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

Enamel microstructure of some fossil and extant murid rodents of India

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Abstract. Spatial arrangement of various enamel types (schmelzmuster) present in the incisors and molars of some fossil and extant murid rodents of India was studied from both the functional and phylogenetic points of view. Hunter-schreger bands (HSBs) along with radial enamel (RE) in mice molars have been found to occupy the entire height of the enamel crown (from the base to the top) on the anterior and the posterior portions. These HSBs tend to be horizontal around the base and inclined apically around the top. A clear distinction between the leading and the trailing edges of chewing surfaces based on the difference in the orientation of prisms has been observed in hypsodont murid molars. On the leading edges, the long axes of prisms originating from the enamel-dentine junction tend to be oriented towards the load, whereas those on the trailing edges turn away from the load. The schmelzmuster in molars of *Mus*, indicate an omnivorous diet, whereas that in *Golunda, Millardia,* and *Bandicota* points to adaptation for an abrasive diet. The Indian bandicoot rat (*Bandicota*) with its large, hypsodont molars has developed horizontally oriented (relative to the occlusal surface) HSBs at the base of the enamel crown. These HSBs have been found in enamel layers oriented both almost parallel and perpendicular to the occlusal surface, an observation that corroborates the presence of horizontal tension at the base of the tooth due to vertical load on the occlusal surface. In the light of the observations made here, a model depicting changes in schmelzmuster in murid rodents through Late Miocene and Plio-Pleistocene times is suggested.

Key words: enamel microstructure, functional morphology, India, Muridae, phylogeny, rodent

Introduction

The enamel microstructure can be studied at various hierarchical levels (Koenigswald and Clemens, 1992; Carlson, 1990). Dental enamel in all mammals is made up of hydroxyapatite '*crystallites*'. These fiber-like crystallites are arranged almost parallel to each other to form bundles called '*prisms*' and these in turn are surrounded by an '*interprismatic matrix*' (IPM) which is also made up of crystallites (Wahlert and Koenigswald, 1985). The crystallites of IPM may or may not run parallel to the prism they surround (Martin, 1990). Because of the difference in the orientation of prism and interprismatic crystallites, distinct prism boundaries called as '*prism sheathes*' are formed. The path of a prism can be traced from the enamel-dentine junction (EDJ), through the entire thickness of the enamel, terminating at the outer surface. '*Enamel types*' are defined by the spatial arrangement of groups of prisms. The part of the enamel in which prisms run parallel to each other is termed '*radial enamel*' (RE) (Koenigswald, 1977). In many mammals, prisms are arranged in layers or zones, and when prisms of alternate layers run in different directions, a decussating structure is produced called '*Hunter-Schreger bands*' (HSBs) (Korvenkontio, 1934). Complexly interwoven bundles of prisms that are not arranged in discrete layers are called '*irregular enamel*' (Koenigswald and Clemens, 1992; Koenigswald, 1997) and prisms with a strong lateral deviation relative to the enamel surface are termed '*tangential enamel*' (Koenigswald, 1977). The three-dimensional arrangement of different enamel types within a tooth define its '*schmelzmuster*' (Koenigswald, 1980) and the variation of schmelzmuster from tooth to tooth defines the '*dentition*' level of the enamel microstructure hierarchy.

The enamel microstructure of rodent incisors is quite different from that of their molars due to their special functional requirements (Koenigswald *et al.*, 1987, 1994). Rodent incisors are ever-growing, and their main function is to cut and dig. In the majority of rodents, incisor enamel, which covers only the labial portion, is made up of outer radial enamel and inner HSBs oriented transversely to the long axis. Usually HSBs occupy at least 50% of the

enamel thickness of rodent incisors, but in murid and many caviomorph rodents HSBs can occupy up to 80% (Martin, 1992). The thickness of individual bands of prisms also differs among taxa. A uniserial HSB is 1-2 prism thick, pauciserial 2-4 prisms thick, and multiserial more than 4 prisms thick (Korvenkontio, 1934; Martin, 1993). Murid rodents have only uniserial HSBs.

The main objectives of the present work are 1) to document the complexity of the enamel microstructure in some of the Plio-Pleistocene murids and their extant counterparts collected from India, and 2) to trace the functional adaptation back in time based on comparison of fossil and Recent forms. There are certain morphological characters (such as hypsodonty, relative width of molars and orientation of transverse crests) in murid molars which can be correlated with a grazing diet (Crabb, 1976; Meulen and Musser, 1999). This grazing property of mammalian molars is also reflected at the enamel microstructure level (Rensberger, 1973 1975; Pfretzchner, 1994; Janis, 1988; Fortelius, 1985; Weijs, 1994). Therefore, an attempt has been made here to discover the dietary adaptations (grazing or browsing) of extinct murids from their schmelzmuster, a determination which has important implications for palaeoclimatic reconstruction.

Material and methods

Specimens examined include fossil and Recent murid rodents housed at the Vertebrate Palaeontology Laboratory, Centre of Advanced Study in Geology, Panjab University, Chandigarh, India; around one hundred Recent mice specimens were provided by T. Sharma, BHU, Varanasi, India and *Megacricetodon* specimens were provided by T. Bolliger, Palaeontological Institute, Zurich.

Genus: *Mus*. Species: *M. booduga, M. dunni, M. musculus musculus, M. m. domesticus, M. m. tytelri, M. saxicola. M. flynni, M. linnaeusi and Mus* sp. Material: Upper and lower first left molars and incisors of *M. m. tytelri* (specimen numbers HMD-13, 12, 5, 10, 6, 9, MMt - 1&4); *M. m. musculus* (MMC1, 2, 3 from Czechoslovakia, Mdwsb 4, 5 WSB strain European, HMV-4, 6 from Varanasi); *M. musculus bactrianus* (JP-2, 3, 4 house mouse from Jodhpur); *M. m. casteneus* (NKM-20 from Kathmandu, Nepal; HMNG-2, house mouse from Narpat Ganj, HMMD, from Madras, HMMM-3 from Mysore, HMGW-1, 3, 8, 9, HMGI-1, 3 from Gangtok wild and indoors respectively); *M. booduga/ M. dunni* (MBV-1, 2, 3 from Varanasi MBY-1, 3, 4 from Mysore, MDV3, 1-Type I, MDM5, 6-Type II, MDM1, 3-Type III); *M. saxicola* (upper molar and lower incisor, MS-33); *M. flynni* (upper and lower incisors and first molars, MFI-1, 2, MFM-1, 2,SM-6, 25, Late Pliocene Siwaliks around 2.5 m.y.); *M. linnaeusi* (lower jaw,
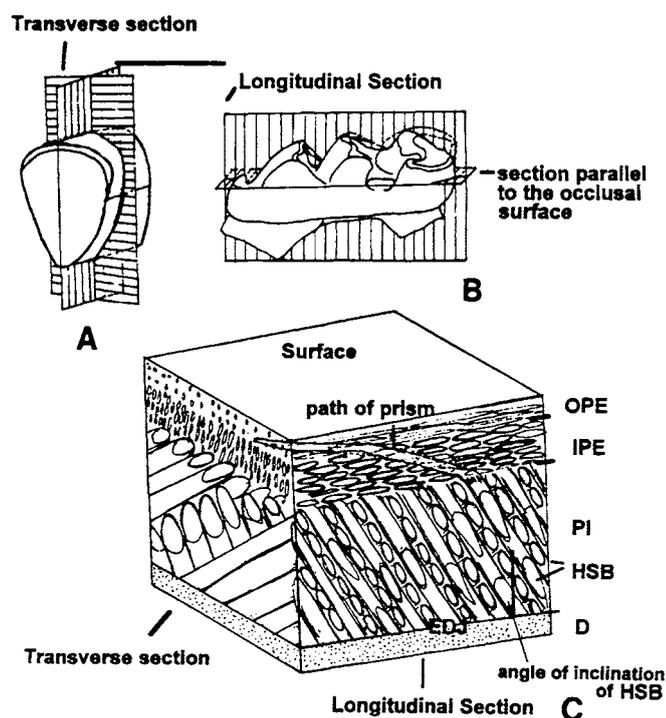
Figure 1. Schematic diagram showing sections in this study. A. Transverse and longitudinal sections of incisor. B. Longitudinal section and section parallel to occlusal surface of molar. C. Model of incisor enamel microstructure showing prism orientation. Abbreviations: D = dentine; EDJ = enamel dentine junction; HSB = Hunter-Schreger bands; PI = portio interna; OPE = outer portio externa; IPE = inner portio externa. PI with HSBs (portio interna with Hunter-Schreger bands) and angle of inclination of HSBs.

VPL/RP-GII, 2 m.y.); *Mus* sp. (upper and lower incisors (MS-1, 2).

Genus: *Bandicota*. Species: *B*. sp. cf. *B. bengalensis, B. indica, B. sivalensis*. Material: *B*. sp. cf. *B. bengalensis* incisors from Pleistocene Narmada valley deposits. *B. sivalensis* upper jaw (VPL/RP-SM-78) from Tatrot Formation (Late Pliocene). *B. indica* (extant form).

Genus: *Golunda*. Species: *G. tatroticus, G. kelleri, G.* sp., *G. ellioti*. Material: Upper and lower incisors and second lower molar (VPL/RP-M2A).

Genus: *Millardia*. Species: *M. meltada* (extant), cf. *Millardia*. Material: Incisors and molars of the Recent form and those collected from Late Pliocene Siwalik deposits.

Genus: *Parapelomys*. Species: *Parapelomys robertsi*. Material: Lower jaw (VPL/RP-SM-58, Late Pliocene Siwalik deposits). A cricetid, *Megacricetodon gregarius* (15-13 m.y.) from La Grive (France). Fifteen to 20 specimens (including molars and incisors) of each extant species mentioned were studied. In the case of fossil taxa, only a few specimens (2 to 5) were used in the present study.

Isolated fossil incisors were identified by comparisons
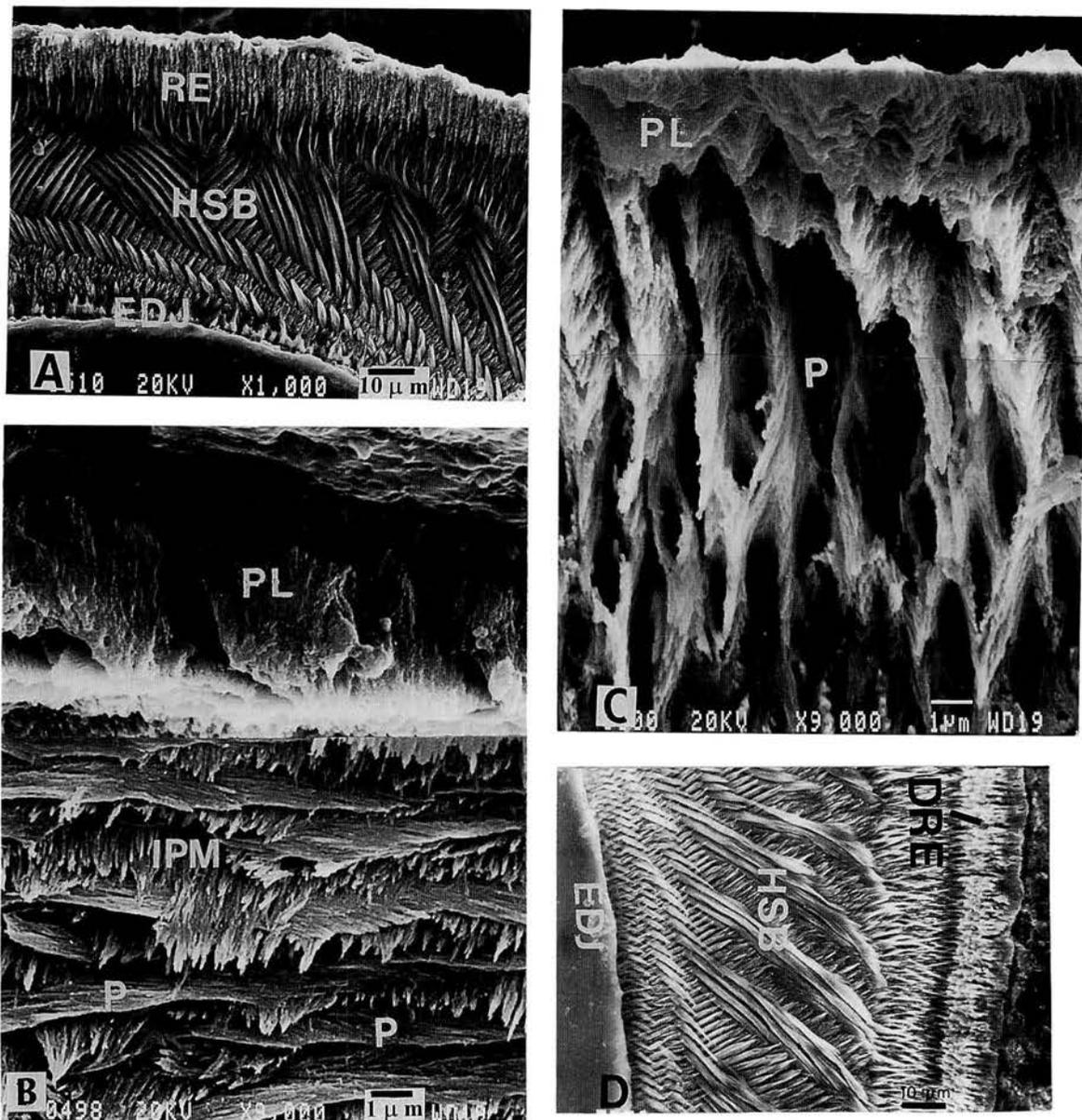
Figure 2. Enamel microstructure in the incisors of some extant *Mus*. **A.** Transverse section of upper incisor of *Mus musculus tytelri*. **B.** Longitudinal section of upper incisor (tip on left-hand side) of *Mus musculus tytelri* showing only part of radial enamel. **C.** Outer radial enamel of upper incisor of *Mus musculus tytelri* in transverse section. **D.** Transverse section of upper incisor of *Mus (Pyromys) saxicola*. Abbreviations: PL = plex; P = prism; IPM = interprismatic matrix; other abbreviations as same as in Figure 1.

with those of their closest extant relatives. For enamel microstructure studies, the molars and incisors were embedded in polyester resin. Based on the area of investigation, sections (longitudinal, transverse, tangential and sections parallel to the occlusal surface of the dentition) were made (Figure 1) and studied both under stereoscopic and scanning electron microscopes. Some of the molars were sectioned parallel to the occlusal surface at particular (approximately 0.25–0.5 mm) intervals of depth (serial sectioning method) for mapping of the schmelzmuster (spatial

arrangement of various enamel types in the whole tooth). In order to view the same part of the enamel of the same molar position of different *Mus* species, all the teeth were aligned and oriented inside one slab of polyester resin and sectioned at the same depth. Sections were polished and etched with mild acid, 5% HCl. Mapping of enamel types was carried out initially by using a light microscope and later the polished surfaces were coated with gold in order to study them under the scanning electron microscope (SEM). The scheme proposed by Koenigswald and Clemens (1992)
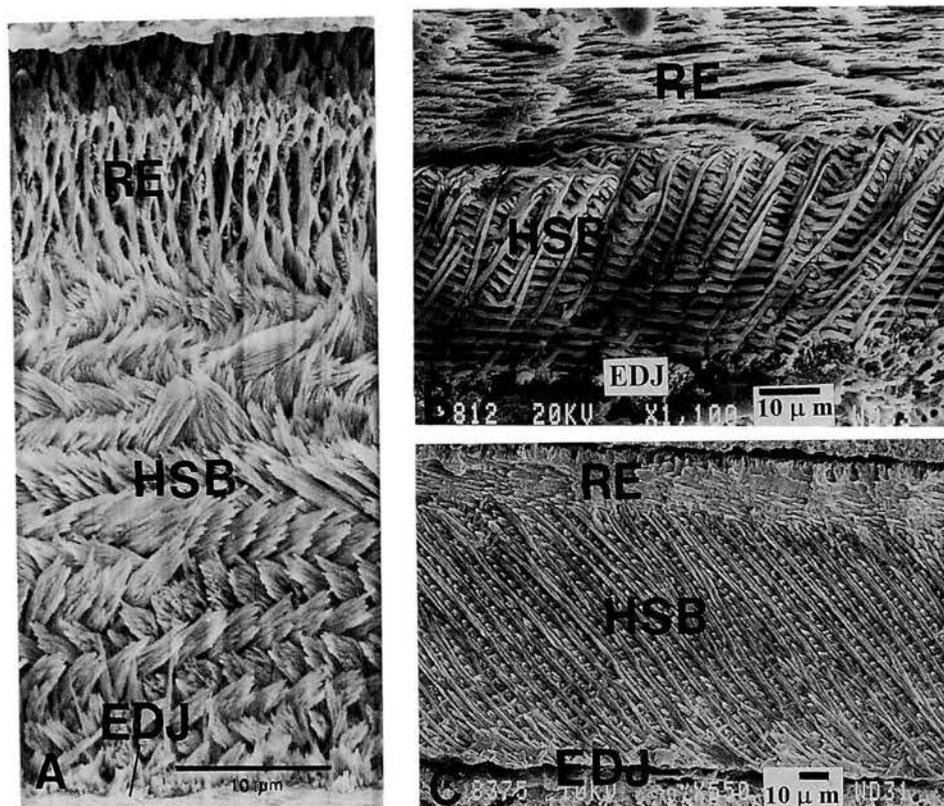
Figure 3. Enamel microstructure in incisors of some fossil *Mus*. **A.** Transverse section of upper incisor of *Mus flynni* (from Late Pliocene Siwalik sediments). **B.** Longitudinal section of upper incisor (tip on right-hand side) of *Mus flynni*. **C.** Longitudinal section of lower incisor (tip on left-hand side) of *Mus flynni*. Abbreviations as same as in Figures 1 and 2.

to study enamel microstructure including various structural complexities and murid dental terminology proposed by Jacobs (1978) has been followed here.

