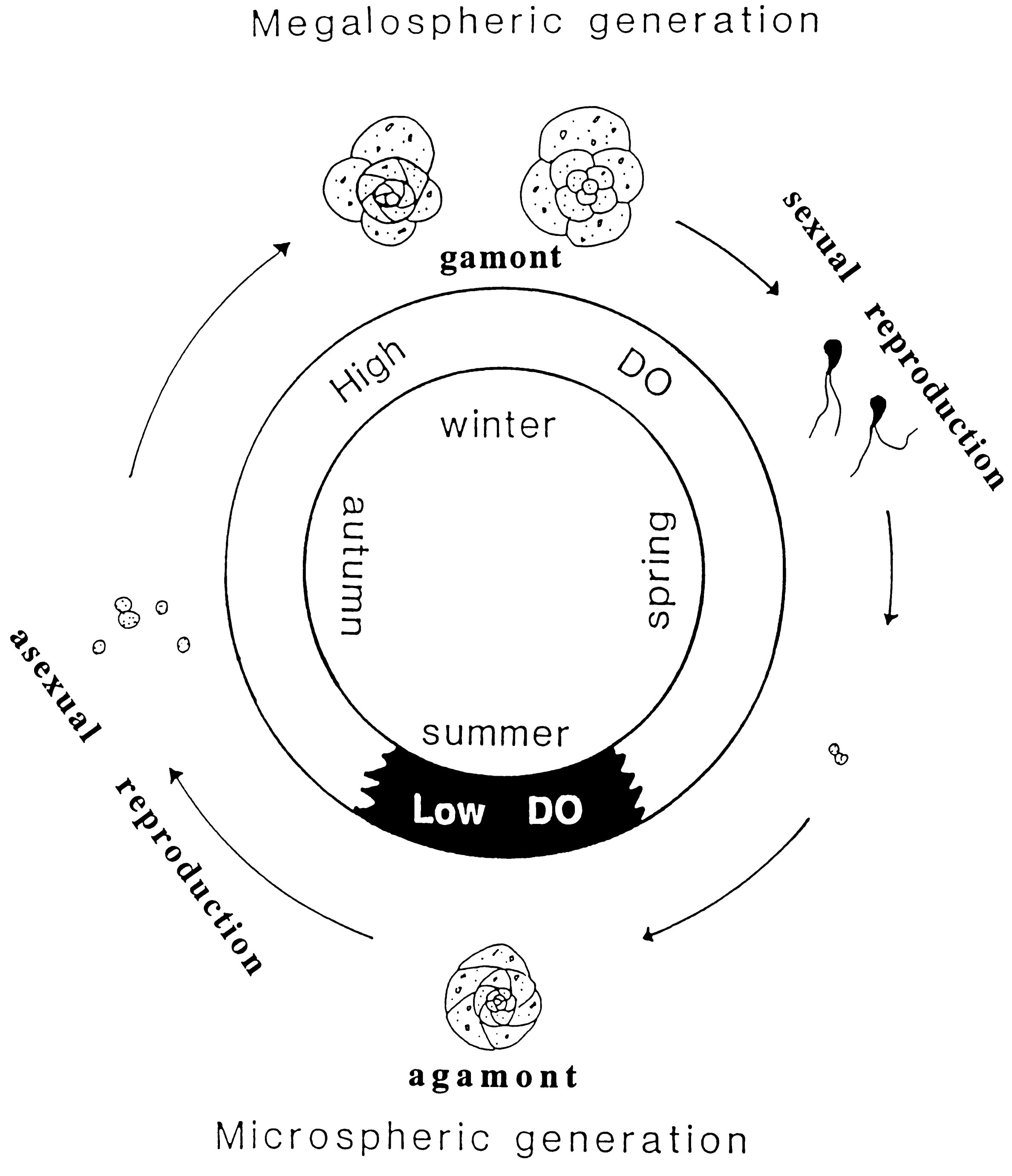

Figure 8. Integrated life cycle of *T. hadai* Uchio in relation to seasons. The figure is revised from figure 15 of Matsushita and Kitazato (1990).

cultures, in order to clarify the nature of ambient factors that induce or control reproduction.

The asexual reproduction process of *T. handai* is mostly the same as that in *T. inflata* (Angell, 1990). However, the duration of reproduction is different in the two species. *Trochammina hadai* took about 6 hours, whereas *Trochammina inflata* required ca. 24 hours (Angell, 1990).

Juvenile individuals of *T. hadai* consist of only one chamber when they leave the cyst. However, both *T. inflata* (Angell, 1990) and *T.* cf. *T. quadriloba* Hoeglund (Salami, 1976) have 2-3 chambers at the time when the juveniles left the mother test, the same as most investigated calcareous foraminifera such as *Ammonia beccarii* (Linné), *Elphidium crispum* (Linné), *Pararotalia nipponica* (Asano), *Glabratella* spp., *Bolivina* spp.,

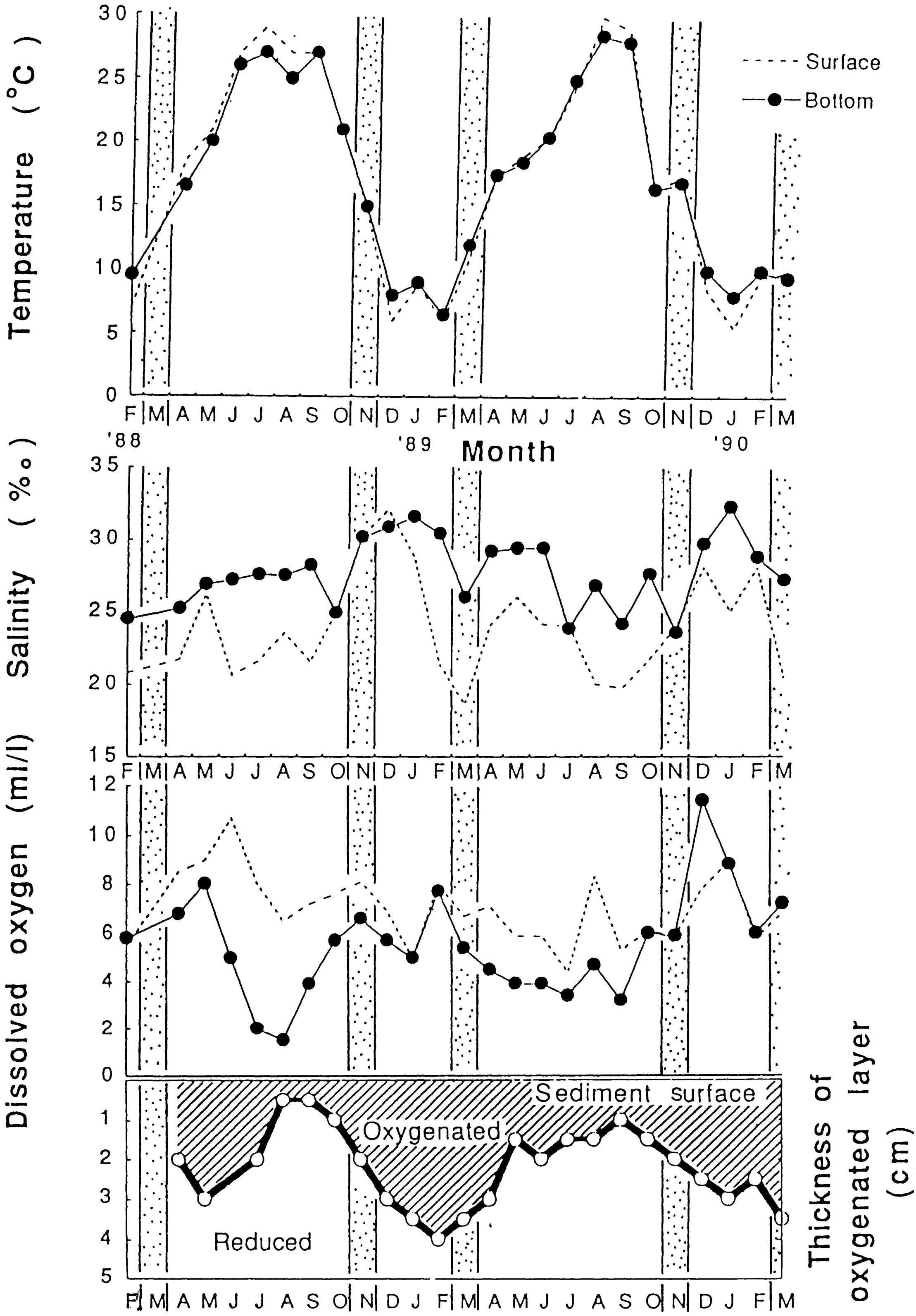

Figure 9. Seasonal changes of water temperature, salinity, dissolved oxygen and thickness of oxygenated layer in the sediments at a fixed station at Hamana Lake during 1988 through 1990. Solid lines show the values for bottom water just above the sediment-water interface. Broken lines show surface conditions. Shaded area shows the main reproductive seasons.