Observations

Upper incisors of all the *Mus* species studied, including the fossil specimens in transverse section, contain uniserial HSBs (portio interna or inner enamel) that are apically inclined and occupy more than 70% of the total thickness of the enamel layer. The typical uniserial HSBs are arranged transversely to the long axis of the incisor. Outer enamel (portio externa) is divided into two parts: an inner part of radial enamel consisting of apically oriented prisms and vertical IPM, and an outer part consisting of dense prisms and IPM (etched prismless external layer or PLEX) (Figure 2A-D). This differentiation of the portio externa is not found on fossil upper and lower incisors, where the portio externa consists only of radial enamel (Figure 3A–C). Prisms have a lensoid shape in cross section. Crystallites of interprismatic matrix (IPM) run perpendicular to those of prisms, providing a strong interlocking system (Figure 2B).

HSBs (portio interna) on lower incisors occupy a greater portion of the enamel and are inclined less steeply than those on the upper incisors. Therefore, in transverse section more bands are encountered on the lower incisors.

On the upper and lower molars of mice, the occlusal surface is covered by occlusally oriented prisms of radial enamel (Figure 4A, B). On leading edges of cusps, these prisms converge with their long axis pointing towards the cutting edge (Figures 5, 6D, 7). On trailing edges, radial enamel with interrow sheets emerges from the EDJ with prisms oriented towards the cutting edge. Often in sections parallel to the occlusal surface or on slightly ground lower molars, HSBs emerging from the EDJ are inclined towards the occlusal surface (Figures 4, 6D, E). As we move towards the base of the molar, they tend to become horizontal and parallel to the occlusal surface (Figures 4, 7A, C, D). At the very base, the HSBs occupy almost the total thickness of the enamel running from the EDJ to the outer part (Figure 7C). Prisms of alternate bands decussate at a high angle and crystallites of IPM are at right angles to those of the prisms (Figure 6E). This layer is followed by radial enamel containing prisms oriented

Figure 4.   Schematic diagrams showing sections of first upper and lower molars of *Mus musculus*. A. Occlusion of first upper and lower molars of *Mus musculus* showing prism orientation. B. Model showing prism orientation at tip and base of anterior most cusp on first lower molar.
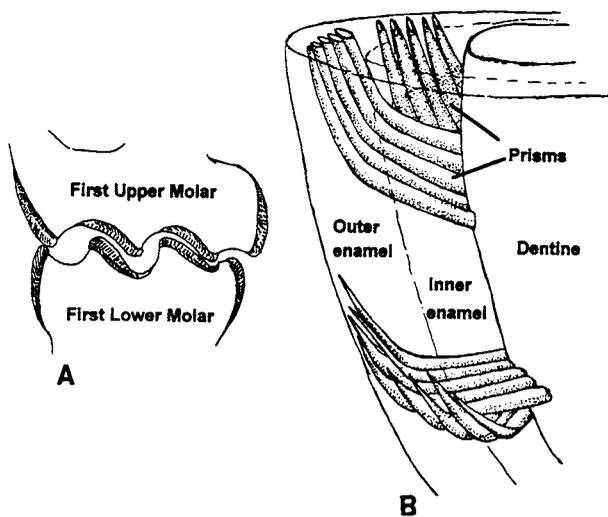

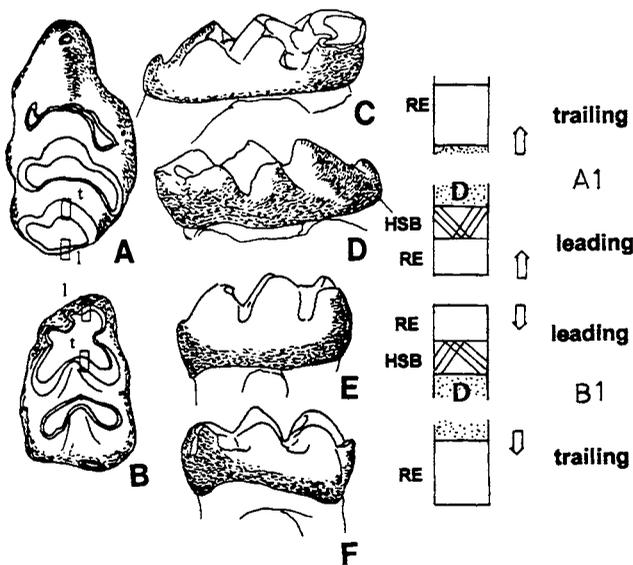Figure 5.   Schematic diagrams of *Mus musculus* first upper and first lower molars. A, occlusal; C, labial; D, lingual views of first upper molar and B, occlusal; E, labial; F, lingual views of first lower molar of *Mus musculus* with approximate distribution of HSBs. Blowups of A (A1) and B (B1) showing differentiation of leading and trailing edge. Arrows indicating load direction. Abbreviation same as in Figures 1 and 2.

occlusally.   In longitudinal sections of upper and lower molars, the HSBs run from the base to the tip of the anterior and posteriormost cusps, a structure similar to that seen on incisors (Figures 6A, 7C, D).   These horizontal HSBs are also found on the labial and lingual walls but are con-

centrated around the roots.   Therefore, HSBs cover the anterior, posterior and lingual sides of the upper first molars where major roots are found (Figure 5).   Enamel on transverse cusps apart from the anterior ones (anterostyle, lingual and labial anterocones on the upper first molars and labial and lingual anteroconids on the lower first molars) and posterior ones (hypocone and metacone on the upper molars and posterior cingulum on the lower) lack HSBs (Figures 6A, B, F, 7B).   Where a prestyle is present on the lingual anterocone, HSBs are developed on it, running perpendicular to the cusp axis away from the EDJ (Figure 6C).

Upper and lower molars of fossil mice (Pliocene, Siwaliks) also show HSBs running from the root to the crown (Figure 8A-G).   At the base of the tooth these HSBs are horizontal, but near the cap they incline occlusally.   In *Megacricetodon gregarius* (from the Middle Miocene deposits of Switzerland) the HSBs occupy more than half (from the root-crown junction) of the upper molar crown (Figure 8H).

In *Bandicota* sp. cf. *B. bengalensis*, the longitudinal section of the upper incisor shows uniserial HSBs inclined apically at an angle of around 40°.   The crystallites of IPM are at right angles to those of the prisms.   The prisms of alternate bands decussate at an angle less than 90°.   At the EDJ, the IPM crystallites run vertically (relative to the EDJ) and then they change course to run perpendicular to the prisms.   At the outer enamel, the crystallites of IPM again become almost vertical as the prisms bend apically.   The outer radial enamel is around 25% of the total thickness (Figure 9A).   The HSBs of lower incisors are inclined at around 45° to the long axis of the tooth.   Prisms of alternating bands decussate very strongly (around 90°).   Crystallites of IPM are at a right angle to those of the prisms.   The outer radial enamel occupies only 15% of the total thickness.   IPM crystallites of the outer enamel run vertically.   Prisms of the radial enamel in the lower incisors have a higher inclination towards the outer surface than those of the upper incisors (Figure 10).

On the molars of extant species of *Bandicota*, except for the very minor portion of the base, the entire enamel, including the grinding edges of the occlusal surface, is composed of radial enamel.   At the base of the anterior portion the enamel curves beneath the molar and becomes almost parallel to the occlusal surface (Figure 11A).   In contrast to incisors, where the outer layer consists of radial enamel and the inner layer of HSB, here the outer enamel contains HSBs and the inner enamel is radial which is modified and appears similar to an interrow sheet (layers of IPM between rows of prisms) (Figure 11B, C).   A small portion of the enamel at the base on the posterior margin, which is vertically oriented (relative to the occlusal surface), is also occupied by HSBs (Figure 11E).   In the first lower molar the leading and trailing edge differentiation is quite clear
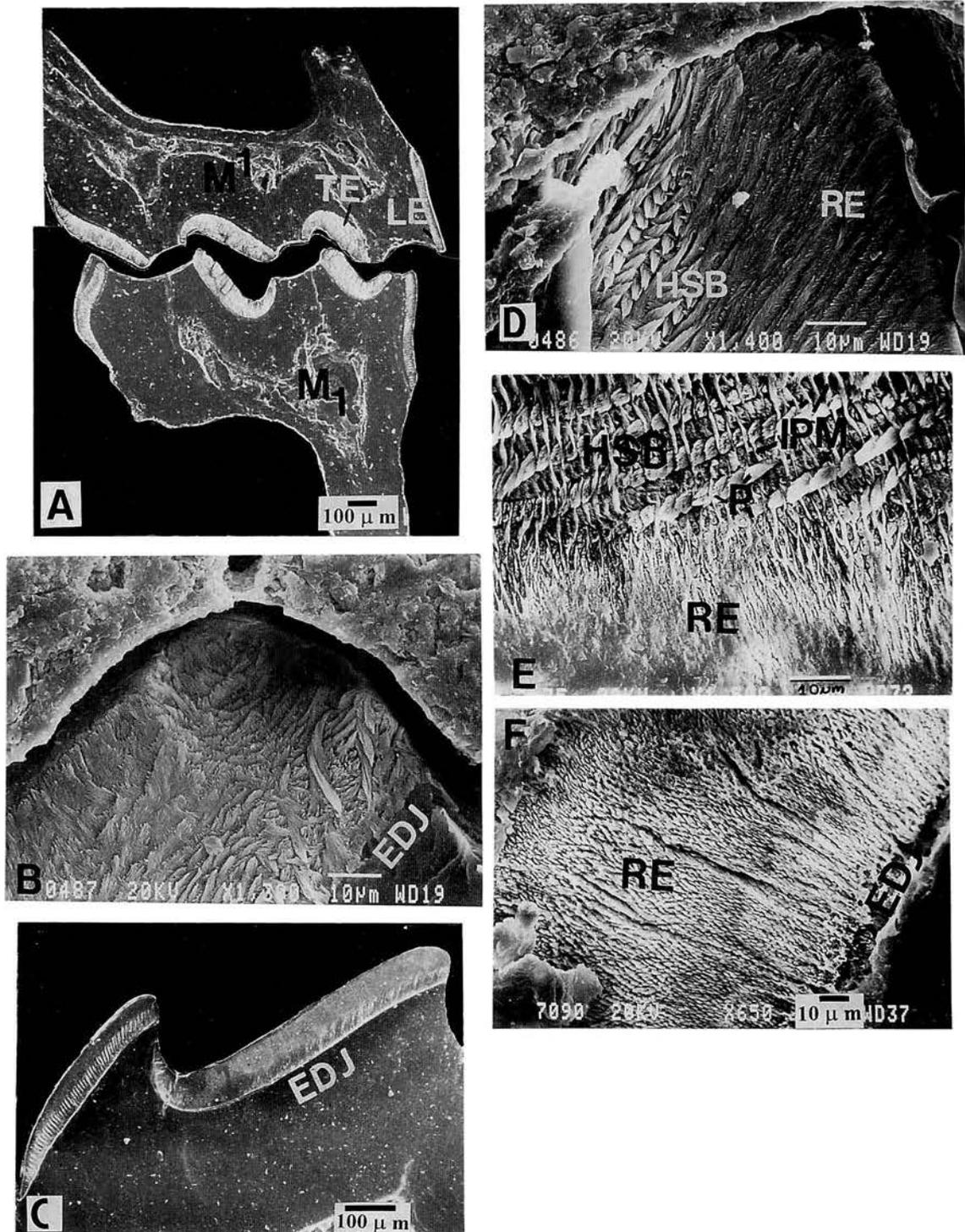
Figure 6.   Enamel microstructure in molars of some extant *Mus.*   **A**. Longitudinal sections of first upper (M¹) and lower (M₁) molars of *Mus musculus tytelri*.   **B**. Trailing edge in longitudinal section of first upper molar of *Mus musculus tytelri* (another specimen).   **C**. Longitudinal section of first upper molar of *Mus saxicola* showing prestyle and lingual anterocone.   **D**. Longitudinal section of first upper molar of *Mus musculus tytelri* showing leading edge.   **E**. Section parallel to occlusal surface of first upper molar of *Mus musculus tytelri*, showing leading edge.   **F**. Section parallel to occlusal surface of first upper molar of *Mus musculus tytelri*, showing trailing edge.   Abbreviations same as in Figures 1 and 2.
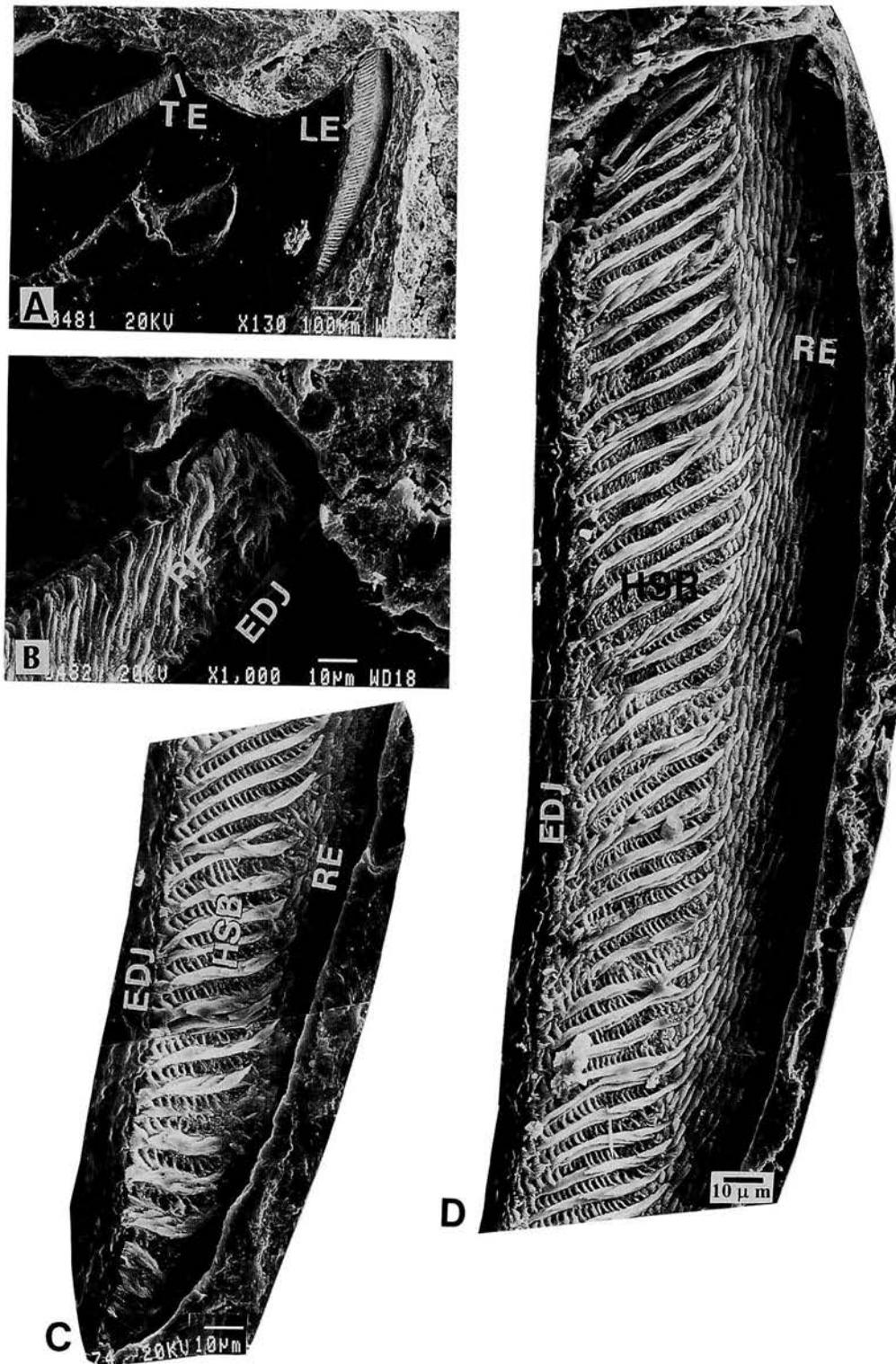
Figure 7. Enamel microstructure in first lower molars of *Mus musculus tytelri*. **A**. Longitudinal sections showing anterior part. **B**. Trailing edge in longitudinal section (magnified portion of **A**). **C**. Lower part of leading edge in longitudinal section (magnified portion of **A**). **D**. Upper part of leading edge in longitudinal section (magnified portion of **A**). Abbreviations same as in Figures 1 and 2.
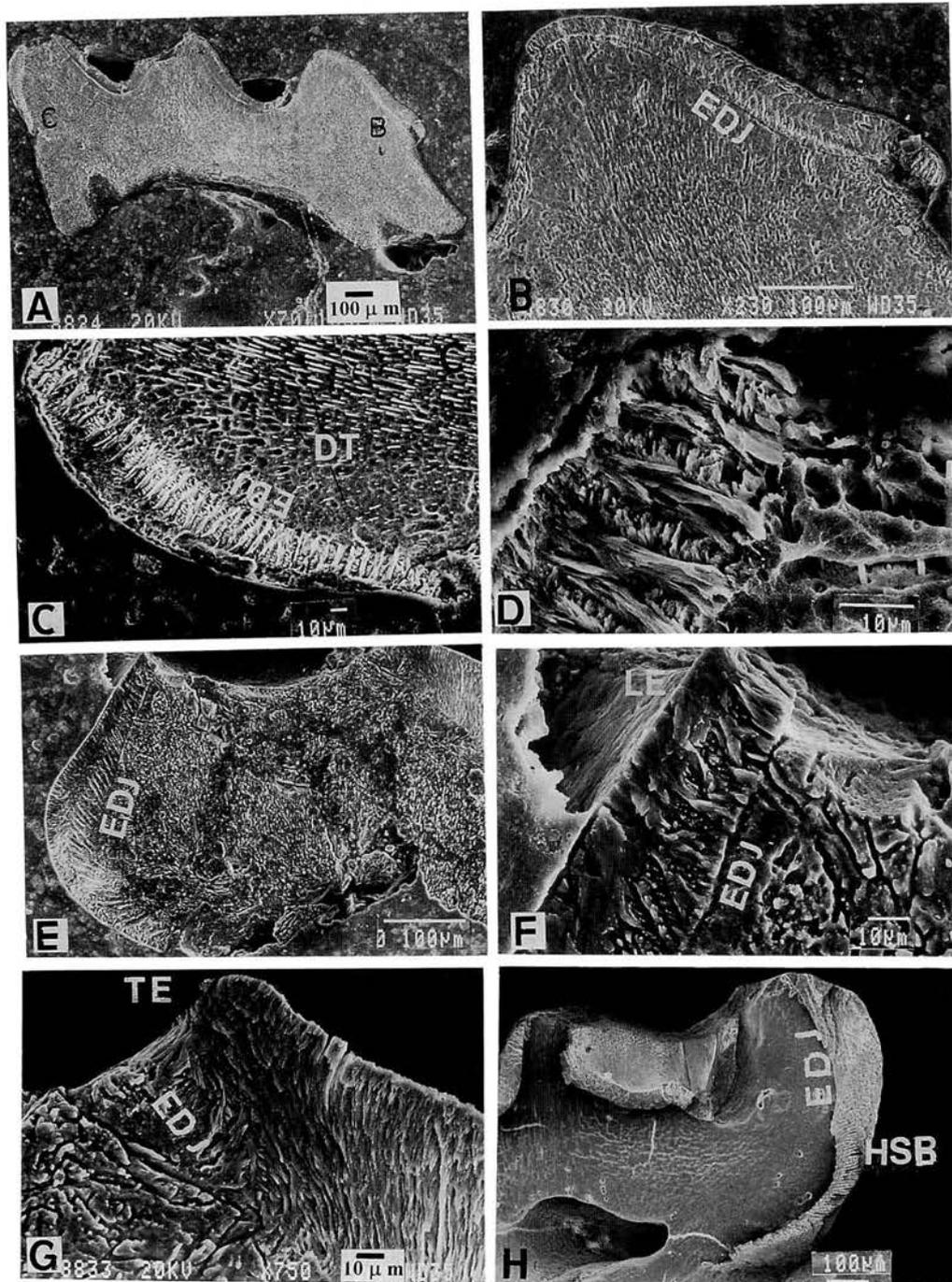
Figure 8. Enamel microstructure in molars of some fossil muroid rodents.   **A–G.** *Mus flynni* (from Pliocene Siwalik deposits of India).
A. Longitudinal section of first upper molar of *Mus flynni*.   **B.** Anterior part of first upper molar in longitudinal section (magnified portion of **A**, in-
dicated by **B** on **A**).   **C.** Posterior part of first upper molar in longitudinal section (magnified portion of **A**, indicated by **C** on **A**).   **D.** Tip of posterior
part of first upper molar in longitudinal section (magnified portion of **C**).   **E.** Anterior part of first lower molar in longitudinal section.   **F.** Tip of
leading edge in longitudinal section (magnified portion of **E**).   **G.** Tip of trailing edge in longitudinal section (magnified portion of **E**).
H. *Megacricetodon gregarious* (from Miocene deposits at La Grive, France).   Oblique section (parallel to probable jaw movement direction) of first
upper molar of *Megacricetodon gregarius*. Abbreviations same as in Figures 1 and 2.
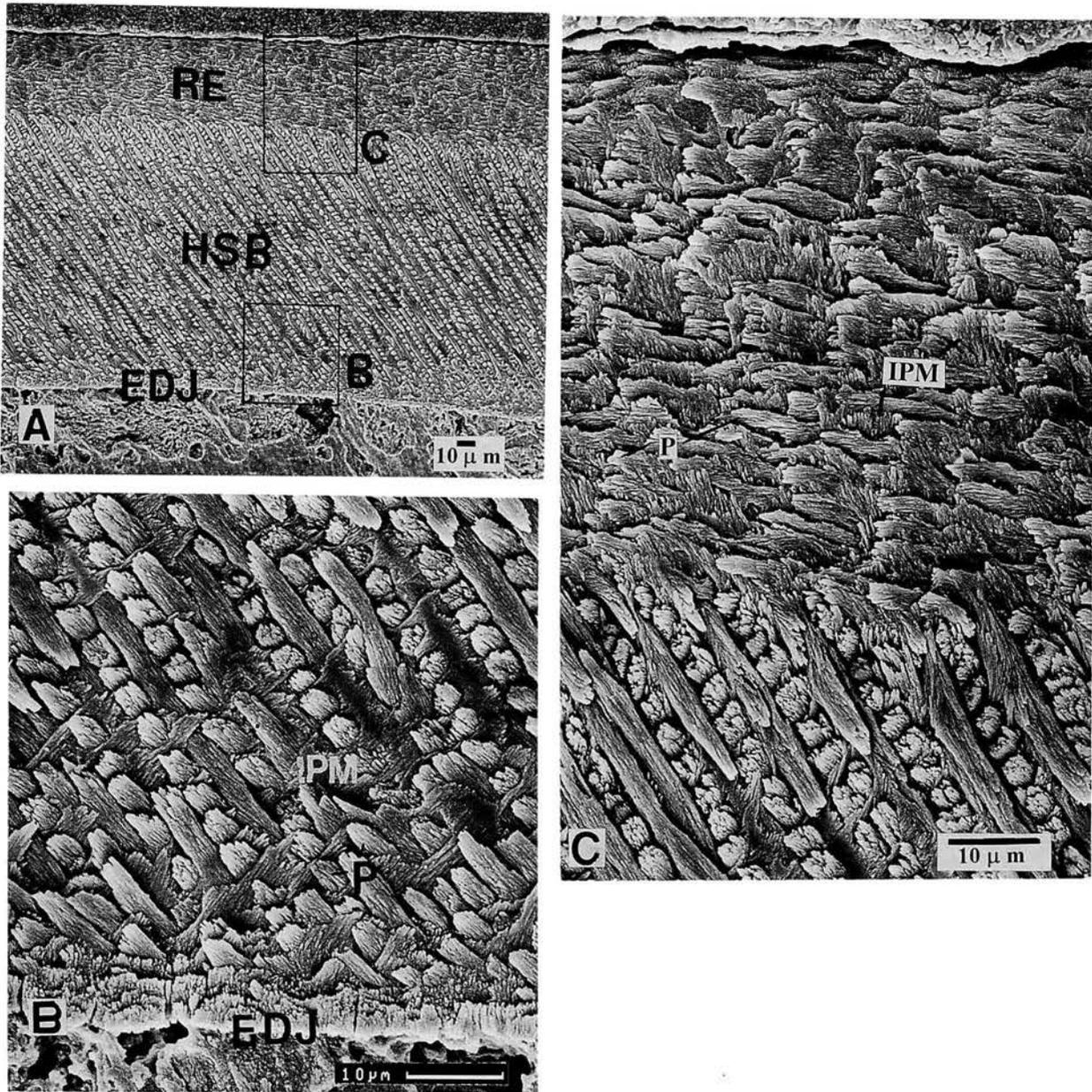
Figure 9. Enamel microstructure in upper incisor of *Bandicota* sp. cf. *B. bengalensis* (Upper Pleistocene, Narmada Valley). **A.** Longitudinal section of upper incisor (tip on left-hand side). **B** and **C.** Close-up of lower and upper parts of longitudinal section. Abbreviations same as in Figures 1 and 2.

(Figure 11F, G). Here the prisms in the leading edge originating from the EDJ initially bend forward (their c-axis) occlusally and later turn in the same direction as the load (Figure 11F). Those in the trailing edge run away from the load occlusally (towards the worn surface, Figure 11G). All the species of *Bandicota* studied here show similar patterns.

Upper incisors of *Golunda kelleri* and *G. tatroticus* (fos-sils) have thick outer enamel (radial enamel) occupying around 30% of the total thickness of enamel (Figure 12A, B). The transversely arranged HSBs are inclined apically by 25°. Prisms of alternate bands decussate at right angles, and the crystallites of IPM are at right angles to the prisms in the third dimension (Figure 12E). HSBs on lower incisors have an inclination of around 35° (Figure 12F).
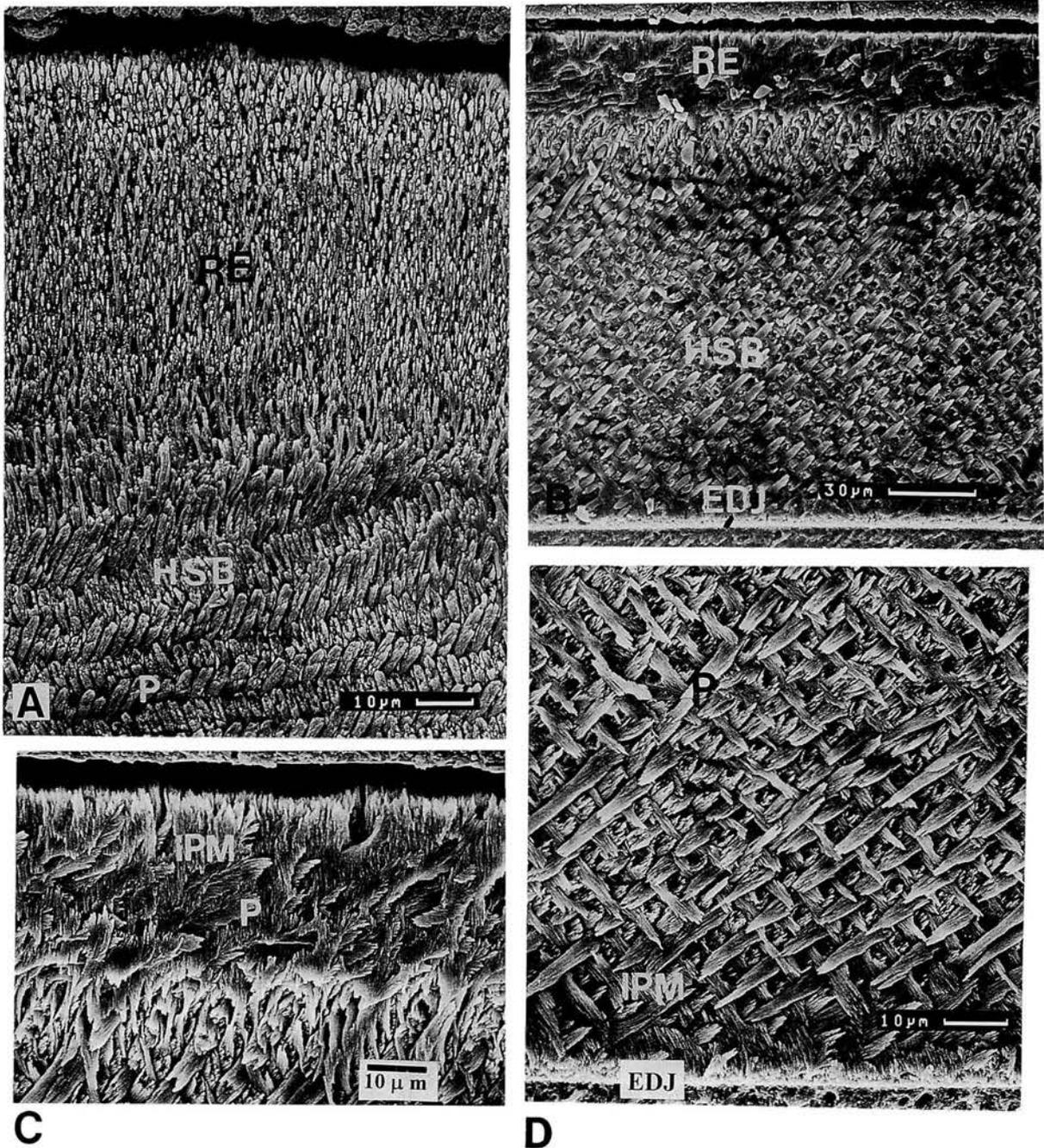
Figure 10.   Enamel microstructure in incisors of *Bandicota* sp. cf. *B. bengalensis* (Upper Pleistocene Narmada Valley).   **A.** Transverse section of upper incisor.   **B.** Longitudinal section of lower incisor (tip on right-hand side).   **C** and **D.** Upper and lower parts of longitudinal section, close-up of **A** and **B**, respectively.   Abbreviations same as in Figures 1 and 2.