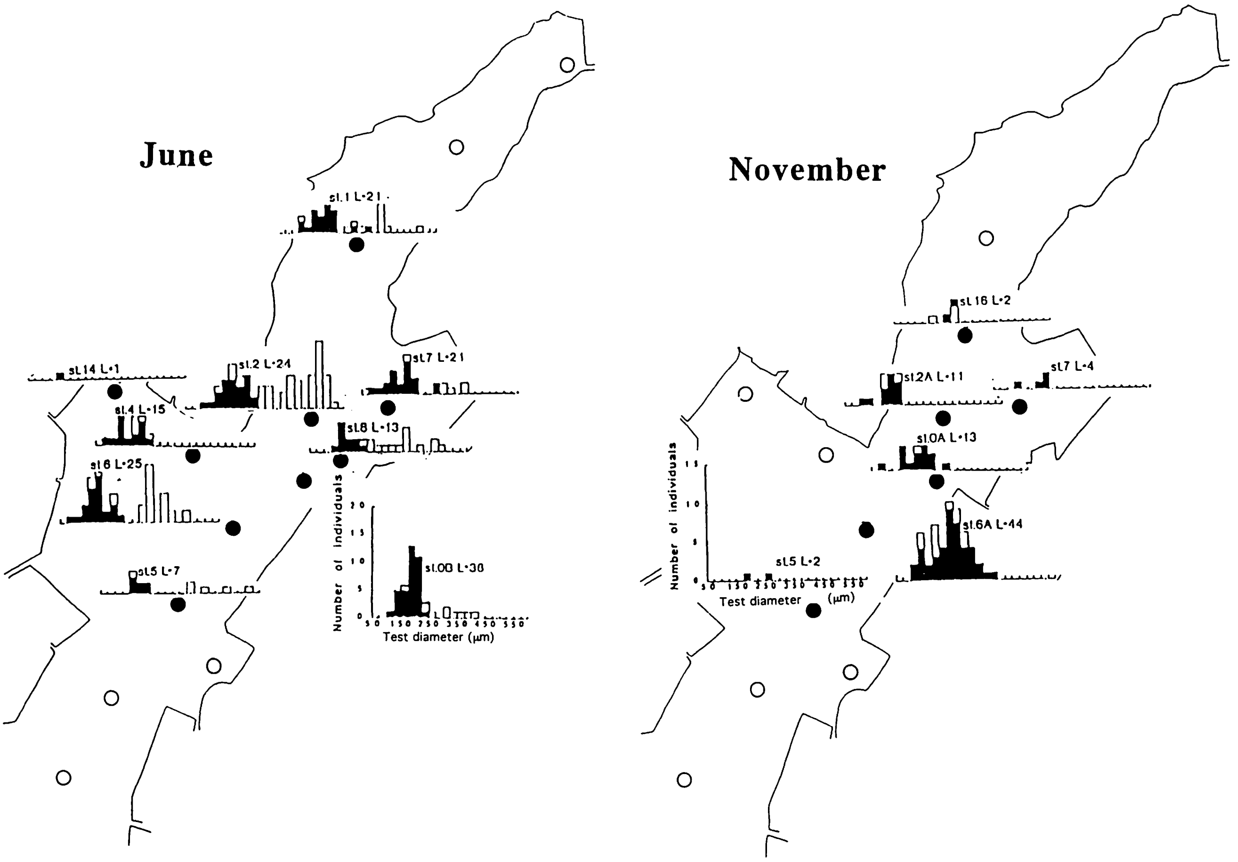

Figure 10. Geographical distribution of *T. hadai* in June and November, 1990, at the Shonai Inlet, Hamana Lake. Open circles show the stations where *T. hadai* was not found. Closed circles indicate the stations where *T. hadai* were found. Histograms show size distribution of *T. hadai* at each station. Open bars of the histograms beside the stations show the number of dead individuals ; closed bars show the number of living individuals. L is the number of living individuals per 10 cm^2.

and others (Kitazato, unpublished observations).

We observed that *Trochammina hadai* collected carborundum grains and cemented the grains, using an organic cement, to the surface of gamont cells to construct an agglutinated test. Bender (1992) proposed six constructional stages during chamber formation for agglutinated foraminifera that secret calcitic cement. We probably observed only initial parts of the chamber formation process. It is probable that chamber wall construction by gamont juveniles is a mixture of stages 1 through 3 of Bender (1992), though in our observations gamont juveniles simply construct an agglutinated wall on the cell surface without actually forming a new chamber. Further studies are needed for correlating correctly our observations, including constructional stages of chamber formation, with those of Bender (1992).

The seasonal distribution of this species may reflect the mode of reproduction in *T. hadai*. Microspheric agamont generations of *T. hadai* are spread widely throughout the inlet in June. The megalospheric generation was dispersed in November. However, the distributional ranges of the megalospheric generation was narrower than those of the microspheric generation (Figure 10). These variations in the seasonal distribution of *T. hadai* might be explained by the difference in modes of dispersion in the sexual and asexual progeny of this species. Agamont juveniles can disperse widely during sexual reproduction because the gametes are able to swim of float in the water. In contrast, gamont individuals tend to be concentrated in a rather narrow area in the lake, because gamont juveniles disperse only by rhizopodia in and on sediments. The average moving velocity of *T. hadai* is 14 μm/minute (Kitazato, 1981). This means that *T. hadai* is able to migrate only 2 cm per day.

A widespread distribution may be advantageous for keeping high survival rates under stressful summer abiotic conditions, which include bottom anoxia due to strong water column stratification (Matsushita and Kitazato, 1990). During summer the density of living *T. hadai* individuals decreases drastically throughout the inlet. Surviving agamonts reproduce asexually in autumn. This means that a relatively small numbers of agamonts found the succeeding gamont generation.

Acknowledgments

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1013

Taxonomy and distribution of the subfamily Ancistrolepidinae (Gastropoda: Buccinidae) from the Plio-Pleistocene of Japan

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Abstract. Four species of *Ancistrolepis* and one of *Clinopegma* are newly obtained and described from Plio-Pleistocene strata in the Japan Sea borderland: *Ancistrolepis masudaensis* Nomura, *A. grammatus* (Dall), *A.* sp. aff. *A. hikidai* (Kuroda), *A.* sp. and *Clinopegma borealis* Tiba. Among the ten species of Plio-Pleistocene Ancistrolepidinae, *A. masudaensis. A. peulepsis, A. koyamai* and *C. fragilis* are extinct. The first three species belong to the *Ancistrolepis eucosmius* group now living in the eastern North Pacific. They suffered extinction during the late Pleistocene cold-climate maxima because of their distribution being restricted to the Japan Sea borderland. On the other hand, in addition to occurring in the Plio-Pleistocene in the Japan Sea borderland, *A. grammatus, C. borealis* and *Bathyancistrolepis trochoideus* Dall survive in the Okhotsk and Bering Seas as well as in the subarctic Pacific Ocean. Recent higher water temperatures and a shallower sill depth may prevent the above three species from migrating back into the Japan Sea.

Key words: Taxonomy, distribution, Ancistrolepidinae, Pliocene, Pleistocene

Introduction

The buccinid subfamily Ancistrolepidinae is a group of cold-water species now living mainly off Hokkaido and in the Okhotsk and Bering Seas. Unlike *Neptunea, Buccinum* and other buccinids, this group did not invade the Arctic and North Atlantic basins after the opening of the Bering Strait during Pliocene time (Titova, 1993). This subfamily was established by Habe and Sato (1972) as Ancistrolepisinae, based on characteristics of the radula. When Goryachev (1987) revised the so-called Buccinidae, he correctly used the subfamily name of Ancistrolepidinae.

According to Habe and Sato (1972), this subfamily consists of the following five genera: *Ancistrolepis* Dall, *Clinopegma* Grant and Gale, *Neancistrolepis* Habe and Sato, *Bathyancistrolepis* Habe and Ito and *Pseudoliomesus* Habe and Sato. Thereafter, Tiba and Kosuge (1982) considered *Bathyancistrolepis* as a subgenus of *Ancistrolepis*, and stated that the type species of *Neancistrolepis* should be included in the genus *Clinopegma*. When Kantor (1988) studied the shell morphology and radula of *Clinopegma*, he considered it a subgenus of *Ancistrolepis*. Moreover, Goryachev (1987) added *Sulcosisus* Dall and *Japelion* Dall to this subfamily. Recently, Egorov and Barsukov (1994) included the genus *Parancistrolepis* (type genus of the subfamily Parancistrolepidinae) in the Ancistrolepidinae. However, they did not indicate the reason why *Sulcosinus, Japelion* and *Parancistrolepis* should be included in the Ancistrolepidinae. In this paper, we follow Habe and Sato's concept of the subfamily.

When Gladenkov *et al.* (1988) summarized the taxonomy of buccinids from the Neogene of Kamchatka, they discriminated the *Ancistrolepis grammatus* group from the type *A. eucosmius* group on the basis of large shell size and prominent T-shaped cords as independently noticed by Naruse (1952). Gladenkov *et al.* (1988) considered that the *grammatus* group belongs to the genus *Neancistrolepis* Habe and Sato (1972). However, the type species of *Neancistrolepis*, *N. beringiana* (Dall), differs from the *grammatus* group in its rather obsolete spiral ribs.

Thereafter, Titova (1993) regarded the *grammatus* group as belonging within *Ancistrolepis* and discussed the early evolution of the Ancistrolepidinae. According to her, this group includes the following Recent species: *Ancistrolepis grammatus* (Dall), *A. hikidai* Kuroda, and *A. kawamurai* Habe and Ito. On the other hand, the *Ancistrolepis eucosmius* group has a small ovate shell and includes some Recent eastern North Pacific species such as *A. eucosmius* (Dall), *A. californicus* Dall, and others. She also suggested that the *eucos-*

mius and *grammatus* groups evolved independently and most genera of Ancistrolepidinae originated in cold-water environments. However, Plio-Pleistocene fossils were not sufficiently considered by her.

Up to this time, the following species and subspecies of Ancistrolepidinae have been described from Plio-Pleistocene strata of Japan: *Ancistrolepis masudaensis* Nomura, *A. peulepis* Kanehara, *A. koyamai* (Kuroda), *A. eucosmius koyamai* Habe and Ito, *Bathyancistrolepis trochoideus* Dall, *B. t. tokoyodaensis* Ozaki, *Clinopegma fragilis* Kuroda, *C. borealis* Tiba and *C. unicum* (Pilsbry) (Kuroda, 1931; Suzuki, 1935; Nomura, 1937; Kanehara, 1937; Ozaki, 1958; Noda, 1962; Noda *et al.*, 1984; Amano, 1984; Noda and Amano, 1985; Matsui, 1985; Baba, 1990; Matsuura, 1992). The first four species belong to the *Ancistrolepis eucosmius* group (Gladenkov *et al.*, 1988). In the Plio-Pleistocene, no species of the *A. grammatus* group has been recorded. With the exception of *Bathyancistrolepis trochoideus*, each species of Ancistrolepidinae occur only at one or a few localities.

Fortunately, we collected some specimens of the *Ancistrolepis grammatus* group from Plio-Pleistocene strata in Honshu and Hokkaido. Moreover, *A. masudaensis* and *Clinopegma borealis* were found from new localities in Honshu. In this paper, after describing these specimens, we discuss their distribution and biogeographic significance.

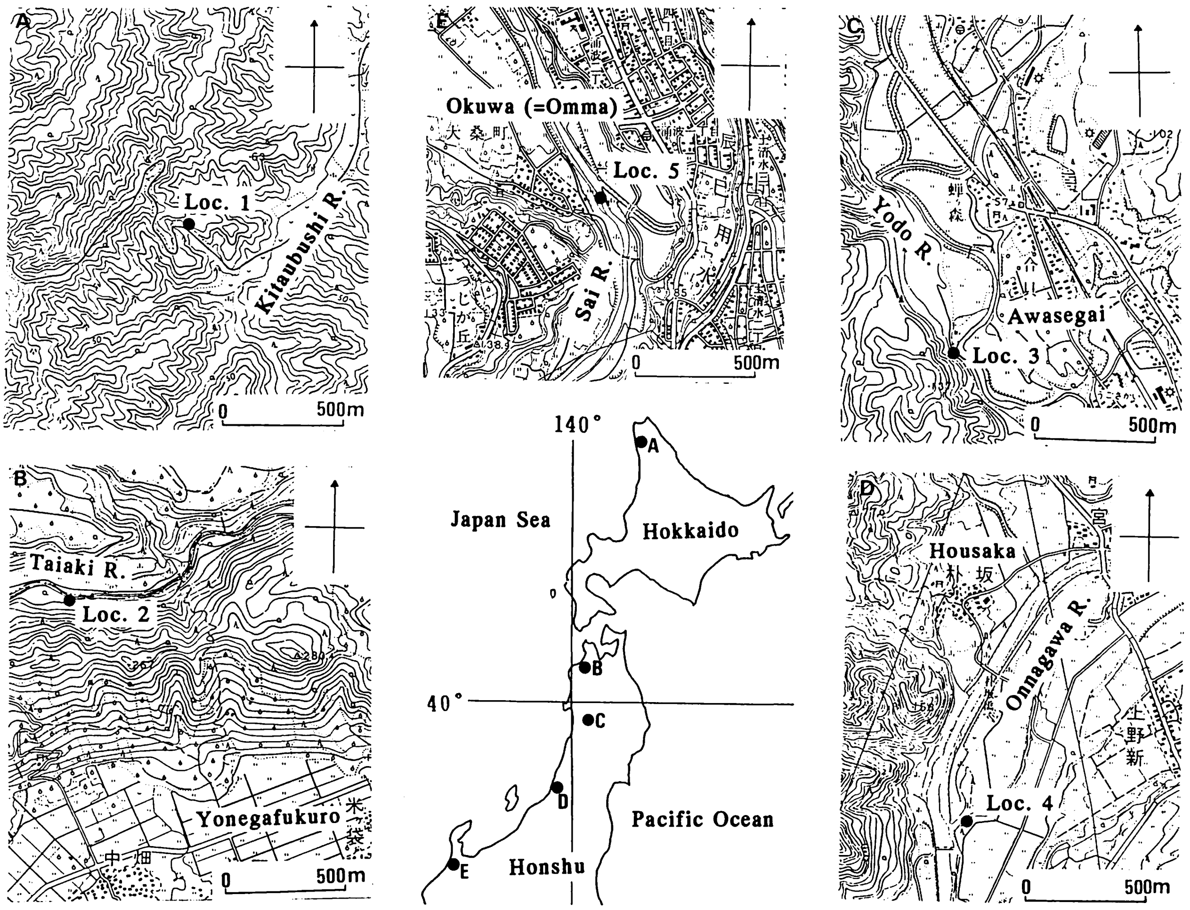
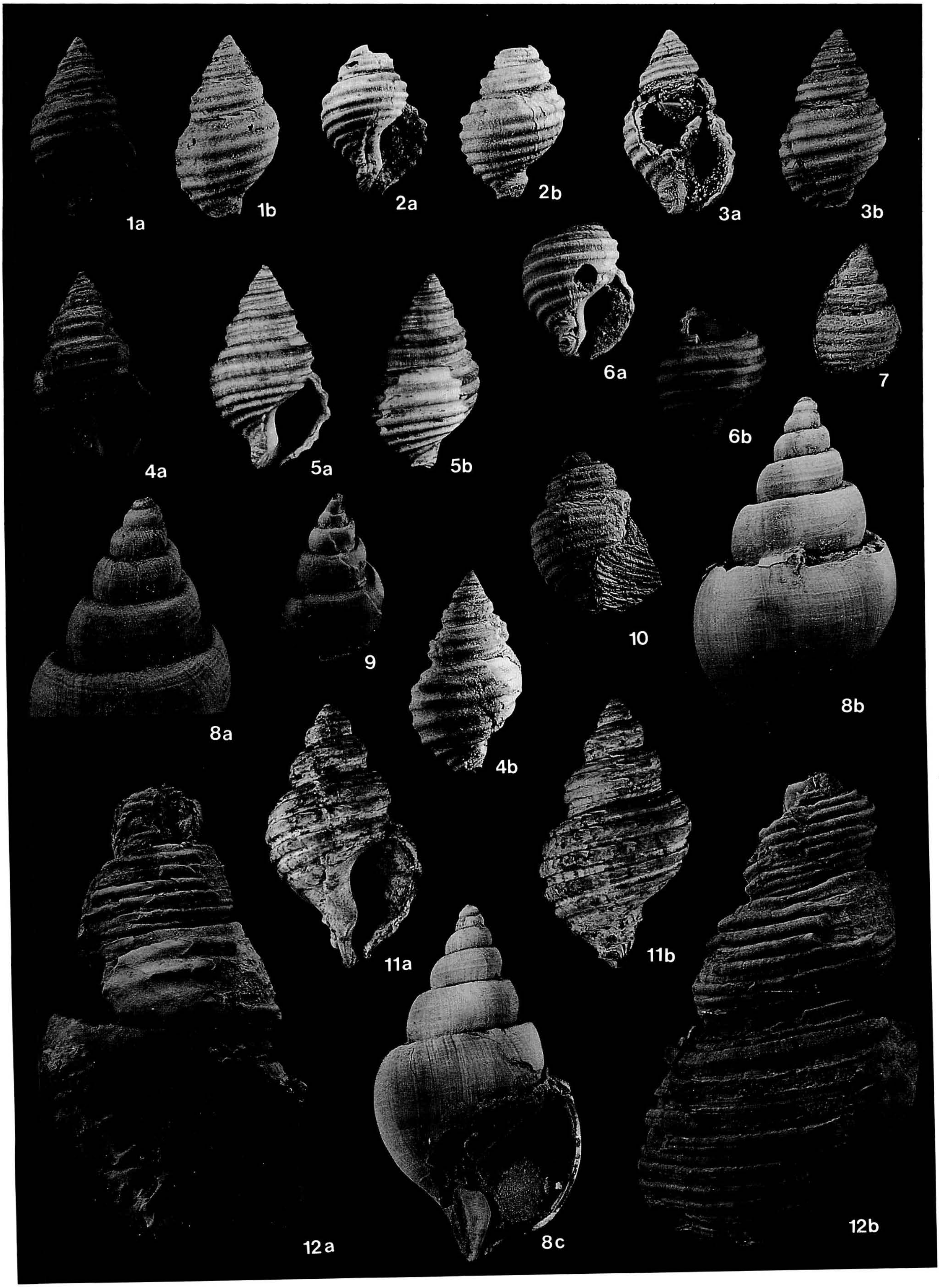


Figure 1. New localities of Plio-Pleistocene Ancistrolepidinae (using the topographical maps "Furaoi", "Iwakisan", "Echigoshimoseki", "Ugosakai" and "Kanazawa", scale 1 : 25,000 published by Geographical Survey Institute of Japan).

Figure 2. 1-6. *Ancistrolepis masudaensis* Nomura, 1a-b, 3a-b: JUE nos. 15565-1, -2, Loc. 3, Tentokuji Formation, ×1.7, 2a-b: JUE no. 15566-1, ×2, 6a-b: JUE no. 15566-2, ×1.5, Loc. Roadside cliff at Shohei Bridge near Masuda, Akumi County, Yamagata Pref., Kannonji Formation, 4a-b: Loc. Kakuma, Kanazawa City, Ishikawa Pref., Omma Formation, collected by Dr. N. Matsuura, ×1.5, 5a-b: SHM no. 12636, Holotype, ×1.7. **7, 10.** *Ancistrolepis koyamai* (Kuroda), 7: JUE no. 15567, Loc. Riverside cliff near Ohata, Nakajo village, Nagono Pref., Joshita Formation, ×1.2, 10: JC 610067, Holotype, ×1. **8, 9.** *Clinopegma borealis* Tiba, 8a-c: 8a, ×1.5, 8b-c, ×1, JUE no. 15568-1, 9: JUE no. 15568-2; Lon. 4., Kuwae Formation, ×1. **11a-b.** *Ancistrolepis peulepis* Kanehara, IGUT 10988, Loc. 84-01 of Noda and Amano (1985), Yuchi Formation, ×1.5. **12a-b.** *Ancistrolepis* aff. *hikidai* Kuroda, JUE no. 15569, Loc. 2, Higashimeya Formation, ×0.8.


1a
1b
2a
2b
3a
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6a
7
4a
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5b
6b
10
9
8b
8a
4b
11a
11b
12a
8c
12b

New localities of Ancistrolepidinae

Five species were newly collected from the following five localiteis (Figure 1). These localities, with stratigraphical and facies details, are described below.

Loc. 1. Large roadside cliff about 850 m east of the pass between Kitaubushi and Kitakawaguchi, Teshio town, northwestern Hokkaido (fossil locality of Noda *et al.*, 1983); siltstone bearing many calcareous concretions; lower part of Yuchi Formation.

Loc. 2. Riverside cliff about 3.2 km upstream of Taiaki River from its junction with the Iwaki River, Hirosaki City, Aomori Pref.; siltstone; Higashimeya Formation.

Loc. 3. Large riverside cliff along Yodo River, about 500 m southwest of Awasegai, Kyowa town, Akita Pref. (Loc. T8 of Ogasawara *et al.*, 1986); pebble-bearing fine-grained sandstone; Tentokuji Formation.

Loc. 4. Riverside cliff of small creek of Onnagawa River, about 600 m south of Housaka Bridge, Sekikawa village, Niigata Pref.; siltstone; Kuwae Formation.

Loc. 5. River bank 260 m downstream of Sai River from the Megane Bridge, Kanazawa City, Ishikawa Pref. (sixth sedimentary cycle of Omma Formation by Kitamura and Kondo, 1990); fine-grained sandstone; middle part of Omma Formation.

Taxonomy

Family Buccinidae Rafinesque, 1815
Subfamily Ancistrolepidinae Habe and Sato, 1972
Genus ***Ancistrolepis*** Dall, 1895

Ancistrolepis masudaensis Nomura, 1937

Figures 2-1—6

Ancistrolepis masudaensis Nomura, 1937, p. 177, pl. 24, figs. 14a, b.

Ancistrolepis eucosmius koyamai Habe and Ito. Matsuura, 1992, pl. 5-15 (2), fig. 4.

Type Specimen.—Holotype, SHM no. 12636 (Figures 2-5a-b).

Type locality.—Masuda, Akumi County, Yamagata Pref.

Material.—Three specimens collected from Loc. 3 (lower Pliocene Tentokuji Formation).

Description.—Shell small, ovate-fusiform, solid, with low spire. Whorls six, with two small and smooth protoconch whorls. Penultimate whorl ornamented with three to four rounded spiral ribs, separated by nearly equal interspaces. Body whorl sculptured by seven to eight spiral cords, separated by slightly narrower interspaces. Subsutural ribs distinct, just below well marked suture. Whole surface occasionally covered by distinct growth lines. Aperture ovate, nearly equal in length to spire. Inner side of outer lip crenulated in correspondence with spiral ribs. Adapical channel narrow and deep. Inner lip with rather thick callus. Canal short, recurved, forming rather distinct fasciole.

Measurements (in mm).—

Specimens	Height	Diameter	NSB*	NSP**
JUE no. 15565-1	19.0	11.2	8	4
JUE no. 15565-2	19.1	11.2	7	3

* Number of spiral cords on body whorl, ** Number of spiral cords on penultimate whorl

Remarks.—Only a single specimen was described by Nomura (1937) from the Plio-Pleistocene Kannonji Formation. Morphological examination of the holotype (Figures 2-5a-b) and two specimens (Figures 2-2a-b, 6a-b) which we collected from the same formation near Masuda shows that *Ancistrolepis masudaensis* is characterized by a small, ovate-fusiform shell, with low spire, 7-8 spiral cords on the body whorl and 3-4 spiral cords on the penultimate whorl. As described above, all these characteristics are the same in the Tentokuji specimens.