Serial sectioning parallel to the occlusal surface on a *G. tatroticus* lower second molar reveals the differentiation of the schmelzmuster at different levels.   Slight grinding and etching led to the exposure of the metaconid, which shows presence of radial enamel with interrow sheets at the EDJ with prisms oriented towards the cutting edge.   The outer radial enamel has prisms running occlusally at a higher angle (Figure 13A–D).   Further grinding reveals the presence of HSBs (Figure 14A–D) with the leading edge having radial enamel on the push (compression) side and HSB on the pull (extension) side (Figure 14A).   But the trailing edge of the metaconid still retains the same pattern of radial
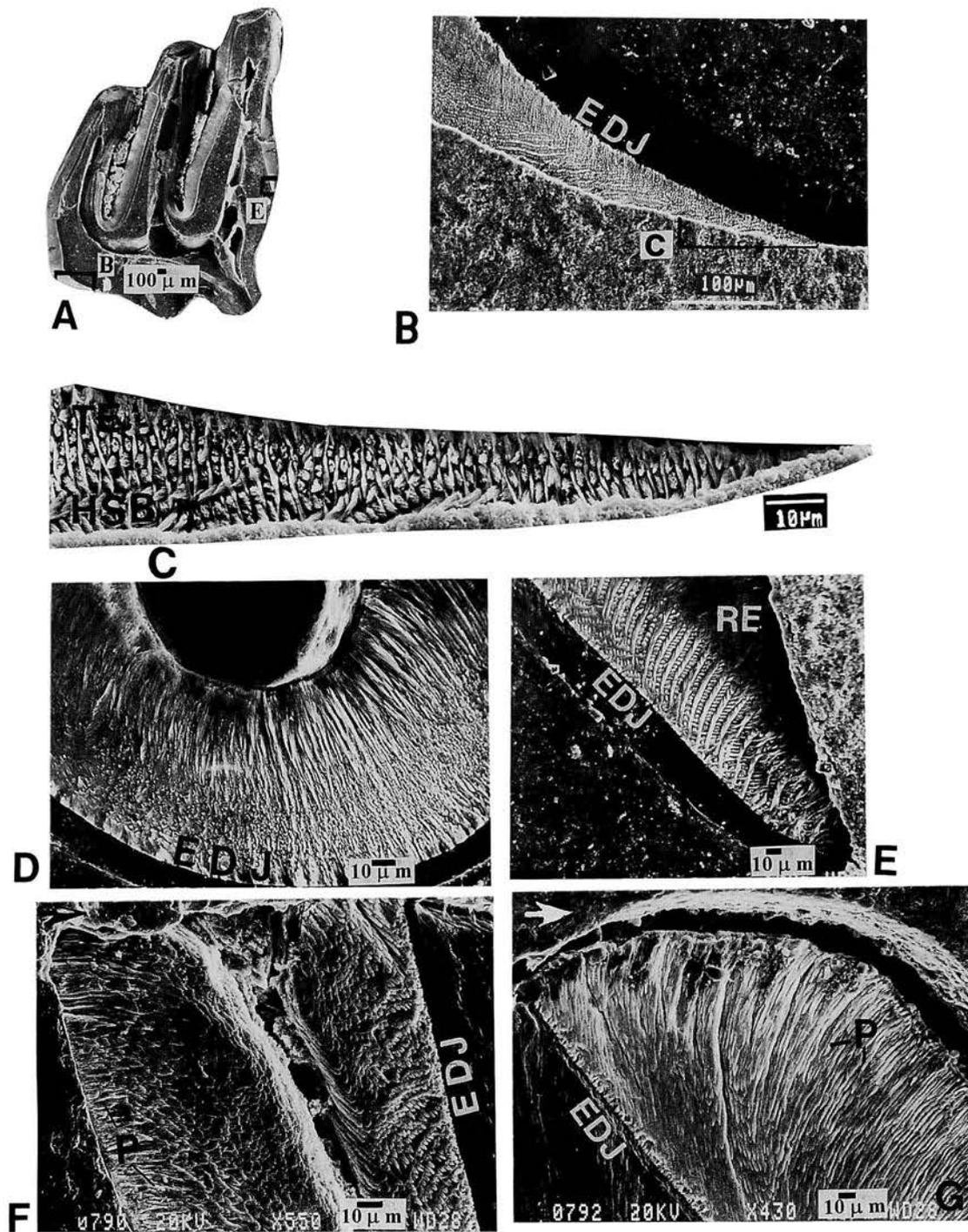
Figure 11. Enamel microstructure in molars of *Bandicota bengalensis* as seen in longitudinal section. **A**. Longitudinal section of first upper molar. **B**. HSBs as seen at base of first upper molar (magnified portion of A, indicated by B on **A**). **C**. HSBs at base of first upper molar, further magnified from a portion on B (indicated by C on B). **D**. Enamel fold as seen on first upper molar (magnified portion of A). **E**. HSBs as seen at posterior end of base of first upper molar (magnified portion of A, indicated by E on **A**). **F**. Longitudinal section of leading edge of first lower molar. **G**. Longitudinal section of trailing edge of first lower molar. Arrow indicates load direction. Abbreviations same as in Figures 1 and 2.
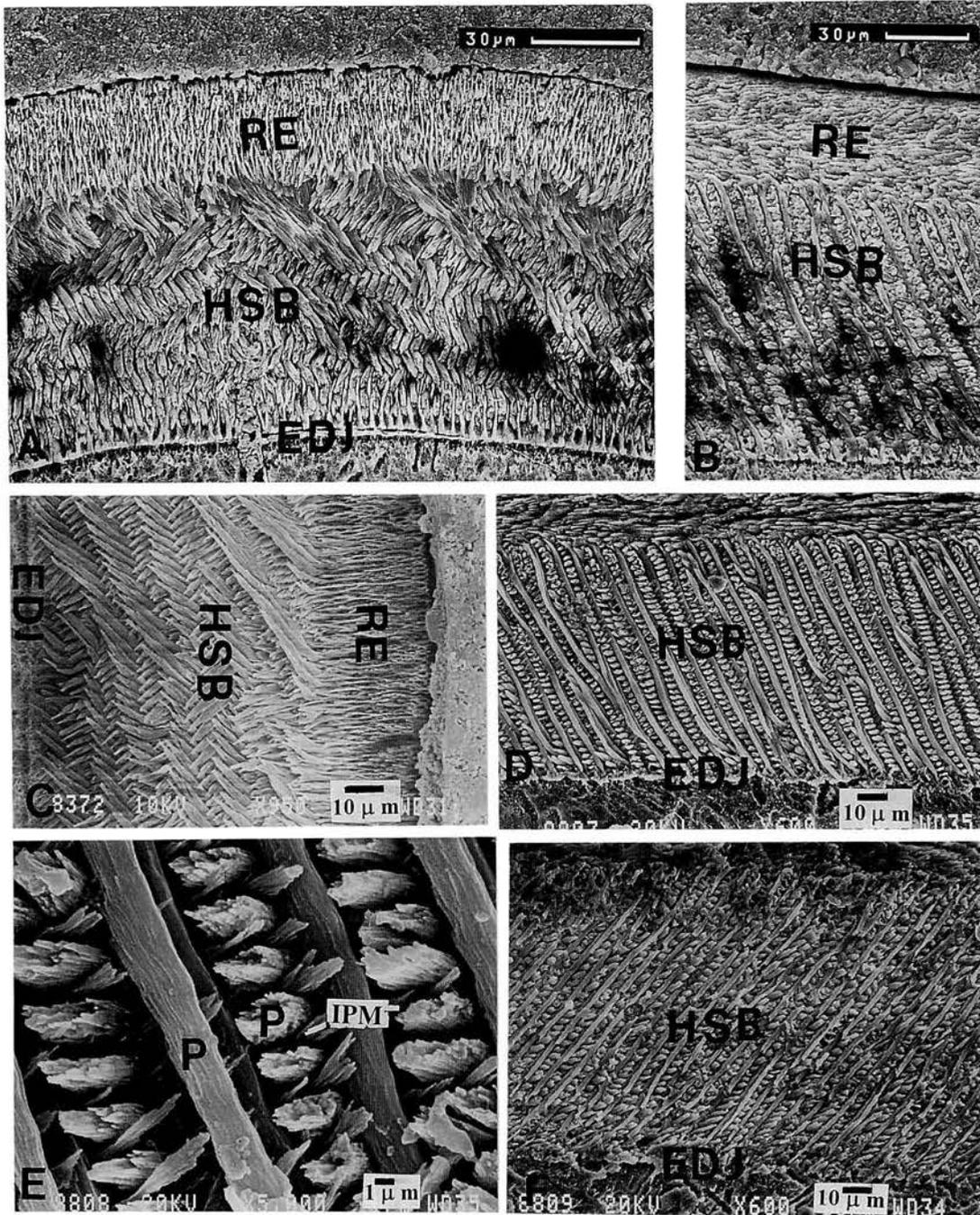
Figure 12. Enamel microstructure in incisors of *Golunda kelleri* and *G. tatroticus*. **A.** Transverse section of upper incisor of *Golunda kelleri* (Late Pliocene Siwaliks). **B.** Longitudinal section of upper incisor (tip on left-hand side) of *Golunda kelleri*. **C.** Transverse section of upper incisor of *Golunda tatroticus* (Late Pliocene Siwaliks). **D.** Longitudinal section of upper incisor (tip on left-hand side) of *Golunda tatroticus*. **E.** HSBs in longitudinal section (magnified portion of HSBs as seen on **D**). **F.** Longitudinal section of lower incisor (tip on right-hand side) of *Golunda tatroticus*. Abbreviations same as in Figures 1 and 2.
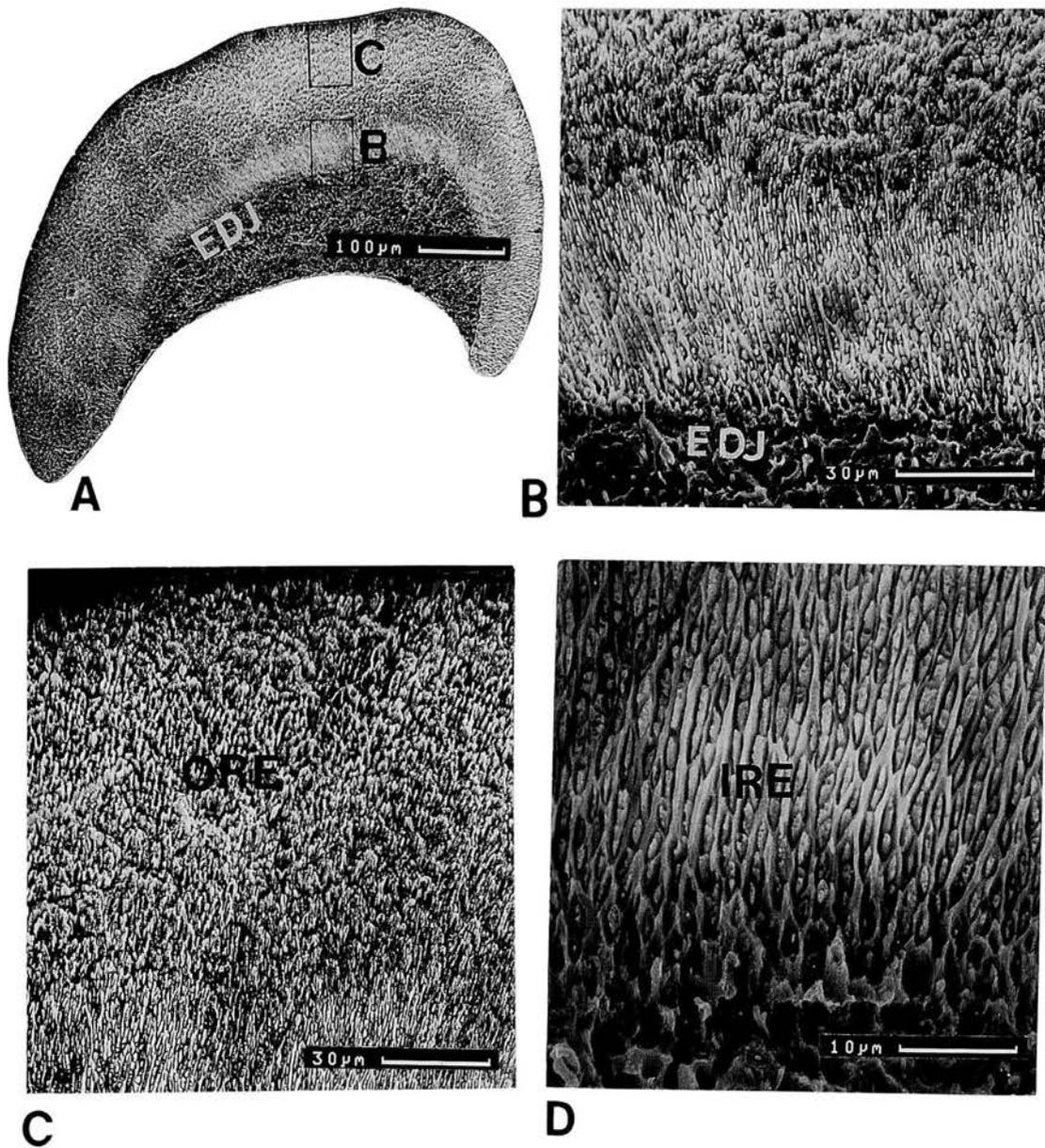
Figure 13. Enamel microstructure in second lower molar of *Golunda tatroticus*, in sections parallel to occlusal surface.   **A**. Enamel microstrcuture in metaconid (as seen after removal of ~.5 mm of enamel and dentine from occlusal surface).   **B**. Inner part of enamel (magnified portion of A).   **C**. Outer part of enamel (magnified portion of A).   **D**. Radial enamel further magnified from a portion of B.   Abbreviations same as in Figures 1 and 2.

enamel as seen before (Figure 14E, F).   At the base of the crown and around the roots, more of the area of the enamel is occupied by horizontal HSBs (Figure 15A–D).   The rest of the upper and lower molars show a very similar pattern.

The lower incisor of the extinct *Parapelomys robertsi* shows less inclined HSBs (several bands can be seen) in transverse section (Figure 16E).   A very thin outer radial enamel with IPM running vertically (Figure 16F) to the

enamel surface from the EDJ has been observed.   As compared to *Golunda*, to which it is closely related (Patnaik, 1997), it has less inclined HSBs.