Matsuura (1992) illustrated a single specimen (Figures 2-4a-b) from the Omma Formation at Kakuma, Ishikawa Prefecture under the name of *Ancistrolepis eucosmius koyamai* Habe and Ito [*non A. koyamai* (Kuroda)]. The specimen has two protoconch whorls, a low spire, nine spiral cords on the body whorl and three spiral cords on the penultimate whorl. These traits are shared with *Ancistrolepis masudaensis*. *A. eucosmius koyamai* is characterized by having a high spire and minute interstitial threads which are never seen in *A. masudaensis*.

Comparisons.—The present species resembles *Ancistrolepis koyamai* (Kuroda), *A. peulepis* Kanehara, *A. kamtchaticus* (Ilyina) and *A. eucosmius* (Dall).

Ancistrolepis koyamai (Figures 2-7, 10) was originally described from the Pliocene Takafu Formation in northern Nagano Prefecture under the generic name of *Buccinum* by Kuroda (1931). It resembles *A. masudaensis* in shell shape, size and similar number of spiral cords (eight on body whorl and three on penultimate). However, *A. koyamai* has rather a flat area just below the suture and broader spiral cords than *A. masudaensis*. *Ancistrolepis peulepis* (Figures 2-11a-b) was proposed from the Pliocene Yuchi Formation in northwestern Hokkaido by Kanehara (1937). This species can be distinguished from *A. masudaensis* by its larger shell, six broad spiral cords on the body whorl and by having a flat-bottomed groove just below the suture.

Ancistrolepis kamtschaticus was established by Ilyina (1939) under the name *Buccinum strigillatum* Dall var. *kamtschatica* from the Middle Miocene Kavran Suite (=Etolon Suite). This species is allied to *A. masudaensis* and *A. peulepis* in its shell form and in having four spiral cords on the penultimate whorl. According to Gladenkov *et al.* (1988), *A. kamtschaticus* has more numerous spiral ribs (8-10) on the body whorl than the later two species.

The Recent species *Ancistrolepis eucosmius* (Dall) can be easily distinguished from *A. masudaensis* by having many interstitial spiral threads over the whole surface.

Distribution.—Pliocene Tentokuji Formation; Plio-Pleistocene Kannonji Formation; lower Pleistocene Omma Formation, all in Honshu.

Ancistrolepis grammatus (Dall, 1907)

Figures 3-2—4

Chrysodomus (*Ancistrolepis*) *grammatus* Dall, 1907, p. 158; Kosuge, 1972, pl. 17, fig. 8.
Ancistrolepis grammatus (Dall). Dall, 1925, p. 3, pl. 30, fig. 8; Kuroda, 1931, fig. 6; Shikama, 1957, p. 35, pl. 10, figs. 8a-b; Habe and Ito, 1968, p. 3, 6-7, pl. 1, fig. 1; Tiba and Kosuge, 1981, p. 5, 6; Okutani *et al.*, 1988, p. 107; Bogdanov and Sirenko, 1993, p. 52, pl. 52, figs. 1, 2.
Ancistrolepis grammatus yamasakii Kuroda, 1944, p. 237-238, pl. 7, fig. 1; Habe and Ito, 1965, p. 56-57, pl. 16, fig. 8.
Ancistrolepis grammata grammata (Dall). Habe and Ito, 1965, p. 57, text-fig. 23.
Ancistrolepis grammata (Dall). Habe and Sato, 1972, pl. 1, fig. 8.
Ancistrolepis (*Ancistrolepis*) *grammatus grammatus* (Dall) Egorov and Barsukov, 1994, p. 6, fig. 16H.
Ancistrolepis (*Ancistrolepis*) *grammatus yamazakii* Kuroda, Egorov and Barsukov, 1994, p. 7, figs. 3I, 16E-G.

Type specimen.—Holotype, USNM no. 110472.

Type locality.—Tsugaru Strait (300 fms.).

Materials.—Two imperfect specimens obtained from Loc. 5 (lower Pleistocene Omma Formation).

Description.—Shell medium-sized, thin, with more than five subtabulated whorls. Protoconch large, with two whorls. Surface of each spire whorl covered by six prominent T-shaped cords. Body whorl sculptured by eleven weathered but strong cords. Subsutural groove narrow and rather deep. Inner lip with thin callus. Fasciole not so large and smooth.

Measurements (in mm).—

Specimens	Height	Diameter	NSB*	NSP**
JUE no. 15571	—	—	—	6
JUE no. 15572	55.9+	32.9+	11	6

* Number of spiral cords on body whorl, ** Number of spiral cords on each whorl except for the last

Remarks.—Our specimens can be identified with the recent species *Ancistrolepis grammatus* (Dall) especially by the form and number (5-6 on penultimate, 8-13 on body whorl in modern form) of spiral cords. They slightly differ from some typical specimens of the species in having a lower spire and narrower interspaces between cords. The Recent species shows wide variations in spire height, and in number and shape of the spiral cords (Tiba and Kosuge, 1981). Therefore, the Omma Formation specimens fall within the shape range of the Recent species.

Ancistrolepis grammatus yamasakii was discriminated from the typical *grammatus* by Kuroda (1944) because of its narrower and more numerous (13) spiral cords. Tiba and Kosuge (1981, p. 8) treated this subspecies as a variety of *A. grammatus*. As *A. grammatus* shows a wide range of varia-

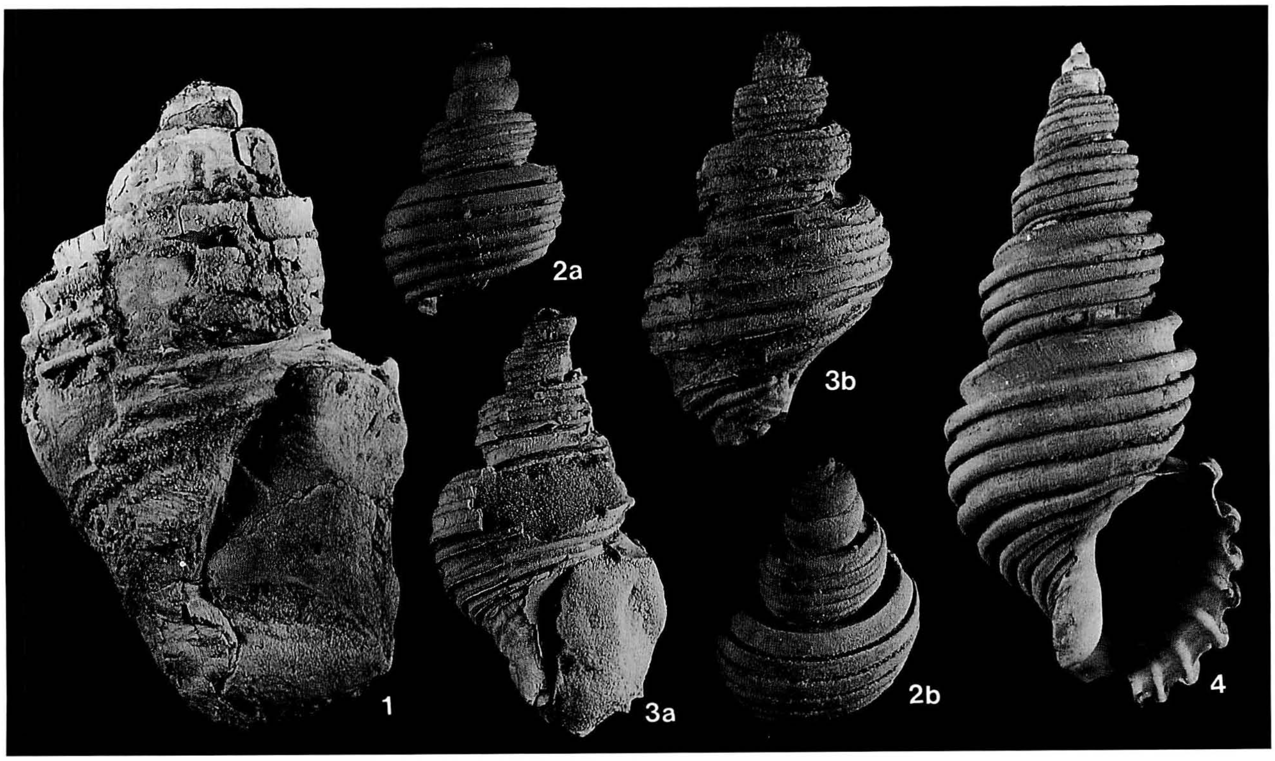

Figure 3. 1. *Ancistrolepis* sp., JUE no. 15570, Loc. 1, Yuchi Formation, ×1. **2-4.** *Ancistrolepis grammatus* (Dall), 2a: ×1.5, 2b: ×1.55, JUE no. 15571, 3a-b: JUE no. 15572, Loc. 5, Omma Formation, ×1, 4: JUE no. 15573, Loc. off Rausu, Hokkaido, Recent, ×1.

tion in its shell shape, form and number of spiral cords, we agree with Tiba and Kosuge's opinion.

Comparisons.—*Ancistrolepis hikidai* Kuroda differs from *A. grammatus* in having more numerous spiral cords (8 on penultimate and 13-15 on body whorl) and a larger body whorl.

Distribution.—Lower Pleistocene Omma Formation in Honshu ; Recent Tsugaru Strait (300 fms.), off Rausu and off Abashiri in Hokkaido ; Paramushir and Shumsh Islands (Kurile Islands).

Ancistrolepis sp. aff. ***A. hikidai*** Kuroda, 1944

Figures 2-12a—b

Material.—One imperfect specimen collected from Loc. 2 (upper Pliocene Higashimeya Formation).

Description.—Shell large, thick, with more than four subtabulated whorls. Protoconch absent. Height of body whorl about three-fifths of shell height. Subsutural area narrow and deep. Surface of penultimate whorl ornamented with ten quadrate or rounded spiral cords and one weak rib just below subsutural keel. Body whorl with more than twelve quadrate spiral cords and two rounded interstitial ribs. Spiral cords on body whorl subdivided into two or three parts by shallow grooves. These cords on both whorls broader than interspaces. Aperture partly broken.

Measurements (*in mm*).—

Specimens	Height	Diameter	NSB*	NSP**
JUE no. 15569	106.9+	64.3+	12+	10

* Number of spiral cords on body whorl, **Number of spiral cords on penultimate whorl

Remarks and comparisons.—The present specimen partly resembles the Recent species, *Ancistrolepis hikidai* Kuroda (occasionally misspelled as *A. hikitai*) in having a similar number of spiral cords. However, the following characters are never seen in the Recent form ; rather high spire, some interstitial ribs and shallow grooves on spiral cords. The first two traits can be seen in *A. vietnamensis* Sirenko and Goryachev (1990). The number of spiral cords enables us to separate *A. vietnamensis* (5 on penultimate and 20 on body whorl) easily from the Higashimeya specimen.

Ancistrolepis sp.

Figure 3-1

Material.—One poorly preserved specimen collected from Loc. 1 (lower Pliocene Yuchi Formation).

Description.—Shell large, thin, with more than four whorls ; lacking protoconch whorls. Body whorl very large occupying four-fifths of shell height. Subsutural area broad and flat. Surface of penultimate whorl sculptured by five rounded spiral cords with interspaces broader than cords themselves. Body whorl with ten highly rounded cords separated by broad interspaces.

Measurements (*in mm*).—

Specimens	Height	Diameter	NSB*	NSP**
JUE no. 15570	85.7+	49.6+	10	5

* Number of spiral cords on body whorl, ** Number of spiral cords on penultimate whorl

Remarks and comparisons.—Judging only from the number of cords of this specimen, it is allied to a Recent species, *Ancistrolepis grammatus* (Dall). However, the former differs from the latter in having a large body whorl, a broad and flat subsutural area, and highly rounded spiral cords. Owing to the poor preservation of this specimen, it is too difficult to assign the shell at the species level.

Genus ***Clinopegma*** Grant and Gale, 1931

Clinopegma borealis Tiba, 1969

Figures 2-8—9

Clinopegma borealis Tiba, 1969, p. 135-136, pl. 7, figs. 1-5 ; Tiba and Kosuge, 1982, p. 11-12 ; Amano, 1984, p. 104, figs. 2, 3 ; Matsui, 1985, p. 175, pl. 23, figs. 8a-b.

Sulcosinus borealis (Tiba). Egorov and Barsukov, 1994, p. 20-21, figs. 3N, 5J, 15, 28C.

Material.—Two specimens collected from Loc. 4 (lower Pliocene Kuwae Formation).

Description.—Shell medium in size, consisting of seven whorls including two large protoconch whorls. Spire rather low. Each whorl with angulated shoulder providing narrow and flat subsutural area. Aperture ovate with nearly straight inner lip. Surface smooth except for fine growth lines and weak spiral threads.

Measurements (*in mm*).—

Specimens	Height	Diameter
JUE no. 15568-1	65.1	36.6

Remarks.—Shells of Ancistrolepidinae generally show a wide range in spire height as described above. In spite of its slightly low spire, the present specimen can be safely identified with a Recent boreal species, *Clinopegma borealis* Tiba, because of its similar shell shape and ornamentation. When they described the species, Egorov and Barsukov (1994) includes this species in the genus *Sulcosinus* Dall, without any explanation including detailed information about an operculum and soft body of *Sulcosinus*. The type species of *Sulcosinus* is characterized by a thick callus, deeply channeled suture and conspicuous zigzag ornamentation. None of these traits is observable in *borealis*. Therefore, it is better for *borealis* to be included in *Clinopegma* rather than in *Sulcosinus*.

Comparisons.—The present species is closely related to *Clinopegma orientalis* (Golikov and Gulvin) from the northern Kurile Islands. The latter species differs from the former only in having more distinct ribs, especially on the body whorl.

Distribution.—Pliocene Rumoi Formation in Hokkaido, Sasaoka and Kuwae Formations in Honshu ; Recent off Kamchatka, Bering Sea.

Distribution

The following species of Ancistrolepidinae have been recognized from the Plio-Pleistocene in Japan: *Ancistrolepis masudaensis* Nomura, *A. peulepis* Kanehara, *A. koyamai* (Kuroda), *A. grammatus* (Dall), *A.* aff. *hikidai* Kuroda, *A.* sp., *Bathyancistrolepis trochoideus* Dall, *Clinopegma borealis* Tiba, *C. fragilis* Kuroda, and *C. unicum* (Pilsbry). Among these ten species, four species suffered extinction after the Pleistocene: namely, *A. masudaensis, A. peulepis, A. koyamai* and *C. fragilis*. It is noteworthy that the *A. eucosmius* group shows a high extinction rate.

The extant species of Ancistrolepidinae now live in the lower sublittoral to upper bathyal zone (Table 1). *Ancistrolepis grammatus* has been recorded from off Abashiri, off Rausu and the Okhotsk Sea (Higo and Goto, 1993) (150-300 m depth after Higo and Goto, 1993; 400-800 m after Okutani *et al*., 1988; 88-890 m after Egorov and Barsukov, 1994). *Clinopegma borealis* is found living off Kamchatka and the Bering Sea (Higo and Goto, 1993) (100-300 m in depth after Higo and Goto, 1993). *C. unicum* has been reported from off Kashimanada-Sanriku and southern Hokkaido (Tiba and Kosuge, 1982) (50-200 m in depth after Higo and Goto, 1993; 50-450 m after Okutani *et al*., 1988) and from the southern part of the Okhotsk Sea and Sakhalin (Egorov and Bersukov, 1994) (100-250 m after Egorov and Barsukov, 1994). In contrast with the above boreal species, *Bathyancistrolepis trochoideus* occurs on the Pacific side of

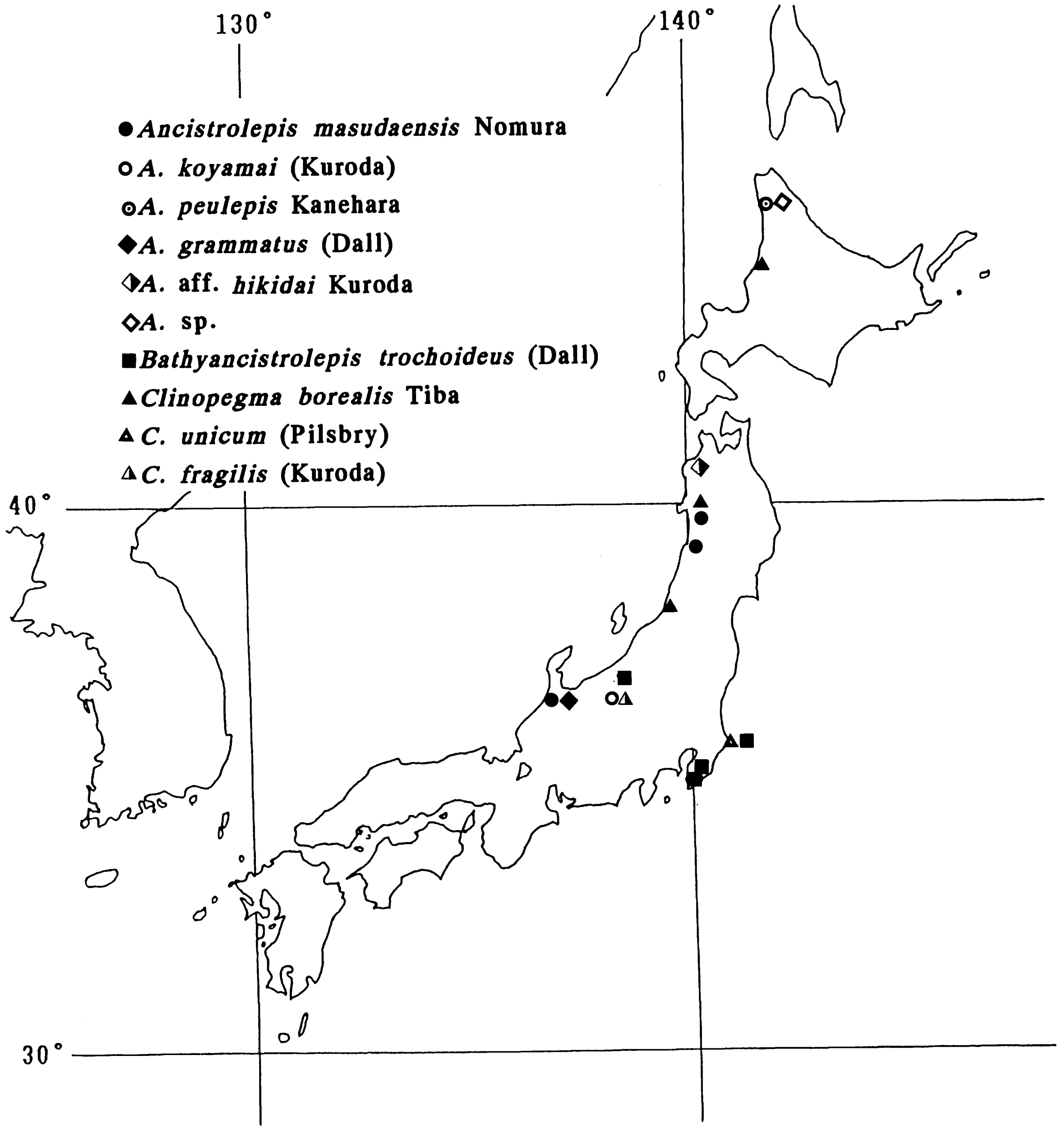

Figure 4. Distribution of Ancistrolepidinae from Plio-Pleistocene strata in Japan.

Table 1. Distribution of some Recent species of Ancistrolepidinae occurring from Plio-Pleistocene strata in Japan.

Species	Geographical distribution	Bathymetric range
Ancistrolepis grammatus	off Abashiri, off Rausu and Okhotsk Sea[1]	150-300 m[1] : 400-800m[2] : 88-890 m[3]
Clinopegma borealis	off Kamchatka and Bering Sea[1]	100-300 m[1]
C. unicum	Kashimanada-Sanriku and Southern Hokkaido[4] :	50-200 m[1] : 50-450[2]
	Southern part of Okhotsk Sea and Sakhalin[3]	100-250 m[3]
Bathyancistrolepis trochoideus	Kumanonada, Sagami Bay and off Sanriku[4]	100-1,500 m[1] : 200-2,000 m[2] : 620-2,050 m[3]

[1] Higo and Goto (1993), [2] Okutani *et al.* (1988), [3] Egorov and Barsukov (1994), [4] Tiba and Kosuge (1982)

Honshu ; Kumanonada, Sagami Bay, Kashimanada and off Sanriku (Tiba and Kosuge, 1982) (100-1,500 m in depth after Higo and Goto, 1993 ; 200-2,000 m after Okutani *et al.*, 1988 ; 620-2,050 m after Egorov and Barsukov, 1994).

As shown in Figure 4, all the fossil species occur only in the Japan Sea borderland except for *Bathyancistrolepis trochoideus* and *Clinopegma unicum*. It is significant to note that all the species still extant from Plio-Pleistocene strata on the Japan Sea side of Honshu such as *Ancistrolepis grammatus, B. trochoideus* and *C. borealis* are not found in the Recent Japan Sea. Moreover, the Pliocene localities from which *C. borealis* has been obtained are north of those for *B. trochoideus*. This occurrence is similar to the present-day distributional pattern ; as noted before, *C. borealis* is now found living off Kamchatka and the Bering Sea while *Bathyancistrolepis trochoideus* occurs more southerly.