In cf. *Millardia* (from Late Pliocene Siwalik sediments) upper incisors have HSBs apically inclined (50°).   A lower incisor of the fossil form (Figure 16D) has thicker outer radial enamel than its extant counterpart, *M. meltada* (Figure 16C).   Molars of *Milladia* (both fossil and extant) show a
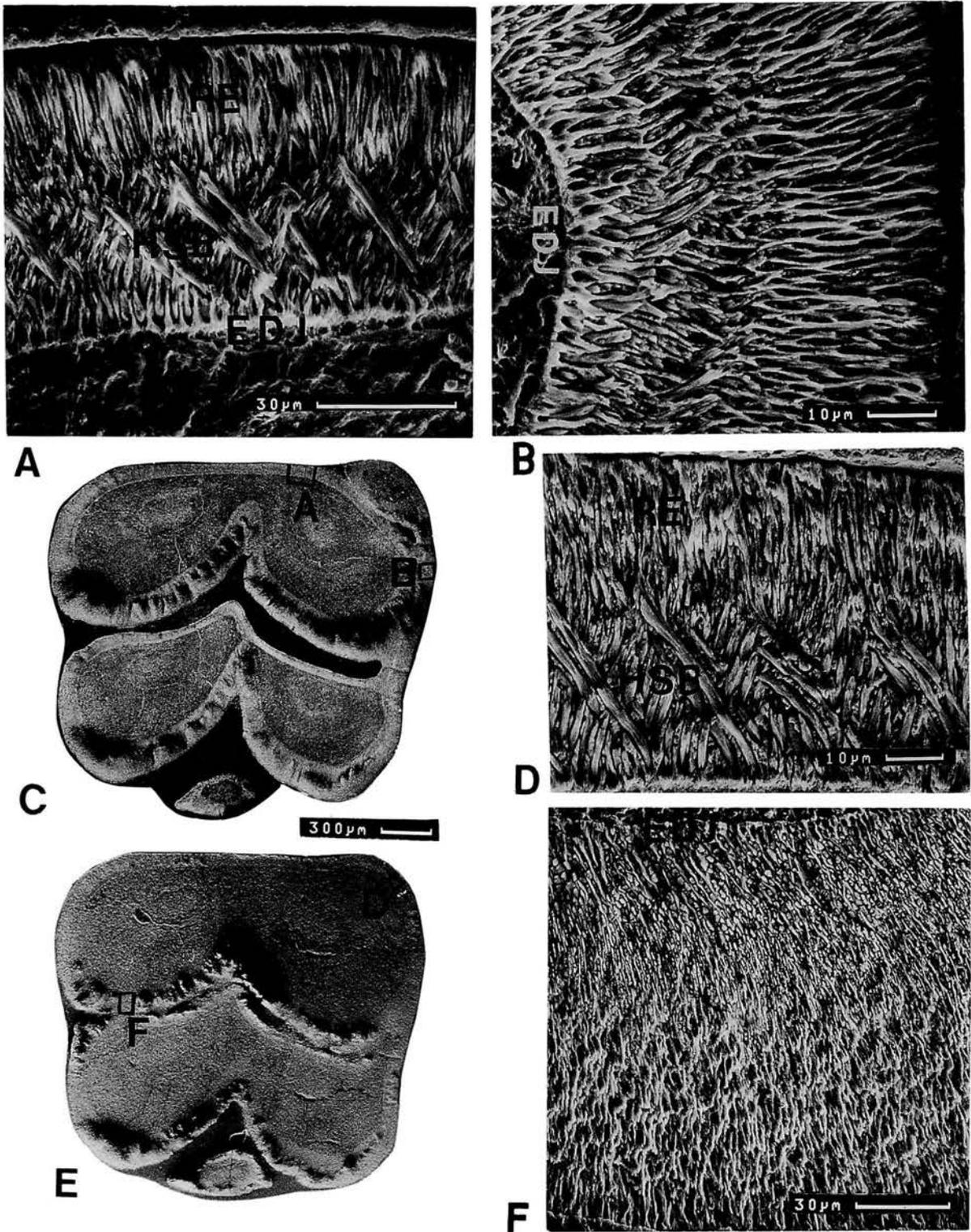
Figure 14. Enamel microstructure in second lower molar of *Golunda tatroticus*, sections parallel to occlusal surface. **A**. Magnified part of leading edge (indicated by A on **C**). **B**. Magnified part of labial side (indicated by B on **C**). **C**. Second lower molar. **D**. Magnified part of leading edge (indicated by D on **E**). **E**. Second lower molar, further polished. **F**. Magnified part of trailing edge (indicated by F on **E**). Abbreviations same as in Figures 1 and 2.
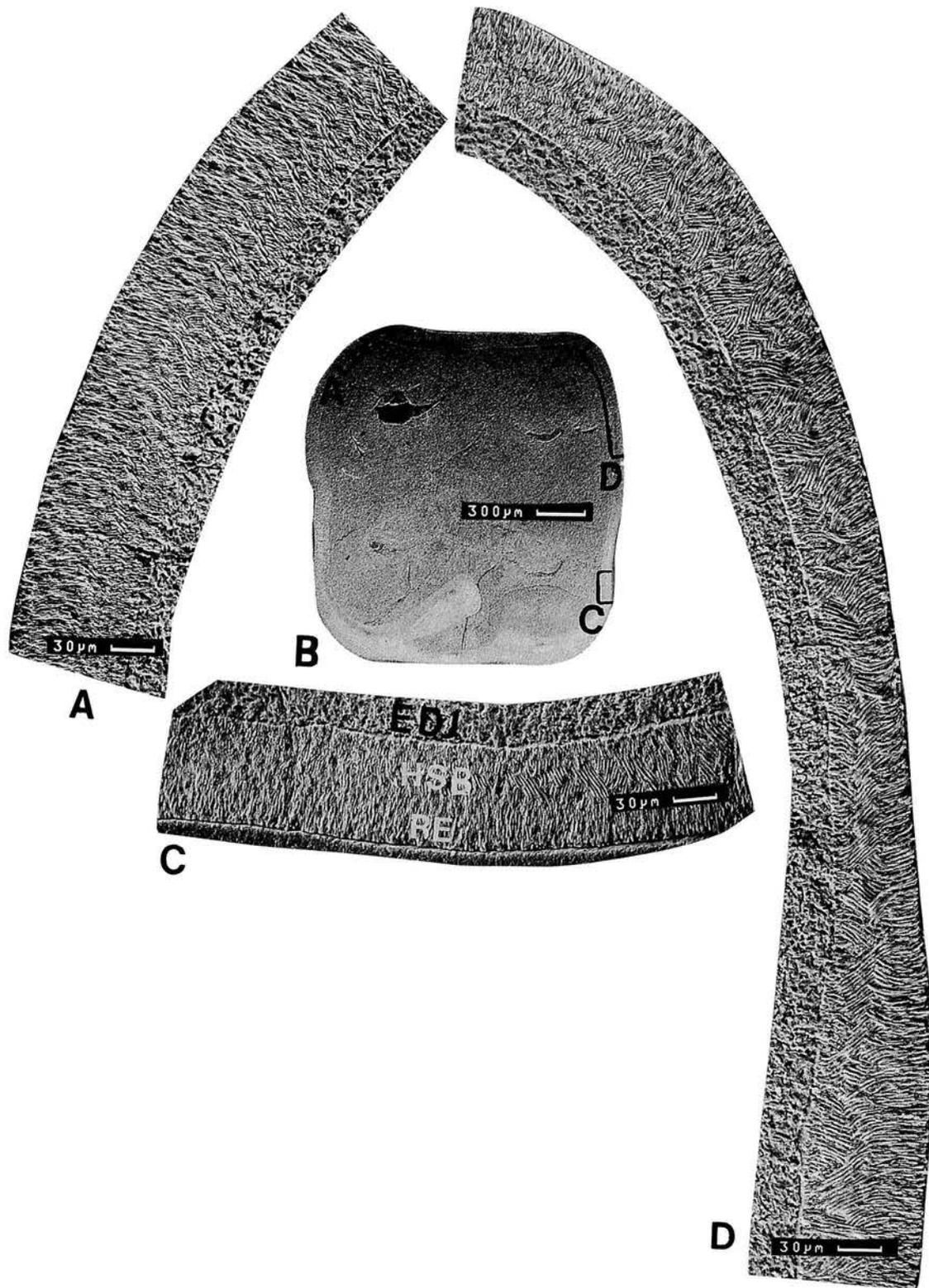
Figure 15. Enamel microstructure in second lower molar of *Golunda tatroticus,* sections parallel to occlusal surface. **A.** A part of HSBs as seen at base of second lower molar (magnified portion of B, indicated by A on B). **B,** Second lower molar polished up to base. **C** and **D.** HSBs at base of molar (magnified portions of **B**, indicated by **C** and **D** on **B**). Abbreviations same as in Figures 1 and 2.
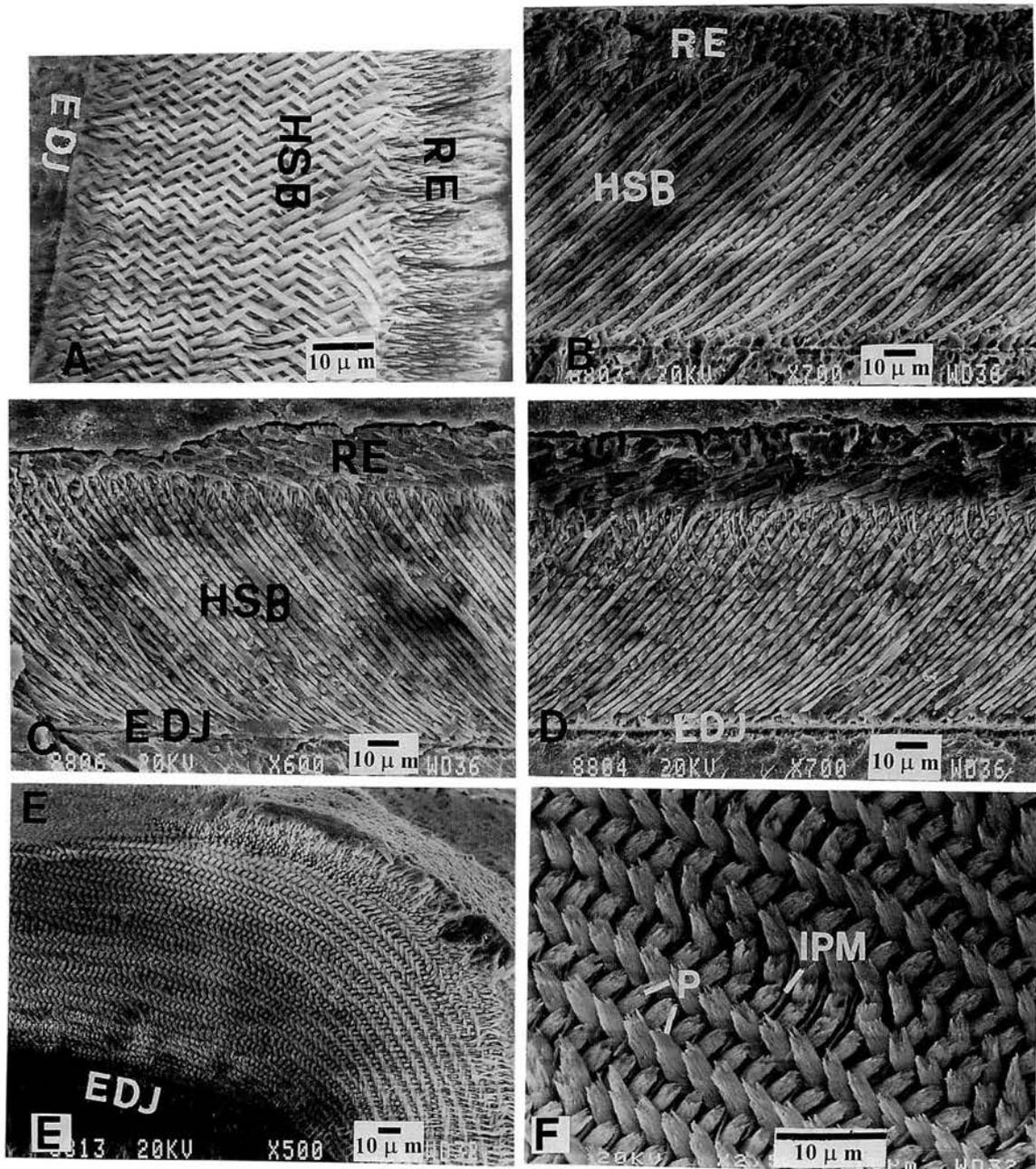
Figure 16. Enamel microstructure in incisors of *Millardia* and *Parapelomys*. **A.** Transverse section of upper incisor of cf. *Millardia*. **B.** Longitudinal section of upper incisor (tip on right-hand side) of cf. *Millardia*. **C.** Longitudinal section of lower incisor (tip on left-hand side) of *Millardia meltada*. **D.** Longitudinal section of lower incisor (tip on right-hand side) of cf. *Millardia*. **E.** Transverse section of lower incisor of *Parapelomys robertsi*. **F.** HSBs, further magnified from **E**. Abbreviation same as in Figures 1 and 2.

very similar structure to that of *Golunda, i.e.*, the lower half of the crown contains inner HSBs and outer radial enamel, and the rest of the crown is occupied by radial enamel.

Discussion

The outer prismless enamel found in all the extant *Mus*

incisors studied here seems to be an etching artifact that could have been produced due to a slight compositional difference between inner and outer radial enamel. Presence of dense outer radial enamel underlain by inner radial enamel and HSBs (which are less resistant to abrasive forces) may facilitate the maintenance of a sharp incisor.

This is the first report of brachydont rodent molars show-

ing HSBs running from the base to the occlusal surface, although on the lingual and labial walls, HSBs occupy only a part of the crown height from the base. Prior to this study only hypsodont and rootless rodent molars have been found to show HSB extending from the base to the top of the crown (Koenigswald, 1980; Koenigswald *et al.*, 1994), although the presence of lamellar enamel with uniserial HSBs covering the base of brachydont molars, such as that of *Cricetus cricetus*, has been noted earlier (Koenigswald and Clemens, 1992; Koenigswald, 1993). Models of stress distribution and prism orientation suggest that horizontal HSBs surround the low-crowned molars in order to provide reinforcement against vertical load and crack propagation (Koenigswald *et al.*, 1987; Pfretzschner, 1988; Pfretzschner, 1994). According to this model, vertical loads on the occlusal surfaces of the upper and lower teeth of mice (Figure 17A) produce horizontal tension in the enamel, which would be at a maximum at the base around the roots. These tensile stresses may lead to expansion of vertical cracks around the walls of the molars. As radial enamel with prisms oriented in one direction is vulnerable to these crack-generating forces, reinforcement of the structure with horizontal HSBs surrounding the base of the molars would inhibit such a development (al in Figure 17). It is possible that the HSBs are developed at the base of the crown to reinforce the thin enamel. But if we look at the HSBs in *Mus* (Figure 7), where they occupy the entire enamel crown of varying thickness, this conjecture does not hold strongly. Another example supporting this view is that of *Megacricetodon*, which has molar enamel comparable in thickness to that of mice, but in which the HSBs occupy only half of the crown height (Figure 8H).

In mice, the effective jaw movement is 'proal' (forward stroke). Except for the posterior portion of the hypocone, all the cusps of the first upper molar point their arcuate and concave end posteriorly. In contrast, except for the anterior portions of the lingual and labial anteroconids on the first lower molar, all the cusps of lower molars point anteriorly. During occlusion, the valleys between lingual and medial cusps and those between the medial and labial cusps of the first upper molars are occupied by the lingual and labial rows of cusps of the first lower molars, respectively. The row containing the hypoconid and the entoconid occupies the space between the second and last row of the first upper molar. During a proal jaw movement with the lower jaw moving forward, sharp cutting edges are formed at the anterior margin by lingual and labial anteroconids. The cutting edge formed in this manner on the molars shows a resemblance to the cutting edge of an incisor, where one can see prisms with their long axis pointing towards the occlusal surface in the outer radial enamel and HSBs inclined apically in the inner part of the enamel. Such cutting edges are also formed at the poste-
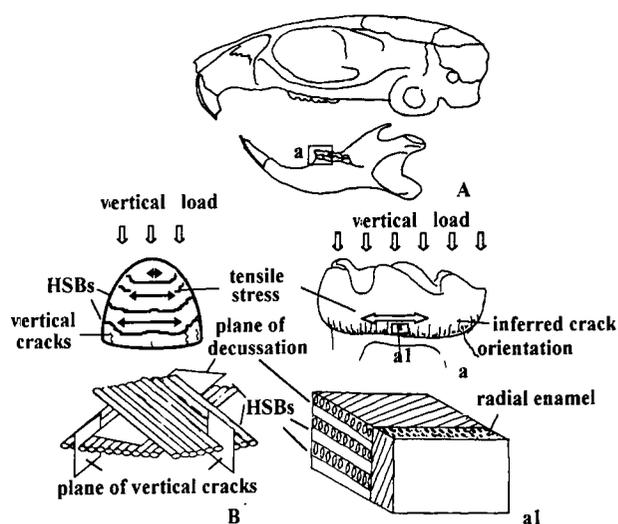
Figure 17. Hypothetical schematic diagram, showing arrangement of HSBs in response to vertical load in molars of mice. A. Sketches of skull and lower jaw of mice; a, first lower molar enlarged; al, schematic model of portion of enamel at base of crown. B. Generalised model showing orientation of HSBs, plane of decussation and plane of vertical cracks in response to vertical load on low-crowned molar (adapted from Pfretzschner, 1988).

rior end of the first upper and lower molars. The cusps and valleys that contain outer radial enamel and inner radial enamel with very thick interrow sheets are resistant to abrasion and may help to grind efficiently when in contact.

Differentiation of the leading and trailing edges of enamel microstructure previously has been observed only in hypsodont rodent molars (both with and without roots). In rodents, hypsodonty has led to lamination of the cusp rows, which has simplified the morphology. In hypsodont rodents the radial enamel has invariably been found on the push sides of the cutting edges (Koenigswald, 1980; Koenigswald *et al.*, 1994). This study shows that the brachydont cuspidate dentition in mice also exhibits such differentiation between leading- and trailing -edge enamel. It is even more conspicuous in heavily worn dentitions where cusps are lost and only enamel folds remain. The presence of radial enamel on the push sides of the leading and trailing edges in mice molars justifies their (radial enamel) abrasion-resisting properties. The cutting and grinding ability of mice molars reflects a rather omnivorous diet, which may include browsing shrubs, eating insects and grazing grasses (Dieterlen, 1972).

In hypsodont *Bandicota*, horizontal HSBs probably serve as a crack-stopping mechanism. These horizontal HSBs have been noticed in both vertically and parallelly oriented enamel relative to the occlusal surface. This may indicate that regardless of the orientation of the enamel, horizontal HSBs are present to counter vertical forces. Also noted is
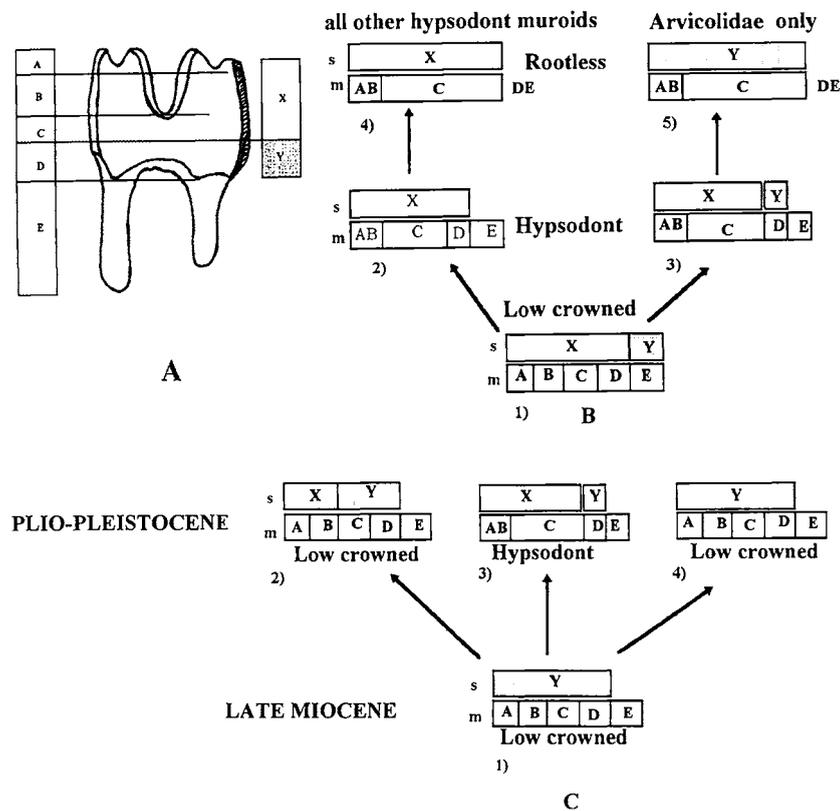
Figure 18. Relationship of molar morphology and scmelzmuster in some muroid rodents. A. Ontogenetic phases of morphology and schmelzmuster of low-crowned muroid molars. B. Difference in heterochrony of morphology (m) and schmelzmuster (s) during evolution from low-crowned (1) to hypsodont (2 and 3) and rootless (4 and 5) molars of muroid rodents. A and B adapted from Koenigswald (1993). C. 1) Low-crowned Late Miocene murids with dominant Y phase (pattern similar to that of *Mus*); 2) Plio-Pleistocene murids such as *Golunda* and *Millardia* with both X and Y phases equally developed; 3) Plio-Pleistocene murids such as *Bandicota* with Y phase reduced and X phase considerably prolonged; 4) Plio-Pleistocene murids such as *Mus*, with dominant Y phase. Explanation of various phases in molar morphology and schmelzmuster: A and B, formation of occlusal surface; C, formation of side walls; D, formation of base of crown; E, formation of roots; X, upper part with radial enamel; Y, circumferential band of lamellar enamel at crown base.

that the development of HSBs takes place from the radial enamel (Koenigswald *et al.*, 1987). Presence of radial enamel (with prisms in leading edges pointing their long axes towards the load) on the occlusal surface would help in resisting abrasion. This feature suggests an adaptation for an abrasive diet.

In brachydont *Golunda* molars, radial enamel is dominant on the occlusal surface. Only after considerable abrasion can one observe differentiation of leading and trailing edges. Radial enamel is found on the push side and HSBs on the pull side of the leading edge. Radial enamel with interrow sheets has been noticed on the push side and radial enamel on the pull side of the trailing edge. Again presence of horizontal HSBs at the base probably strengthens the tooth against progress of vertical cracks. The predominant radial enamel on the occlusal surface points towards a grazing habit.

Koenigswald (1993) studied the evolution of schmelz-muster in molars of low-crowned and hypsodont rodents

(both with and without roots) from the perspective of heterochrony. He argued that low-crowned molars of muroid rodents with a large portion of their crown occupied by radial and a smaller portion by lamellar (uniserial HSB) enamel evolved into hypsodont molars either lacking lamellar enamel altogether (e.g., *Microtia magna*) and/or retaining this small amount of lamellar enamel on the other (e.g., *Nesokia indica*). He observed that in rootless hypsodont molars the radial enamel extends from the base to the top in some species (e.g., gerbil, *Rhombomys opimus*) and that lamellar plus radial enamel extends from the base to the top in others (e.g., arvicolids). Further, he suggested that, in most muroid rodents (except for arvicolids), morphology and schmelzmuster follow the same heterochronic modifications. The base of a low-crowned cricetid molar has lamellar (uniserial HSBs) and radial enamel occupying the inner and outer enamel, respectively (Figures 18A, the 'Y' phase, corresponding to D phase of morphology). The rest of the crown of a cricetid

molar is occupied by radial enamel (Figure 18 A, the 'X' phase, corresponding to A, B and C phases of morphology). According to Koenigswald (1993), the structure seen on low-crowned cricetids gave rise to those observed on hypsodont and rootless muroid rodents; 1) with the entire crown occupied by the 'X' phase and 2) with the entire crown occupied by 'Y' phase (arvicolids). In arvicolids, acquisition of the 'X' phase is accelerated and gives way to the 'Y' phase (Figure 18B).

In the context of the present observations, the heterochrony hypothesis of Koenigswald (1993) is not strongly supported for murids, although it could still be applicable to other muroids, for example, cricetids and arvicolids. In the Indian murids, the 'Y' phase in brachydont mice occupies the whole crown (Figure 18C, 1). Taking into account the temporal and spatial distribution of this structure it is suggested here that this should be regarded as the basic structure for the family Muridae. It extends up to the Recent with the *Progonomys-Mus* lineage. *Mus* originated from *Progonomys* in the Late Miocene (around 5.7 m.y. ago, Jacobs and Downs, 1994). In fact, *Progonomys,* which had a wide distribution during the Miocene (Indo-Pakistan, China, Africa, Europe), is the basic stock that gave rise to all the fossil and extant murids, which includes more than 500 extant species and 120 genera. In contrast to the *Mus* pattern, where the "Y" phase dominates, brachydont *Golunda* and *Millardia,* which are phylogenetically related to the *Karnimata* group (Patnaik, 1997, 2001) of Late Miocene time, have the 'Y' phase restricted to the lower half of the crown and the 'X' phase occupying the rest of the crown (Figure 18C, 4). This structure also extends to the Recent. A different pattern is seen in hypsodont murids. Hypsodonty in murids is first noted in *Dilatomys* of the Pliocene Siwaliks and Late Miocene deposits of Afghanistan (see Sen, 1983; Patnaik ,1997), which appears after the emergence of C4 grasslands in the subcontinent (Cerling *et al.,* 1993). In spite of being hypsodont, cusp patterns of *Dilatomys* are similar to those seen on *Parapelomys-Saidomys* (again related to *Karnimata*) and it has been placed in one group with *Bandicota* and *Hadromys* (Patnaik, 1997). Here, the phase 'X' extends to cover the occlusal surface, and the phase 'Y' is reduced considerably to occupy only a small portion of the base around the roots (Figure 18C, 3).

In this study the genera *Mus, Golunda, Millardia,* and *Bandicota* can be distinguished broadly by variation in schmelzmuster (angle of inclination of HSBs, percentage of HSBs and RE in incisors; extent of distribution of HSBs and prism orientation in molars, etc.). In the genus *Mus,* it was found that closely related species (here belonging to the subgenus *Mus*) do not show any considerable difference at the microstructural level. However, *Mus* (*Pyromys*)

saxicola differs from all the other *Mus* species at the schmelzmuster level, as it shows a slight difference in the shape of the first upper molars (Figure 6C). Nevertheless, it appears that, given similar shape and size of dentition and dietary habits, it is difficult to distinguish closely related species of *Mus* based on enamel microstructure alone.

Conclusions

1. The molars of *Mus* show some sort of specialisation at the microstructure level by having a kind of 'incisor-like' arrangement of HSBs and radial enamel running from the base to the top of the crown, which could be useful in maintaining sharp cutting edges to break down leaves and insects. In addition to this, the low-crowned *Mus* molars also show grinding ability.

2. Predominance of radial enamel on the occlusal surface of molars of *Golunda, Millardia* and *Bandicota* might be indicative of their adaptation for a grassy diet.

3. The results of this paper are in accordance with the hypothesis that the presence of horizontal HSBs counters vertical forces. In *Bandicota,* the HSBs in the enamel are horizontal in spite of the enamel being almost horizontal and parallel to the occlusal surface. Another unique feature of *Bandicota* molars is that HSBs in the enamel layer orientated almost parallel to the occlusal surface occupy the outer part of the enamel whereas the inner part has tangentially oriented radial enamel.

4. For murid rodents a schmelzmuster similar to that of *Mus* should be taken as the basic pattern which could have given rise to patterns similar to the low-crowned *Golunda/Millardia* and hypsodont *Bandicota.*

Acknowledgements

edged.

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Paleobiogeographic significance of *Trominina hokkaidoensis* (Hayasaka and Uozumi) (Gastropoda: Buccinidae) from the basal part of the Tanami Formation (Oligocene) of the Kii Peninsula, southern Japan

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Abstract. The basal part of the Tanami Formation, in the southern part of the Kii Peninsula, southwest Honshu, southern Japan, contains elements of the Asagai-Poronai fauna (late Eocene to early Oligocene age) of northern Japan. These include *Malletia poronaica* (Yokoyama), *Portlandia (Portlandella) watasei* (Kanehara), and *Trominina hokkaidoensis* (Hayasaka and Uozumi). The combination of late Eocene to early Oligocene Asagai-Poronai mollusks and previously known Oligocene to early Miocene mollusks from the Tanami Formation implies that the localities discussed here are of Oligocene age. The presence of *Trominina*, which was widespread in the northern Pacific during Paleogene time, suggests that it migrated from northern Japan and northward to southern Japan, in accordance with the Eocene-Oligocene transition global cooling trend.

Key words: migration, mollusks, Paleogene, *Trominina*

Introduction

The Kumano Group crops out in the southern part of the Kii Peninsula in southwest Honshu, Japan (Figure 1A), and has been assigned to the lower to middle Miocene, on the basis of mollusks and foraminifers (Hisatomi, 1981). However, Katto *et al.* (1976) previously studied mollusks of the Kumano Group in the Tanami area of the Kii Peninsula (Figure 1B) and erected the Tanami and Uematsu Formations (Figure 2), which they assigned to the Oligocene and lower Miocene, respectively, on the basis of mollusks.

The basal part of the Tanami Formation yields many species of the Asagai-Poronai fauna that occurs in the upper Eocene to lower Oligocene of Hokkaido and northeast Honshu, northern Japan (Honda, 1994). The Asagai-Poronai mollusks are *Portlandia (Portlandella) watasei* (Kanehara), *Ampullina asagaiensis* Makiyama, *Beringius hobetsuensis* (Matsui), *Trominina* cf. *T. ishikariensis* (Hayasaka and Matsui), and *Fulgoraria* cf. *F. (Musashia) antiquior* (Takeda) (Katto and Masuda, 1978).

I obtained numerous, but rather poorly preserved molluscan fossils from low cliffs exposed on a wave-cut terrace at Tanosaki, in the basal part of the Tanami Formation (Figure 1B). These are identified as *Malletia*

poronaica (Yokoyama), *Portlandia watasei*, *Acila (Acila) kiiensis* Masuda and Katto, "*Teredo*" sp., *Turritella* sp., and *Trominina hokkaidoensis* (Hayasaka and Uozumi) (Table 1). *Trominina*, which is one of the earliest evolved buccinid genera, appeared in the region including Sakhalin and Kamchatka during late Eocene time (Titova, 1994). It has been widely recorded from upper Eocene to lower Miocene strata in the North Pacific: Japan, Sakhalin, Kamchatka, the Koryak Upland, Alaska, and Washington (Titova, 1994).

In this paper, I document *T. hokkaidoensis* from the basal part of the Tanami Formation and discuss the paleobiogeographic significance of *Trominina* in Japan, as well as the age of the formation based on mollusks.

Geological setting

The Tanami Formation largely consists of pale grey, fine-grained sandstone, grey siltstone, and alternating beds of sandstone and siltstone, and is approximately 1500 m thick (Katto *et al.*, 1976). Its basal granule conglomerate, some 30 cm thick, is unconformably underlain by black mudstone of the Eocene to Oligocene Shimotsuyu Formation in the upper part of the Muro Group. The Tanami Formation is in fault contact with the overlying
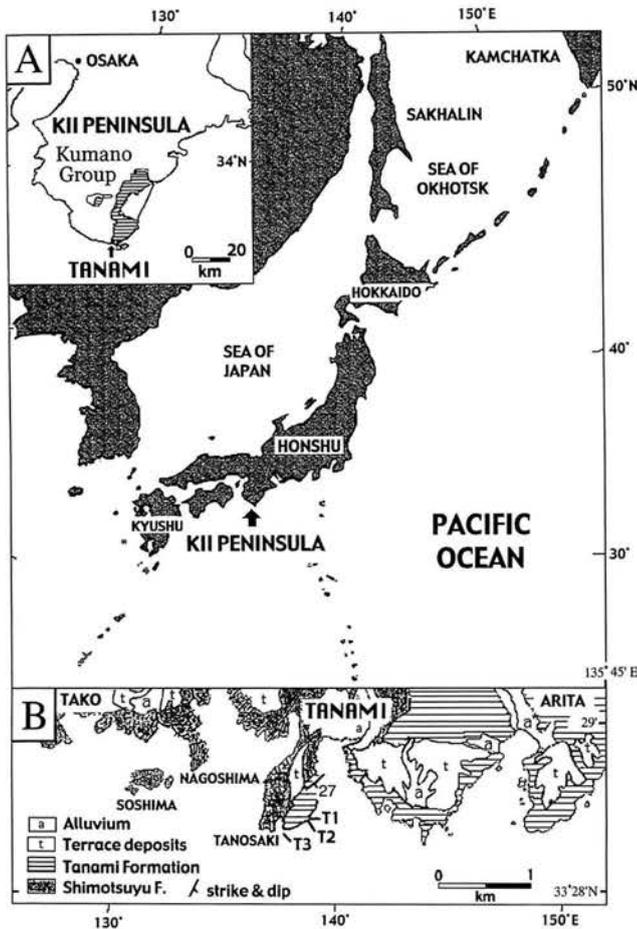
Figure 1. **A.** Map showing the location of the Kii Peninsula, southwest Honshu, Japan. **B.** Geologic sketch map of the Tanami area (simplified from Tateishi *et al.*, 1979). T1–T3, fossil localities.

Figure 2. Stratigraphic classification of the Muro and Kumano Groups, in association with the molluscan faunal succession.

Table 1. Occurrences of fossil mollusks in the Tanami Formation. A, abundant (10 or more individuals); C, common (5 to 9 individuals); F, few (2 to 4 individuals); R, rare (one individual). One individual is defined herein as consisting of more than half of a separated valve or an articulated pair of bivalves, and more than half of a gastropod specimen.

Species	Locality		
	T1	T2	T3
Bivalvia:			
Malletia poronaica (Yokoyama)		R	
Portlandia (*Portlandella*) *watasei* (Kanehara)	C	C	C
Acila (*Acila*) *kiiensis* Masuda et Katto			R
Acila sp.			R
Caryocorbula? sp.			R
"*Teredo*" sp.		A	
Gastropoda:			
Turritella sp.		C	
Trominina hokkaidoensis (Hayasaka et Uozumi)	F	R	

Uematsu Formation (Katto *et al.*, 1976), which contains the Kadonosawa fauna (earliest middle Miocene age; Ogasawara, 2001) (Figure 2).

The upper part of the Muro Group largely contains the Asagai-Poronai fauna, within the Tanami Formation, which includes characteristic elements of this fauna such as *Malletia poronaica*, *Yoldia* (*Yoldia*) *laudabilis* Yokoyama, *Y.* (*Tepidoleda*) *sobrina* Takeda, *Portlandia watasei*, *P.* (*Megayoldia*) *yotsukurensis* Uozumi, *Acila* (*Acila*) *elongata* Nagao and Huzioka, *A.* (*Acila*) *kusiroensis* Nagao and Huzioka, *Cyclocardia akagii* (Kanehara), *C. tokunagai* (Yokoyama), *Orectospira wadana* (Yokoyama), and *Turritella tokunagai* Yokoyama (Mizuno, 1973).

Discussion

Trominina has been recorded from the Paleogene strata bearing the Asagai-Poronai fauna in Hokkaido, northern Japan. Matsui (1957) recorded *T. japonica* (Takeda) from

the upper Eocene Poronai Formation in the Ishikari coalfield, central Hokkaido. The lower Oligocene Momijiyama Formation in the Ishikari coalfield has yielded several species, including *T. hokkaidoensis*, *T. onnaica* (Yokoyama), *T. ishikariensis* (Hayasaka and Matsui), *T. yubariensis* (Hayasaka and Uozumi), and *T. umbelliformis* (Hayasaka and Uozumi) (Hayasaka and Matsui, 1951; Hayasaka and Uozumi, 1954).

In addition, Honda (1989) recorded *T. japonica*, *T. hokkaidoensis*, *T. ishikariensis*, *T. umbelliformis*, and *T. dispar* (Takeda) from the lower Oligocene Ombetsu Group
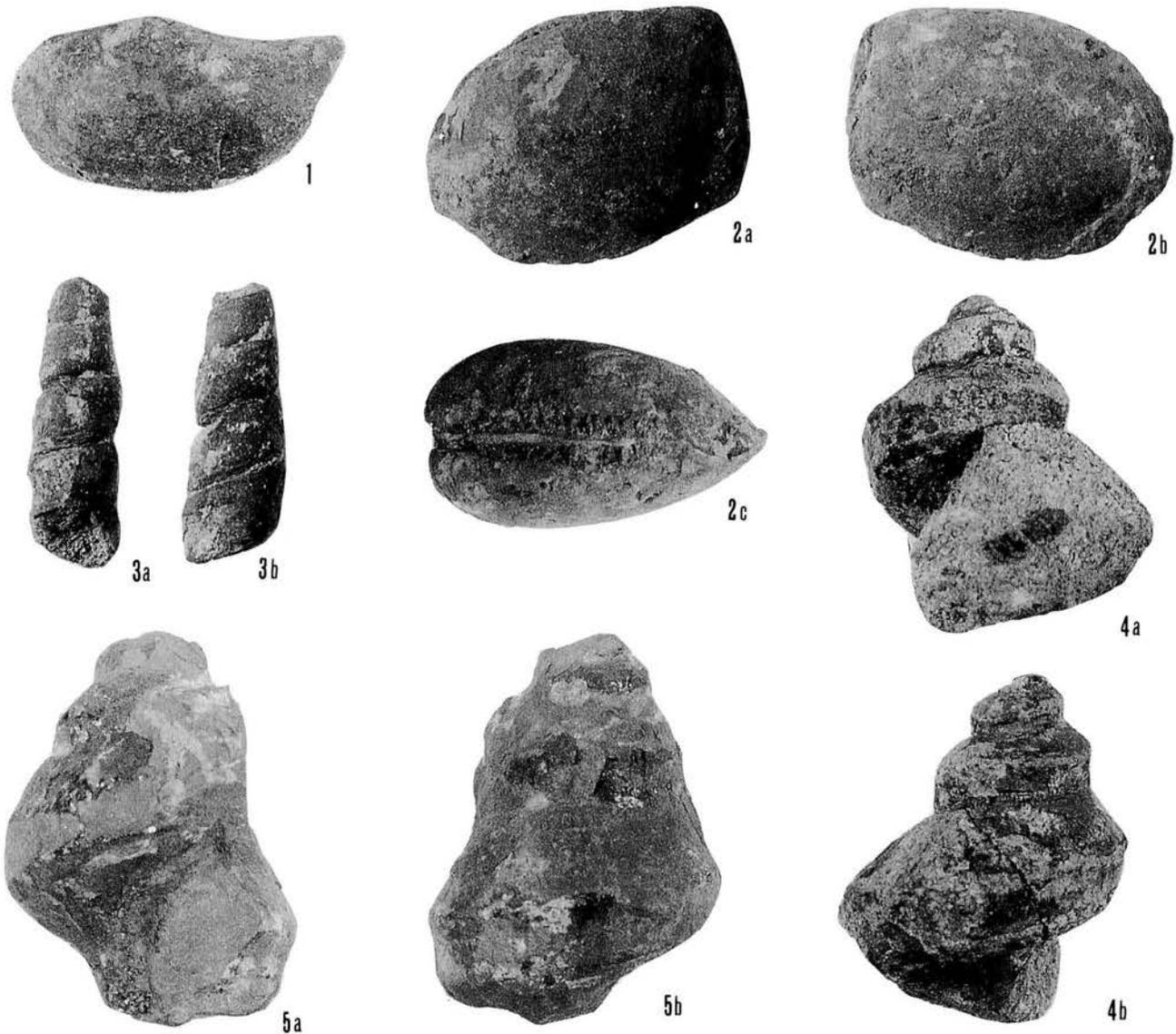
Figure 3. **1.** *Portlandia (Portlandella) watasei* (Kanehara). ×1.4, Loc. T2, MES˙ 1034. **2a-c.** *Acila (Acila) kiiensis* Masuda and Katto. ×1.4, Loc. T3, MES 1035. **3a, b.** *Turritella* sp. ×1.6, Loc. T2, MES 1036. **4, 5.** *Trominina hokkaidoensis* (Hayasaka and Uozumi). 4a, b; ×1.5, Loc. T2, MES 1037. 5a, b; ×1.5, Loc. T1, MES 1038. ˙Abbreviation for the Department of Earth Sciences, Faculty of Education, Mie University.

in the Kushiro coalfield, eastern Hokkaido. The southernmost record of *Trominina* is *T. japonica* from the upper lower Oligocene Yamaga Formation in the Ashiya Group of Kyushu, southern Japan (Tomita and Ishibashi, 1990). This suggests that *Trominina* migrated from Hokkaido and further northward to the Kii Peninsula and Kyushu, southern Japan, in accordance with the Eocene-Oligocene transition global cooling trend. In contrast to these Paleogene records, *T. bicordata* (Hatai and Koike, 1957) from the lower Miocene Hota Group in the Boso Peninsula, central Honshu, is the youngest record of *Trominina* in Japan.