Biogeographic significance

In the Pliocene and early Pleistocene, cold-water species dominated the molluscan faunas of the Japan Sea borderland (Ogasawara, 1994 ; Amano, 1994). Therefore, some boreal populations of Ancistrolepidinae were able to invade the Japan Sea through a northern channel (Tada, 1994) which was more deeper than the modern water passways.

Later, especially during late Pleistocene glacial lowstands, the Japan Sea was enclosed and its deep-sea bottom was euxinic (Tada, 1994). Matoba (1978, 1984) has pointed out that the deep-water benthic foraminiferal fauna suffered drastic extinction during the late Pleistocene. As most larvae of buccinid species including Ancistrolepidinae show nonplanktotrophic development (Amio, 1963 ; Bouchet and Waren, 1994), their ability to disperse is less than that of planktotrophic larvae (Shuto, 1974). In the deteriorated environments of cold-climate maxima, most species of Ancistrolepidinae in the Japan Sea borderland suffered extinction along with the benthic foraminifers. However, *Bathyancistrolepis trochoideus* survived because it also occurred on the Pacific side. *Ancistrolepis grammatus* and *Clinopegma borealis* probably survived in the Okhotsk and Bering Seas. However, unfortunately, this speculation is not supported by the fossil record from the Plio-Pleistocene in Sakhalin and Kamchatka, perhaps because the species are rare.

In the Holocene, with the Tsushima warm current flowing over the hyperoxic bottom water, water temperature at the northern shallow straits increased over that in Plio-Pleistocene times (*see* Amano, 1994). Therefore, boreal *Ancistrolepis grammatus* and *Clinopegma borealis* could not invade the Japan Sea. Why can not *Bathyancistrolepis trochoideus* living on the Pacific side of Honshu migrate into the Japan Sea ?

Fossil occurrences of two species of *Neptunea* are shown in Figure 5. The genus *Neptunea* in phylogenetically close to the genus *Ancistorolepis* (Titova, 1993). Among the Recent Japanese *Neptunea* species, *N.* (*Neptunea*) *intersculpta* (Sowerby) and *N.* (*Barbitonia*) *arthritica* (Bernardi) have been recorded from the Plio-Pleistocene on both the Pacific Ocean side and the Japan Sea side of Northeast Honshu as well as the Japan Sea side of Hokkaido (Masuda and Noda, 1976 ; Nemoto and O'hara, 1979 ; Baba, 1990). Both species are now living around the Japanese Islands. *N. intersculpta* occurs in the Japan Sea and also off Sanriku, Sakhalin and the Kurile Islands (Tiba and Kosuge, 1988) (36-895 m in depth after Golikov, 1963). *N. arthritica* is known from the Japan Sea, Okhotsk Sea and Pacific Ocean side of Northeast Honshu (Tiba and Kosuge, 1988) (0-150 m in depth after Golikov, 1963). These cool-water species can live in shallow waters. This enabled both species of *Neptunea* to go through the Recent northern straits into the Japan Sea. In contrast, because the shallowest depth occurrence of *Bathyancistrolepis trochoideus* is still deeper than that of these *Neptunea* species, the former cannot invade the Recent Japan Sea.

The distribution of Ancistrolepidinae in the Plio-Pleistocene and the Recent reveals that most deep-water elements in the Japan Sea suffered extinction during the Quaternary. Thermal tolerance and bathymetric distribution dictated which species could re-invade the Japan Sea after these extinction events. Moreover, one of the reasons why this group could not invade the Arctic and North Atlantic basins with the Pliocene Beringian transgression is due to their having deeper habitats than *Neptunea, Buccinum* and so on.

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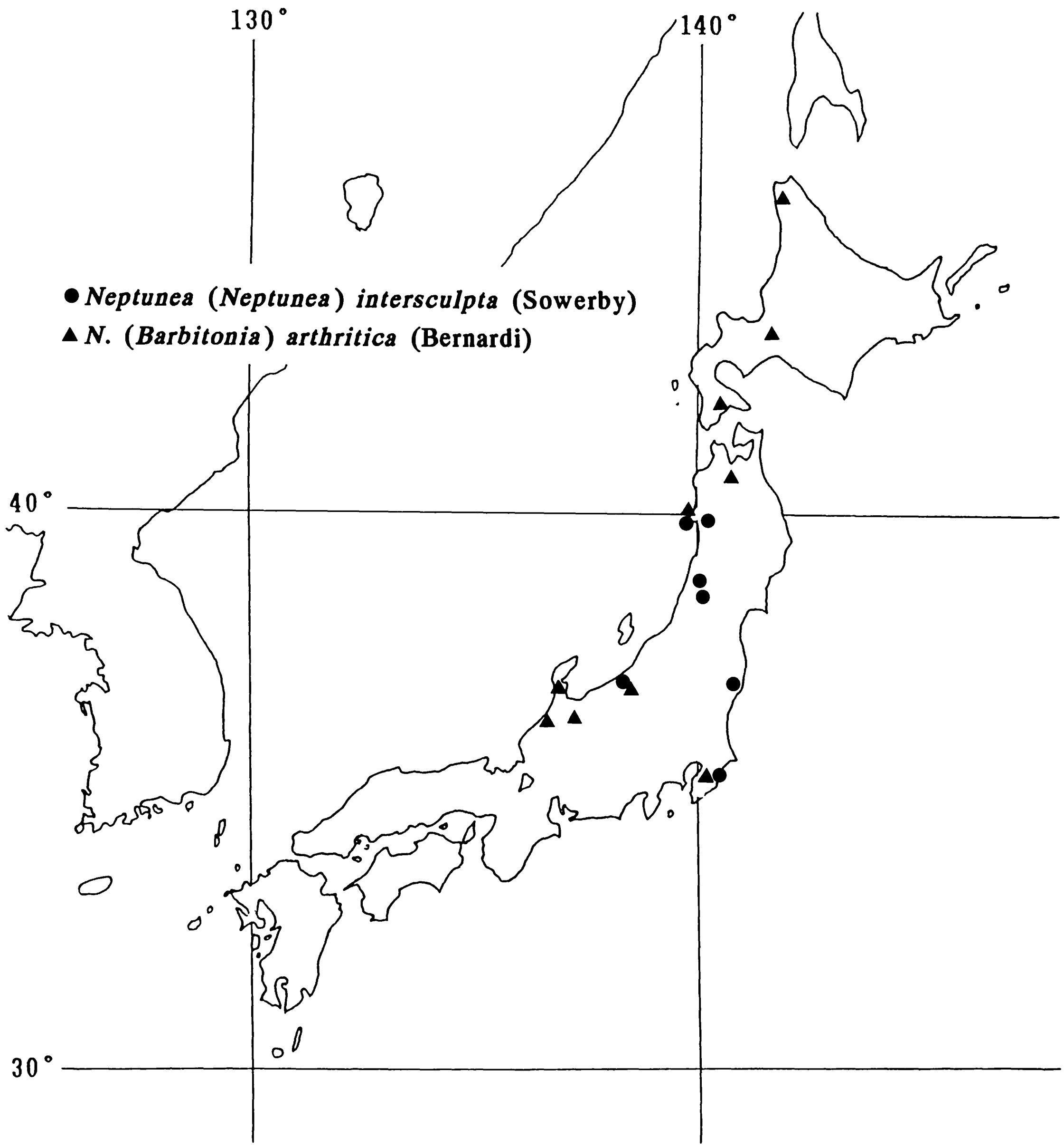

Figure 5. Distribution of two species of *Neptunea* from Plio-Pleistocene strata in Japan.

Nobuomi Matsuura of the Shiramine-mura Dinosaur Museum, Dr. Sadako Takeuch of the Saito Ho-on Kai Museum of Natural History, Mr. Teiji Sato of Murakami High School, and Mr. Tetsuya Tanaka of Joetsu University of Education for their help in examining some fossil specimens.

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1014 A new genus of shrew from the Pliocene of Yinan, Shandong Province, northern China

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Abstract. A large shrew mandible with pigmented teeth obtained from the Pliocene cave sediments of Yinan is referred to a new species of a new genus in the subfamily Soricinae, which is named *Lunanosorex lii*. This species belongs to the tribe Beremendiini of the subfamily. Comparisons with large shrews with pigmented teeth such as *Beremendia, Blarinoides* and *Shikamainosorex* indicate that *Lunanosorex* is clearly distinct from all the shrews. In north China, *Lunanosorex* appeared probably in the middle Pliocene as an indigenous genus, and seems to have been coexistent with *Beremendia* until it became extinct around the end of the Pliocene.

Key words: New genus, new species, *Lunanosorex*, shrew, Pliocene, north China

Introduction

In 1971, Pliocene cave sediments containing a large number of mammalian remains were found on the Qipanshan Hill near Xingtunzhi (=western hill of Shuangquan) in Yinan County (Figure 1). Of the remains, *Kowalskia* (cricetid rodent) and *Ursus* (bear) were subsequently studied (Zheng, 1984; Li, 1993), while others have remained undescribed. We therefore resumed systematic studies of these remains in order to elucidate the mammalian fauna of this locality, which was expected to provide important knowledge on the Pliocene mammalian fauna of north China. In the course of our study, we found that the remains contained an interesting large shrew mandible with pigmented teeth. This mandible shows unique characters which allow it to be referred to a new genus. In this paper, we describe the mandible in detail, and discuss its systematic position.

Geological setting

The sediments completely infill a fissure-like cave which is formed in Ordovician limestone. The plan of the cave is observable, because the ceiling of the cave has been removed. In plan, the cave has a northeast-southwest trend, and is about 15 m long and about 4.8 m in maximum width. The sediments are strongly cemented by carbonates into cemented breccia, sandstone and mudstone. Renewed excavations conducted in October and November 1987 reveal the following sequence in descending order (thickness shown in parenthesis):

Layer 1: Reddish brown breccia (110 cm)
Layer 2: Reddish brown breccia (87 cm)
Layer 3: Reddish brown muddy breccia (115 cm)
Layer 4: Reddish brown muddy breccia (140-170 cm)
Layer 5: Reddish brown muddy sandstone with breccia (50-100 cm)
Layer 6: Brown fine-grained sandstone with breccia (110-120 cm)
Layer 7: Reddish brown fine-grained sandstone (140 cm)
Layer 8: Reddish brown calcareous mudstone with breccia (30 cm)
Layer 9: Brown fine-grained sandstone (more than 30 cm)

The shrew mandible described below was obtained from Layer 6.

Terminology and measuring method

The terminology and measuring method follow those of Jin and Kawamura (1996). All the measurements have been taken with a measurescope (Nikon: MM-11) with an electric digital counter (Nikon: CM-65).

Systematic paleontology

Order Insectivora Bowdich, 1821
Family Soricidae Gray, 1821
Subfamily Soricinae Fischer von Waldheim, 1817
Tribe Beremendiini Reumer, 1984
Genus **Lunanosorex** gen. nov.

Type species.—*Lunanosorex lii* sp. nov., described below.

Name derivation.—Named after Lunan, an area name, meaning the southern part of Shandong Province, plus sorex (Latin) meaning shrew.

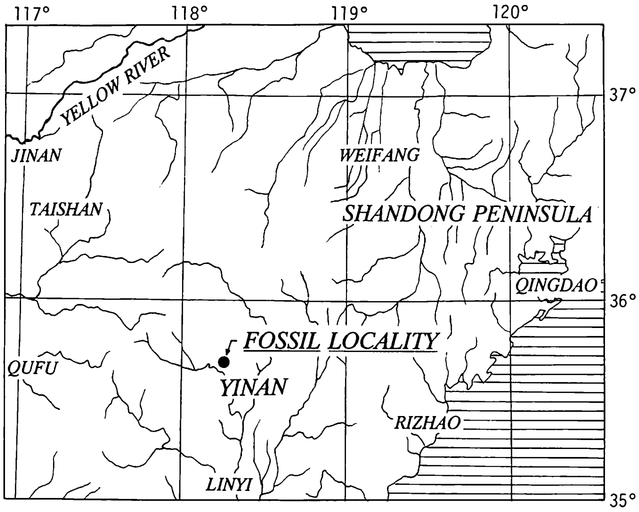

Figure 1. Index map showing the location of the fossil locality.

Diagnosis.—Large shrew with similarity to both *Beremendia* and *Blarinoides*; coronoid process longer and broader than that of *Beremendia*; this process not leaning anteriorly, but its apical part strongly protruding anteriorly; coronoid spicule and external temporal fossa well developed; upper pterygoid fossa indistinct; upper facet narrowly elliptical; interarticular area very broad and having lingual emargination; lower facet placed very anteriorly, and thus invisible in buccal view; internal temporal fossa deeply pocketed, and continuing to mandibular foramen through a small opening; dental formula 1-2-3 for lower teeth; teeth stained red to dark red; antemolars and molars having thick cingulum; P_4 with posterolingual basin; entoconid crest present in M_1.

Included species.—Monospecific, including *L. lii* only.

Geographic and geologic distribution.—Known only from the locality of Yinan; Late Pliocene.

Lunanosorex lii sp. nov.

Figures 2-6

Holotype.—A left mandible with a first lower incisor, A_1, P_4 and M_1 to M_3 (V10813), stored in the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica.

Referred specimen.—The holotype only.

Locality and geologic age.—Qipanshan Hill near Xingtunzhi in Yinan County, Shandong Province; Late Pliocene.

Name derivation.—Named in honor of Professor Li Chuankui, who has contributed to the studies on Cenozoic micromammals of China.

Diagnosis.—Same as for the genus.

Description.—The mandible is completely preserved except for the apical part of the angular process. All the teeth are, however, strongly worn, considerably reducing the height and pigmented area of the cusps and ridges.

Mandible: The horizontal ramus is stoutly built. It attains its maximum height below M_3 in buccal view, and below M_2 in lingual view (Figure 2). The mental foramen is a small opening in a shallow depression on the buccal face of the ramus, and is situated below the hypoflexid of M_1. The symphysis begins at the anterior tip of the ramus, and terminates below the posterior root of M_1. It is formed by two ridges and a deep groove between them. Of the two ridges, the upper one is more prominent. The groove opens only posteriorly, because the ridges are confluent anteriorly. The morphology of the ascending ramus is similar to that of *Blarinoides* in general. The coronoid process is longer and broader than that of *Beremendia* (Figure 3). This process leans greatly to the buccal side (Figure 4), but does not lean anteriorly. The apical part of the process markedly broadens in lateral and dorsal views owing to its remarkable anterior protrusion (Figure 3; 1A and Figure 5). The tip of the process is conspicuously thickened and forms a rounded smooth surface with a small depression on its posterior part. The coronoid spicule is very prominent, and extends diagonally on the buccal face of the coronoid process. The areas above and below the spicule are strongly excavated to form the external temporal fossa. The upper sigmoid notch is high in position, and is relatively shorter than that of *Beremendia*. It is somewhat emarginated ventrally (Figure 3; 1B). There is no pterygoid spicule. The upper pterygoid fossa is indistinct, and is much weaker than in *Beremendia* (Figure 3; 1C). The morphology of the condyle, however, resembles that of *Beremendia* (Figure 5; 2). The upper facet exhibits a narrow transverse elliptic shape. The interarticular area with lingual emargination is very broad, and diverges downward. Its buccal margin is rather straight. The lower facet is formed on the ventral face of the lower part of the condyle. In ventral view, its posterior margin is strongly emarginated as in *Beremendia* (Figure 5; 2). The lower part of the condyle greatly protrudes linguoventrally, and is placed greatly anteriorly (Figure 3; 1D), so that the lower facet cannot be seen from the buccal side (Figure 2A). The internal temporal fossa with an oval outline is very large and deeply pocketed. The mandibular foramen is large but relatively shallow, and extends anteriorly. Its inner wall is penetrated by a small opening which connects this foramen with the internal temporal fossa (Figure 3; 1E). The lower sigmoid notch is not remarkably emarginated as in *Beremendia* and *Blarinoides*. The lower pterygoid fossa forms a broad, shallow furrow extending from the mandibular foramen to the base of the angular process. A small boss is observed below this furrow (Figures 2B and 3).

First lower incisor: The tooth projects straight forward in dorsal view (Figure 6). Its apical part and cutting edge are considerably worn, so that their original shape cannot be observed. The apical part is stained red to dark red. A cingulum is observed along the buccal root-crown junction line. This junction makes an acute buccal angle, and extends to a point somewhat posterior to the posterior margin of P_4 (in *Beremendia*, it is rounded and ends below P_4). On the lingual face of the crown, there is neither cingulum nor longitudinal groove, but a low ridge extending from the tip of the crown to the junction line.

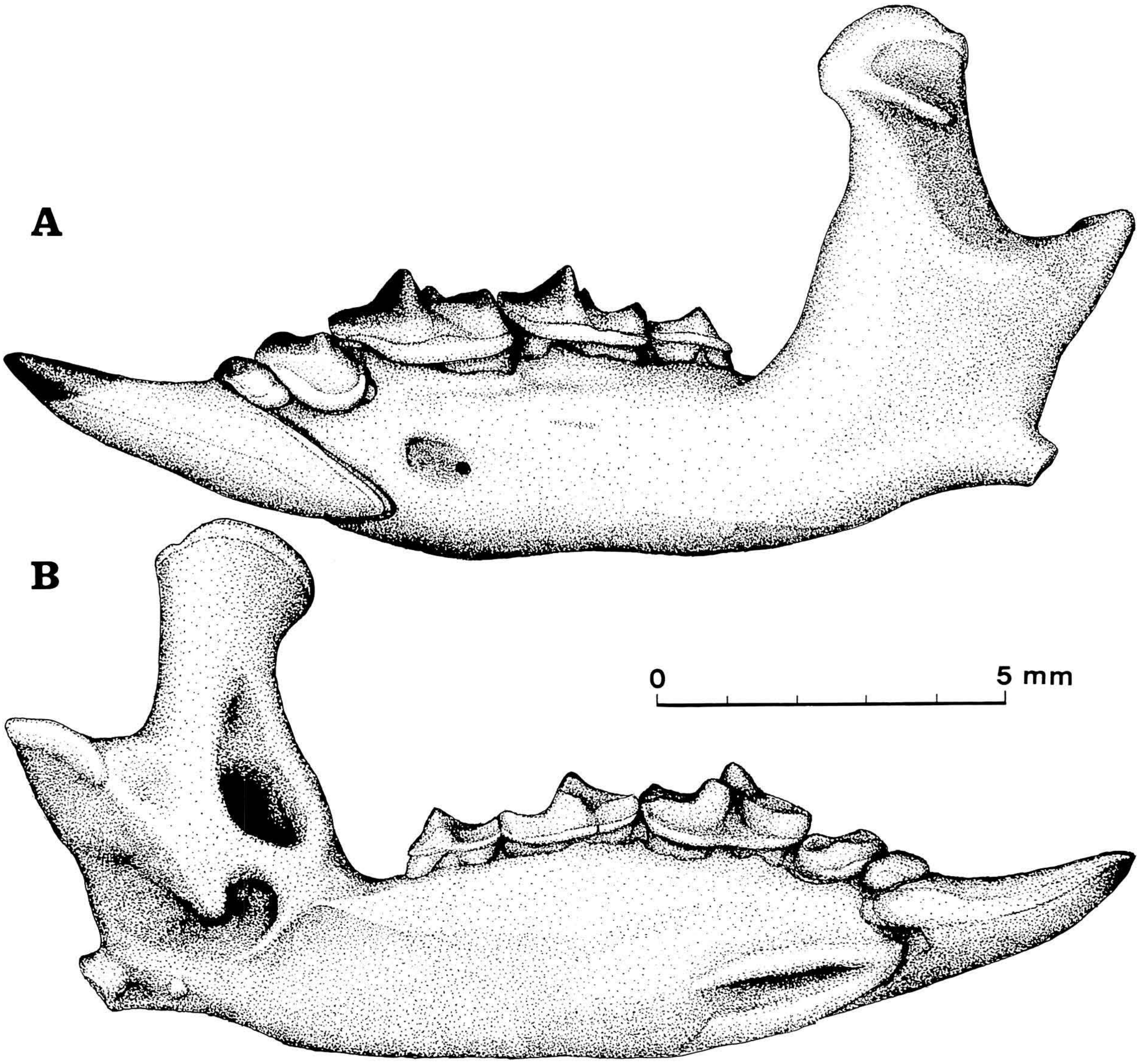

Figure 2. *Lunanosorex lii* gen. et sp. nov. Left mandible with the first lower incisor, A_1, P_4 and M_1 to M_3 (holotype : V10813). A : buccal view, B : lingual view.

A_1 : This tooth is single-cusped, and overlies the first lower incisor. The crown is rounded triangular in occlusal outline. The apical part of the cusp is stained red. A small depression probably corresponding to the posterolingual basin of P_4 is observed just behind the apex of the cusp. The buccal face of the crown protrudes posteroventrally, and has a marked thick cingulum. Another cingulum is present on the lingual face, but it is quite indistinct.

P_4 : The anterior part of this tooth overlaps on the posterior part of A_1. The basic structure, pigmentation and occlusal outline of the crown are roughly similar to those of A_1. The central constriction of the occlusal surface suggests that two cusps were originally positioned near to each other. The posterolingual basin is well developed to form a broad valley extending toward the posterolingual corner of the crown. The posteroventral protrusion of the buccal face of the crown is more developed than in A_1, so that the buccal face largely overhangs the mandible. A very thick cingulum occurs on this face, while the cingulum on the lingual face is thinner and less distinct.