Based on these records of *Trominina*, the presence of

Trominina in the Tanami Formation suggests that the basal part of the Tanami Formation, which also contains the Asagai-Poronai fauna, is of Oligocene rather than Miocene age. Honda *et al.* (1998) recorded the Akeyo fauna (Itoigawa, 1987; early Miocene, ca. 18 to 16 Ma; Figure 2) from the Shimosato Formation of the Ukui area in the southeastern Kii Peninsula. The basal part of the Tanami Formation contains an older fauna than does the partly coeval Shimosato Formation. The Tanami Formation as a whole is assigned to the Oligocene to early Miocene age (Figure 2).

The presence of Asagai-Poronai mollusks in the upper

part of the Muro Group first implied an Oligocene to early Miocene age for these strata (Mizuno, 1973). This is the southernmost record of the Asagai-Poronai fauna; however, it is now known to range from the late Eocene to early Oligocene in Hokkaido and northeast Honshu, northern Japan (Honda, 1994). In addition, Suzuki (1988) assigned the Aikawa Formation, in the upper part of the Muro Group, to the early to earliest middle Eocene age, based on radiolarians. Accordingly, the Shimotsuyu Formation, which is correlative with the Aikawa Formation (Tateishi et al., 1979), is tentatively treated here as an Eocene to Oligocene unit (Figure 2).

Systematic description

Family Buccinidae Rafinesque, 1815
Genus *Trominina* Oyama and Mizuno, 1958

Type species.—Ancistrolepis japonicus Takeda, 1953.

Trominina hokkaidoensis (Hayasaka et Uozumi, 1954)

Figure 3.4, 3.5

Ancistrolepis yudaensis Otuka var. *ishikariensis* Hayasaka and Matsui, 1951, p. 334, pl. 1, fig. 3 (*non* fig. 4).
Ancistrolepis hokkaidoensis Hayasaka and Uozumi, 1954, p. 402, pl. 25, fig. 8, pl. 26, fig. 5.
Trominina hokkaidoensis (Hayasaka and Uozumi). Oyama *et al.*, 1960, p. 63, pl. 10, fig. 2 (reproduced from Hayasaka and Uozumi, 1954); Kanno and Ogawa, 1964, p. 291, pl. 4, fig. 3; Honda, 1989, p. 100, pl. 10, fig. 11.
Neptunea dispar Takeda. Katto and Masuda, 1978, pl. 1. fig. 5.

Material examined.—Three specimens (MES coll. cat. nos. 1037, 1038, 1039).

Remarks.—This species is characterized by a high spire ornamented with one relatively weak but acutely expanded keel on the middle part of the whorl. Hayasaka and Matsui (1951, p. 334, pl. 1, figs. 3, 4) erected *Ancistrolepis yudaensis* Otuka var. *ishikariensis* from the Momijiyama Formation (lower Oligocene) of the Ishikari coalfield, central Hokkaido. Hayasaka and Uozumi (1954) later proposed *Ancistrolepis hokkaidoensis* from the Momijiyama Formation, and they doubtfully cited a specimen (Hayasaka and Matsui, 1951, pl. 1, fig. 3) as *A. hokkaidoensis*. *Trominina hokkaidoensis* differs from *T. ishikariensis* in having a weaker keel on the middle part of the whorl.

Gladenkov *et al.* (1988) synonymized *T. onnaica* (Yokoyama), *T. yubariensis, T. japonica, T. ishikariensis, T. hokkaidoensis, T. umbelliformis,* and *T. bicordata* with *T. angasiana* (Yokoyama) after studying the Eocene to Oligocene buccinids in Kamchatka. *Trominina yubariensis* and *T. umbelliformis* are characterized by a clearly ex-

panded keel on the middle part of the whorl, as is *T. angasiana*. However, *Trominina onnaica, T. japonica, T. ishikariensis, T. hokkaidoensis,* and *T. bicordata* all bear a relatively weak keel, which differentiates them from *T. angasiana*. Although the taxonomy of the above listed species should be further studied, they are considered here to differ from one another by the surface ornamentation and the outline of whorls.

Trominina hokkaidoensis most closely resembles *T. japonica,* known from the middle Eocene to upper Oligocene 'Maoka' Group in southern Sakhalin, Russia (Takeda, 1953; Kano *et al.,* 2000). However, *T. hokkaidoensis* has a more distinctly expanded body whorl than does *T. japonica.* Katto and Masuda (1978, pl. 1, fig. 5) illustrated *Neptunea dispar* from the Tanami Formation, which is assigned here to *T. hokkaidoensis* based on its more acutely elevated spire.

Associated fauna.—The present species is associated with such sublittoral to bathyal dwellers as *Portlandia watasei* and *Turritella* sp. (Table 1).
Occurrence.—Loc. T1, T2.

Acknowledgments

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Migration and speciation of the *Loxoconcha japonica* species group (Ostracoda) in East Asia

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Abstract. Eighty-five fossil and Recent species of the genus *Loxoconcha* (Crustacea: Ostracoda) from East Asia are systematically reexamined. On the basis of carapace morphology, the genus *Loxoconcha* from East Asia is divided into five species groups: *L. pulchra*, *L. optima*, *L. japonica*, *L. uranouchiensis* and *L. japonica* species groups. The migration and speciation patterns of four species of the *L. japonica* species group are as follows. In Late Miocene, *L. lilljeborgii* and *L. tumulosa* were distributed over the Paleo-Indian Ocean. In Early Pliocene time, these species migrated to the Western Pacific and *L. japonica* evolved from populations of *L. tumulosa* by peramorphic evolution. In the Middle Pleistocene, *L. shanhaiensis* evolved from populations of *L. japonica* in the Ryukyu Islands by paedomorphic evolution.

Key words: East Asia, *Loxoconcha*, Ostracoda, paedomorphic evolution, paleobiogeography, peramorphic evolution,

Introduction

The genus *Loxoconcha* was proposed by Sars (1866) with the type species *Cythere rhomboidea* Fischer (1855), based on a Recent specimen from Lervig (= Larvik), South Norway. Since then, about 550 species belonging to this genus have been identified from around the world (Kempf, 1986). The oldest fossil record is from the Eutaw Formation (late Cretaceous) of northwest Selma, Dallas City, Alabama, North America (Crane, 1965). This genus is reported from the Paleogene of four continents: North America (Hazel *et al.*, 1980; Howe, 1963; Carreño and Cronin, 1993), Australia (Mckenzie *et al.*, 1991, 1993), Africa (Cronin and Khalifa, 1979; Ahmad *et al.*, 1991) and Europe (Keij, 1957); thus its distribution had already become worldwide. Today, it is widely distributed in littoral, sublittoral and brackish-water environments throughout the world except for the polar regions (Athersuch and Horne, 1984).

The genus *Loxoconcha* is an evolutionarily successful group, with one of the highest species diversity of all ostracod genera. Its species have adapted to various habitats, often developing morphological characters in adapting to microhabitats.

In East Asia, 85 species of *Loxoconcha* have been described since 1868 when Brady reported two Recent species from Batavia, Java, present-day Indonesia (Brady, 1868). Based on carapace outlines, surface ornamentation patterns, hinge structures and muscle scar patterns, *Loxoconcha* can be classified into five species groups (Figure 1). Morphological similarity among *Loxoconcha* species is affected either by the genotype or environmental interactions or both. It is possible to estimate the relative importance of each by investigating intraspecific morphological variants and their geographical, stratigraphical and ontogenetical variability. In this study, we focus on the neritic *L. japonica* species group. We compare morphological characters among species and evaluate the presumed phylogenetic relationships among species based on inter-specific morphological similarities. Finally, we consider geographic dispersal processes and mechanisms of adaptation to local environments.

Material

This study is based mainly on Recent and fossil faunal-slides housed at Shizuoka University. Collections of *Loxoconcha* come from 35 localities (23 Recent; 12 fossil) which range geographically from Suttsu Bay (Hokkaido, Japan) to Taiwan (Figure 2 and Table 1). All figured specimens have been deposited at the Shizuoka University Museum, Japan (SUM–CO–Number).
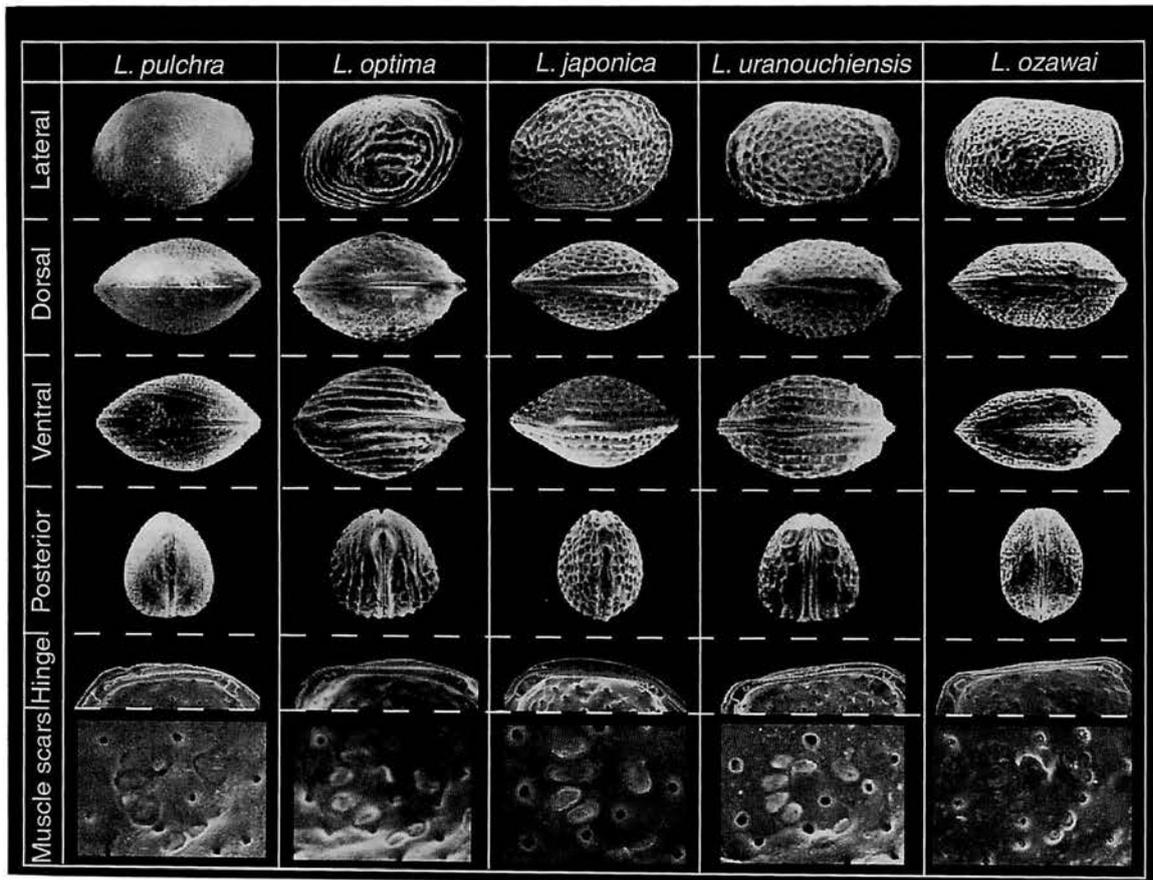
Figure 1.   Five species groups of *Loxoconcha* in the East Asia, defined on the basis of their carapace morphology.   Not to scale.

Morphological classifications of genus *Loxoconcha* from East Asia

Loxoconcha, which includes 85 species from the East Asia, is divided into the following five species groups on the basis of carapace morphology (Figure 1).   They include those species which have not been given species names (indicated by *L.* sp.) and those referred to in quotes in the literature.

Loxoconcha pulchra *species group.* — Carapace subrhomboidal in lateral view.   Surface ornamentation of the carapace consists of concentrically-arranged pits or weak reticulation, except for the dorsal area.   In dorsal view, ornamentation not developed.   In ventral view, five pairs of ridges diverge toward anterior.   Posterior element of hingement is ball-shaped.   Prominent fulcral point.   A total of six species are included: *L. pulchra, L. subcirculata, L. subpulchra, L.* sp. (Hou *et al.,* 1982), *L.* sp. C (Ikeya *et al.,* 1985), "*L. pulchra*" (in Gou *et al.,* 1981).

Loxoconcha optima *species group.*—Carapace subrhomboidal in lateral view.   Surface ornament of the carapace consists of concentrically-arranged ridges or pits as located

around the position of the muscle scar, except for the dorsal area.   In dorsal view, ornamentation not developed.   In ventral view, five pairs of ridges run parallel from anterior to posterior.   Posterior element of hingement is composed of three teeth.   Prominent fulcral point.   A total of sixteen species are included: *L. chinzeii, L. hemicrenulata, L. ikeyai, L. medioconvexa, L. optima, L. orientarica, L. pleistocenica, L. taiwanensis, L. tamakazura, L. tarda, L.* sp. (Hu, 1978), *L.* sp. (Ishizaki, 1984), *L.* sp. (Yajima, 1988), "*L. pulchra*" (in Yajima, 1988), "*L. sinensis*" (in Gou *et al.,* 1981), "*L. sinensis*" (in Zhao *et al.,* 1985).

Loxoconcha japonica *species group.*—Carapace subrhomboidal in lateral view.   Surface ornament of the carapace consists of concentrically- arranged pits or coarse reticulation centered around the muscle scars.   In dorsal view, a pair of ridges converges toward the anterior.   In ventral view,   five pairs of ridges developed that run parallel from anterior to posterior.   Posterior element of hingement is ball-shaped.   Fulcral point not prominent. The following four species are included: *L. japonica, L. lilljeborgii, L. shanhaiensis, L. tumulosa.*

Loxoconcha uranouchiensis *species group.*—Carapace

Table 1. Sample localities for *L. japonica* species group from East Asia. Sample numbers corresponds to those in Figure 2. Abbreviations: Alg. = Algae; M. = Mud; St. = Silt; Sd = Sand; R. = Rock; f. = fine; m. = medium; c. = coarse; mdy. = muddy; sdy. = sandy; gry. = gravelly; L. = late; M. = middle; E. = early; Ls. = Limestone; Pref. = Prefecture; Penin. = Peninsula; Is. = Island; Ja = *L. japonica* ; Sh = *L. shanhaiensis* ; Tu = *L. tumulosa* ; Li = *L. lilljeborgii*.