M_1 and M_2 : The occlusal outline is trapezoidal. The ectolophid is stained red. The trigonid has nearly the same width as the talonid. The protoconid is placed somewhat anterior to the metaconid. The hypoflexid reaches the buccal cingulum. A ridge extending anterolingually from the hypoconid attaches to the posterior face of the protoconid. Another ridge extending lingually from the hypoconid is separated from the entoconid by a very narrow groove at the posterolingual corner of the crown. The entoconid crest is present in M_1. In M_2, however, it is unknown whether the

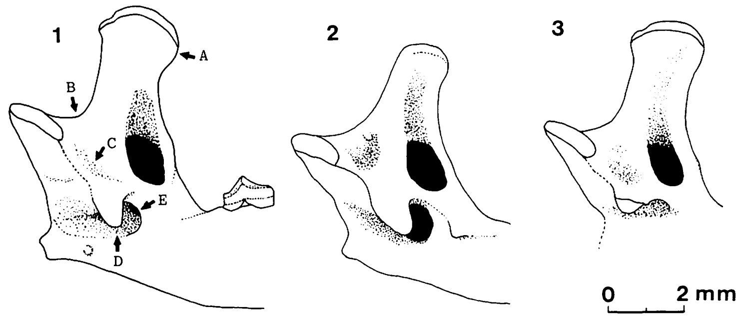

Figure 3. Simplified sketch illustrating the mandibular ascending rami in lingual view, comparing *Lunanosorex lii* gen. et sp. nov. (1), *Beremendia pohaiensis* from Haimao (2), and the shrew mandible from the Yushe Basin (3). **1** : V10813, (**A** : anterior protrusion of the apical part of the coronoid process, **B** : slight ventral emargination of the upper sigmoid notch, **C** : indistinct upper pterygoid fossa, **D** : anterior position of the lower part of the condyle, **E** : small opening on the inner wall of the mandibular foramen), **2** : DH8956, **3** : V8895, 4.

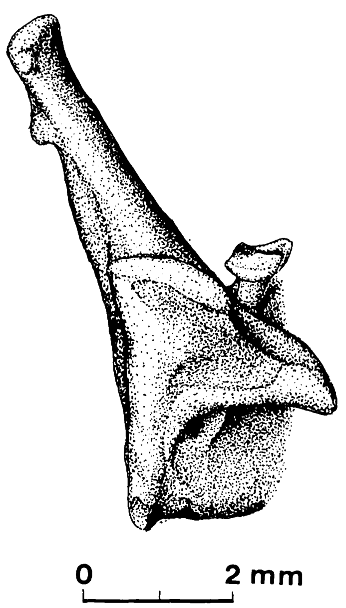

Figure 4. *Lunanosorex lii* gen. et sp. nov. Mandibular ascending ramus in posterior view (V10813).

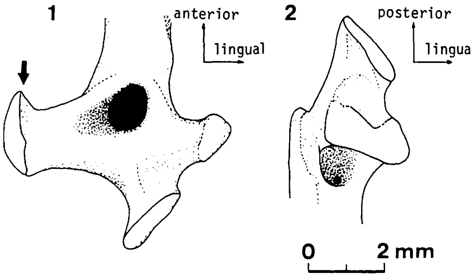

Figure 5. *Lunanosorex lii* gen. et sp. nov. Holotype (V10813). Simplified sketch illustrating the ascending ramus in dorsal view (1) and the condyle in ventral view (2). Arrow indicates the anterior protrusion of the apical part of the coronoid process.

crest is present or not owing to strong wear of the crown. The straight buccal cingulum is very thick and distinct. On the other hand, the lingual one is thinner, less distinct and slightly undulated.

M_3 : The trigonid is preserved, while the talonid is mostly absent, possibly due to wear. The protoconid is situated slightly anterior to the metaconid. As in M_1 and M_2, the buccal cingulum is thick and straight, while the lingual one is indistinct and slightly undulated.

Measurement.—

Length from the mental foramen to the uppermost point of the lower margin of the ascending ramus	7.54 mm
Height of the coronoid process	6.86 mm
Length of the upper facet	1.98 mm
Length from P_4 to M_2	5.83 mm
Length of the first lower incisor	5.86 mm
Length of A_1	1.12 mm
Width of A_1	1.00 mm
Length of P_4	1.83 mm
Width of P_4	1.35 mm
Length of M_1	2.67 mm
Trigonid width of M_1	1.81 mm
Talonid width of M_1	1.78 mm
Length of M_2	2.27 mm
Trigonid width of M_2	1.54 mm
Talonid width of M_2	1.49 mm
Trigonid width of M_3	0.98 mm

Systematic position.—This species has such characters as the internal temporal fossa deeply pocketed, the interarticular area emarginated lingually, and P_4 with posterolingual basin, which are diagnostic of the subfamily Soricinae. Reumer (1984) provided a revised key to subfamilies and tribes of the Soricidae in which he mainly followed the classification by Repenning (1967), but added a new idea to the tribal classification of the Soricinae. This key indicates that the present species belongs to his new tribe, Beremendiini, because it has a broad interarticular area of the

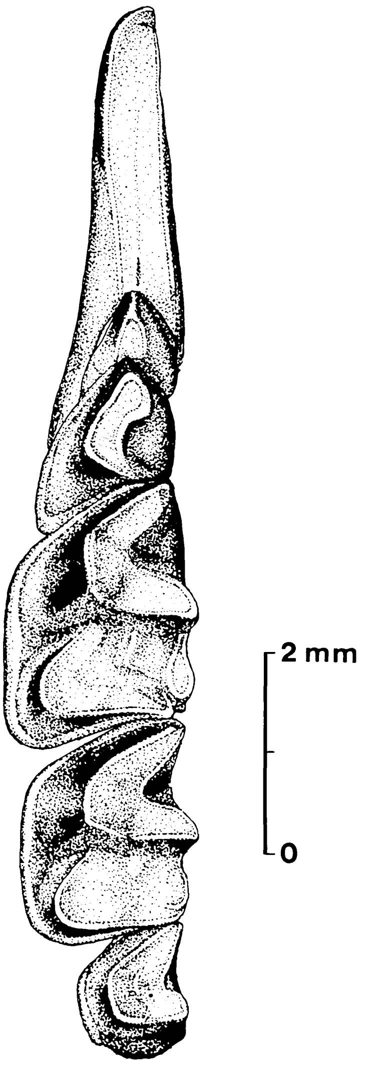

Figure 6. Left lower dentition of *Lunanosorex lii* gen. et sp. nov. Occlusal view of the dentition of the holotype (V10813).

condyle, and a lower facet strongly shifted anteriorly, as well as pigmented teeth and the entoconid crest on M_1. Reumer (1984) considered that the genus *Beremendia* is the only constituent of the tribe. In comparion with the known species of *Beremendia* (*B. pohaiensis*, *B. fissidens* and *B. minor*; see Jin and Kawamura, 1996), the present species differs in having a longer and broader coronoid process whose apical part strongly protrudes anteriorly, stronger coronoid spicule and external temporal fossa, and much weaker upper pterygoid fossa (Figure 3). These differences are considered to be sufficiently generic, because they are greater than those among the species of *Beremendia*. The present species is therefore referred to a second genus of Beremendiini, *Lunanosorex*, which is newly recognized here.

Comparison and discussion.—As already described in the diagnosis, *Lunanosorex* is a large shrew with pigmented teeth which shows similarity to both *Beremendia* and *Blarinoides*, but the differences from these genera are also distinct. Those from *Blarinoides* are exclusively described here, because those from *Beremendia* are mentioned above. *Blarinoides* differs in having a distinct pterygoid spicule, an upper pterygoid fossa strongly excavated, lingual emargination of the interarticular area slighter, P_4 with a unique tetrahedral shape and without a posterolingual basin, and M_1 without entoconid crest.

Two genera of large soricines with heavily pigmented teeth have been hitherto described from East Asia. They are "*Peisorex*" from the middle Pliocene and early Pleistocene of north China and *Shikamainosorex* from the middle and late Pleistocene of Japan. As already demonstrated by Jin and Kawamura (1996), the former is synonymous with *Beremendia*, and thus the same differences as those mentioned above are observed between "*Peisorex*" and *Lunanosorex*.

On the basis of the description by Rzebik-Kowalska and Hasegawa (1976) and the observation of comparative specimens (Y. Kawamura's collection), *Shikamainosorex* differs from *Lunanosorex* in having the tip of coronoid process not protruding anteriorly, shorter upper facet, lower incisor extending more posteriorly, A_1 larger relative to P_4, indistinct buccal cingula of A_1 and P_4, M_1 with a thicker buccal cingulum, and no entoconid crests in the lower molars.

The comparisons above indicate that *Lunanosorex* is easily distinguishable from *Blarinoides* and *Shikamainosorex* as well as from *Beremendia*. *Lunanosorex* is, however, similar to *Blarinoides* and *Shikamainosorex* in the general morphology of the ascending ramus, while it resembles *Beremendia* in the shape of the mandibular condyle and the presence of the entoconid crest in M_1. More complete materials including upper dentition are necessary to elucidate its affinity to other soricine genera.

Additionally, a mandibular ascending ramus recently described from the middle Pliocene in the Yushe Basin (V8895, 4; fig. 1 of Flynn and Wu, 1994) is very similar to *Lunanosorex* in having a long and broad coronoid process, strong coronoid spicule and external temporal fossa, although this specimen is somewhat smaller, the anterior protrusion of the apical part of its coronoid process is much weaker, and its upper pterygoid fossa is better developed than in *Lunanosorex* (Figure 3). Flynn and Wu (1994) did not determine its taxonomic position, probably because it is fragmentary. In our opinion, however, this specimen is possibly congeneric with *Lunanosorex*, or even conspecific with *L. lii*.

As regards the constituent genera of Beremendiini, *Beremendia* first appeared in the early Pliocene of Europe, but its ancestor is unknown in Europe (Reumer, 1984). Somewhat later in north China, *Lunanosorex* appeared, but its ancestor is also unknown as far as the pre-Pliocene fossil records of East Asia are concerned. It probably coexisted with *Beremendia* in the late Pliocene of north China. *Lunanosorex* seems to have become extinct before the beginning of the Pleistocene, while *Beremendia* survived until the early Pleistocene there.

Conclusions

The large shrew mandible with pigmented teeth from the Pliocene of Yinan is allocated to the tribe Beremendiini of the subfamily Soricinae. This tribe was previously considered to comprise only one genus, *Beremendia*. The mandible is referable to a new species of a new genus named *Lunanosorex lii*, because the differences between the mandible and that of *Beremendia* are sufficiently generic. *Lunanosorex* is, therefore, considered to be the second genus of the tribe. In addition to the comparison with *Beremendia*, it is compared with the large shrews, *Blarinoides* and *Shikamainosorex*, known from the Pliocene of Europe and the Pleistocene of Japan, respectively. *Lunanosorex* is easily distinguishable from these two genera, and its relative affinity to *Beremendia* is suggested. *Lunanosorex* inhabited north China together with *Beremendia* in the later part of the Pliocene, and possibly became extinct before the beginning of the Pleistocene.

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