Recent materials

Sample number	Localities	Latitude (N)	Longitude (E)	Depth (m)	Remarks	Species
1a	Suttu Bay	42°48.9′	140°18.0′	22	R.	Ja
1b	〃	42°47.8′	140°16.2′	34	f.-Sd.	Ja
1c	〃	42°47.2′	140°18.7′	9	R.	Ja
1d	〃	42°47.2′	140°15.6′	26	f.-Sd.	Ja
1e	〃	42°46.7′	140°17.9′	11	f.-Sd.	Ja
1f	〃	42°46.7′	140°15.6′	17	f.-Sd.	Ja
1g	〃	42°46.2′	140°16.5′	7	c.-Sd.	Ja
1h	〃	42°46.2′	140°15.0′	5	c.-Sd.	Ja
2	Otsuchi Bay	39°19.6′	141°55.0′	15	c.-Sd.	Ja
3	Imagawa	38°24.6′	139°28.1′	0	Alg.	Ja
4	Aikawa	38°02.4′	138°14.3′	0	Alg.	Ja
5	Hayase	35°37.0′	135°54.7′	1	Alg.	Ja
6	Kagoshima	35°39.5′	134°46.8′	0	Alg.	Ja
7	Off Shimane	36°13.9′	133°06.0′	96	mdy., f.-m.-Sd.	Ja
8	Misaki	35°09.5′	139°37.0′	0	Sea glass	Ja
9	Osezaki	35°06.3′	138°47.4′	1	Alg.	Ja
10	Ago Bay	34°57.1′	136°40.5′	7	f.-Sd.	Ja
11	Hanesaki	33°22.0′	134°02.4′	0	Alg.	Ja
12	Uwajima Bay	33°10.8′	132°29.9′	5	v. c.-Sd.	Ja
13	Tsuyasaki	33°47.4′	130°27.7′	2	m.-Sd.	Ja
14	Danjyo Islands	32°01.9′	128°23.1′	86	f.-Sd.	Ja
15	Okawa-minato	31°14.6′	130°24.8′	0	Alg.	Ja
16	Tanega-shima Is.	30°10.3′	130°52.7′	96	c. shelly-Sd.	Ja
17	Amami-o-shima Is.	28°07.5′	129°22.0′	4	coral Sd.	Ja, Sh
18	Tokuno-shima Is.	27°51.6′	128°57.7′	0	Alg.	Ja, Tu
19	Yoron Is.	27°02.9′	128°27.3′	0	Alg.	Ja, Sh, Tu, Li
20a	Nago Bay	26°34.1′	127°56.4′	38	m.-St.	Sh
20b	〃	26°39.3′	127°51.5′	59	m.-Sd.	Ja, Sh
20c	〃	26°37.7′	127°52.2′	22	m.-Sd.	Ja, Sh
20d	〃	26°36.1′	127°53.5′	40	c.-Sd	Ja, Sh
20e	Nakagusuku Bay	27°19.2′	127°52.0′	4	sdy.-M.	Ja, Li
20f	〃	26°16.8′	127°50.3′	6	gry.-Sd.	Sh, Li
20g	〃	26°15.9′	127°54.3′	21	Sd.	Ja, Sh, Tu, Li
20h	〃	26°15.3′	127°53.1′	4	gry.-Sd.	Ja, Sh
20i	〃	26°15.0′	127°52.3′	20	Sd.	Ja, Sh
20j	〃	26°12.8′	127°55.0′	48	Sd.,-M.	Ja, Sh, Li
20k	〃	26°12.5′	127°52.9′	28	mdy.-Sd.	Ja, Sh, Li
20l	〃	26°10.1′	127°52.8′	22	Sd.	Ja, Sh
20m	〃	26°07.8′	127°53.9′	70	gry.-Sd.	Ja, Sh, Li
21	Off Miyako Is.	24°47.9′	127°37.4′	124	c.-Sd.	Sh
22	Sekisei-sho	24°27.4′	124°03.3′	167	f.-Sd.	Ja, Sh
23	Hengchun Penin.	21°56.0′	120°49.0′	0	Alg.	Sh, Tu

Fossil materials

| Sample number	Formation (age)	Localities	Latitude (N)	Longitude (E)	Remarks	Species
a	Hamada (L. Pleistocene)	Shimokita Penin.	41°10.3′	141°16.4′		Ja
b1	Sawane (Pliocene)	Sado Is.	37°59.6′	138°15.6′		Ja
b2	Sawane (Pliocene)	〃	37°59.3′	138°15.9′		Ja
c1	Hiradoko (L. Pleistocene)	Noto Penin.	37°27.0′	137°18.2′		Ja
c2	Miyainu (L. Pleistocene)	〃	37°20.2′	137°13.8′		Ja
c3	Numashiro (L. Pleistocene)	〃	35°19.4′	139°15.4′		Ja
d1	Ninomiya (L. Pleistocene)	Oiso Hill	35°18.9′	139°15.1′		Ja
d2	〃	〃	35°18.4′	139°15.4′		Ja
d3	〃	〃	35°18.2′	139°15.7′		Ja
e	Takahama (Holocene)	Fukui Pref.	35°29.2′	135°33.3′		Ja
f	Hamamatsu (Holocene)	Hamana-ko	34°44.8′	137°36.5′		Ja
g	Ananai (Plio-Pleistocene)	Shikoku	33°29.4′	133°56.7′		Ja
h	Shimo-jiro (M. Pleistocene)	Okino-erabu Is.	27°24.5′	128°38.3′		Sh
i	Maja (E. Pliocene)	Kume Is.	26°22.6′	126°47.4′		Ja
j1	Yonabaru (L. Pliocene)	Okinawa Is.	26°09.7′	127°46.7′		Ja
j2	Chinen Sand (E. Pleistocene)	Okinawa Is.	26°07.3′	127°43.8′		Ja
k	Tungshiao (L. Pleistocene)	Taiwan	24°36.0′	120°43.0′		Sh
l1	Hengchun Ls. (L. Pleistocene)	Taiwan	21°59.0′	120°43.0′		Ja, Sh, Li
l2	Hengchun Ls. (L. Pleistocene)	Taiwan	21°55.0′	120°51.0′		Sh, Tu
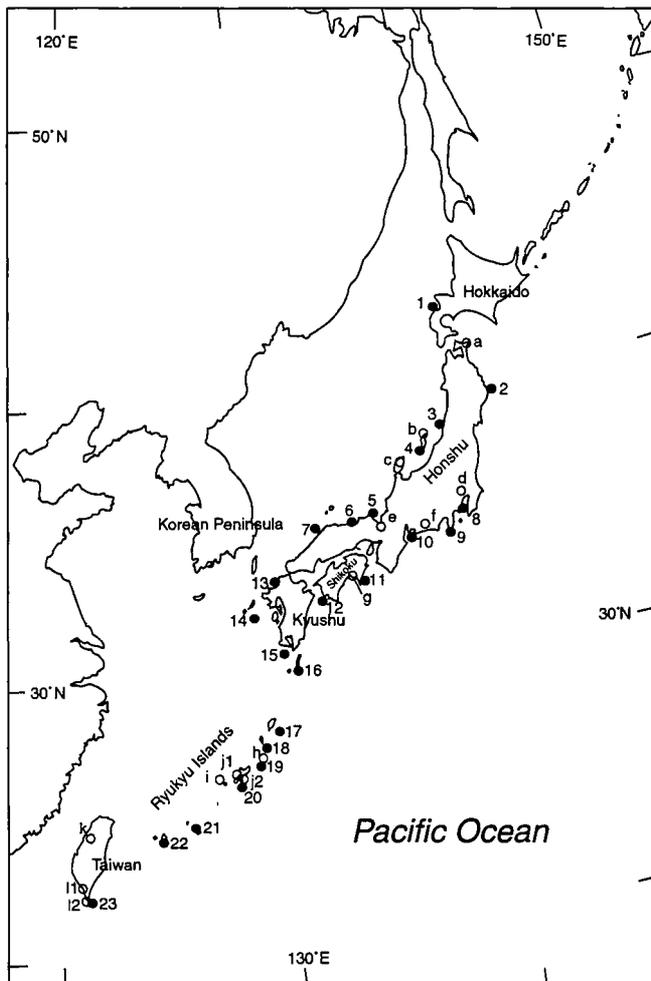
Figure 2. Map showing sampling localities. Numbers and lower case letters correspond to the sample numbers in Table 1.

subrhomboidal to oblong in lateral view. Surface ornament of the carapace consists of reticulation. In dorsal view, the carapace is covered with irregular reticulation. In ventral view, three- or four-pairs of ridges run parallel from anterior to posterior, the most ventral pair being developed only in the anterior region. Posterior element of hingement is ball-shaped. Prominent fulcral point. A total of forty-three species are included: *L. bispinosa, L. bizenensis, L. brevia, L. crassela, L. crispatum, L. epeterseni, L. hanachirusato, L. harimensis, L. hattorii, L. kattoi, L. kitanipponica, L. malayensis, L. nozokiensis, L. paiki, L. pashihaiensis, L. prolaeta, L. sinensis, L. tata, L. tosaensis, L. tosamodesta, L. triconicula, L. uranouchiensis, L. ventispina, L. viva, L. xuwenensis, L. yinggehaiensis, L. zamia, L. zhejiangensis, L.* sp. A (Huh, 1992), *L.* sp. B (Ishizaki, 1968), *L.* sp. B (Lee, 1990), *L.* sp. C (Huh, 1992), *L.* sp. 2 (Yamane, 1998), "*L. hattorii*" (in Cai, 1982), "*L. hattorii*" (in Wang and Zhang, 1987), "*L. kattoi*" (in Ruan and Hao, 1988), "*L. sinensis*" (in Gou *et al.*, 1981), "*L.*

sinensis" (in Ruan and Hao, 1988), "*L. uranouchiensis*" (in Cai and Chen, 1987), "*L.* cf. *uranouchiensis*" (in Gou *et al.*, 1983), "*L. uranouchiensis*" (in Tabuki *et al.*, 1987), "*L. uranouchiensis*" (in Yamane, 1998), "*L. viva*" (in Wang *et al.*, 1988).

Loxoconcha ozawai *species group.*—Carapace subrhomboidal to oblong in lateral view. Surface ornamentation of the carapace consists of weak reticulation. In dorsal view, the carapace is covered with weak, irregular reticulation. In ventral view, two pairs of weak ridges converge toward anterior. Posterior element of hingement is ball-shaped. Prominent fulcral point. The following sixteen species are included: *L. binhaiensis, L. elliptica, L. fujianensis, L. gigantea, L. hataii, L. ocellata, L. ozawai, L. subkotoraforma, L.* sp. (Ikeya *et al.*, 1992), *L.* sp. (Tsukagoshi and Kamiya, 1996), *L.* sp. B (Huh, 1992), *L.* sp. B (Ishizaki, 1971), *L.* sp. D (Huh, 1992), *L.* sp. 1 (Ozawa, 1996), *L.* sp. 1 (Yamane, 1998), "*L. sinensis*" (in Zhao and Wang, 1988).

Natural history of *Loxoconcha japonica* species group

Morphological characters

In order to characterize the *L. japonica* species group, four species of the group were compared in terms of carapace morphology (Figures 3, 4), pore system (Figure 5), appendages (Figure 6) and male copulatory organ (Figure 7). The following summarizes the morphology of this species group.

Carapace outline.—Carapace subrhomboidal in lateral view. Dorsal margin straight and sloped toward anterior or arched dorsally; anterior margin with an oblique curvature; ventral margin slightly concave at mid-anterior area; posterior margin curved toward the dorsal. Caudal process protrudes prominently toward posterodorsal. In dorsal and ventral view, carapace diamond- to wedge-shaped. In posterior view, carapace elliptical to egg-shaped. Large sexual dimorphism; in lateral view, male more elongate.

Carapace ornamentation.—Surface of the carapace is entirely ornamented with pits or coarse reticulation in lateral view. The ornamentation is concentrically arranged, consisting of eight rings centered around the position of the muscle scar. Posteroventral alate ridge and/or posterodorsal protuberance are/is sometimes developed. In ventral view, five pairs of ridges run parallel from the anterior to posterior margins. In dorsal view, a pair of ridges converges toward the anterior. In posterior view, on the ventral side of the posterior margin, four pairs of short ridges are developed that consist of reticulations arranged parallel to the posterior margin. On the dorsal side of the posterior margin, on the other hand, radially-developed ridges centered near the position of the caudal process intersect ridges that parallel the posterior margin.

Hinge.—Gongylodont. In left valve, anterior element is
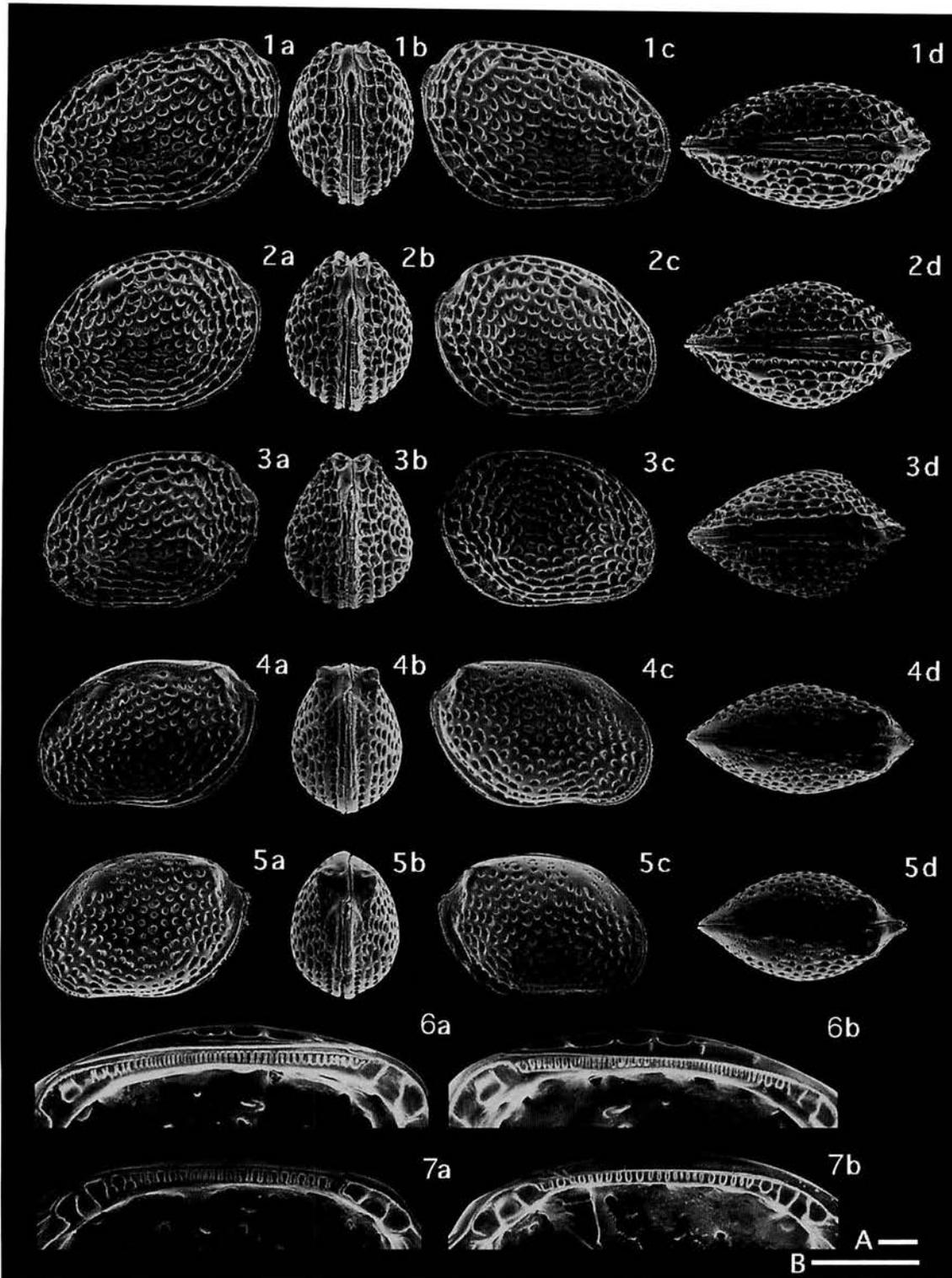
Figure 3. 1–3, 6. *Loxoconcha japonica* Ishizaki, 1968. 4, 5, 7. *Loxoconcha lilljeborgii* Brady, 1868. 1. A male carapace of the same specimen in external left lateral view (**a**), posterior view (**b**), right lateral view (**c**) and dorsal view (**d**) from sample no. 8 (SUM–CO–1269). 2. A female carapace of the same specimen in external view (**a–d**) from sample no. 8 (SUM–CO–1270). 3. A female carapace of the same specimen with alate ridge at the posteroventral area in external view (**a–d**) from sample no. 17 (SUM–CO–1271). 4. A male carapace of the same specimen in external view (**a–d**) from sample no. 19 (SUM–CO–1305). 5. A female carapace of the same specimen in external view (**a–d**) from sample no. 19 (SUM–CO–1306). 6. Hingement of female right (**a**) (SUM–CO–1272) and left (**b**) (SUM–CO–1273) valves from sample no. 19. 7. Hingement of female right (**a**) (SUM–CO–1307) and left (**b**) (SUM–CO–1308) valves from sample no. 19. Scale bars = 100 μm (A for 1–5; B for 6, 7).
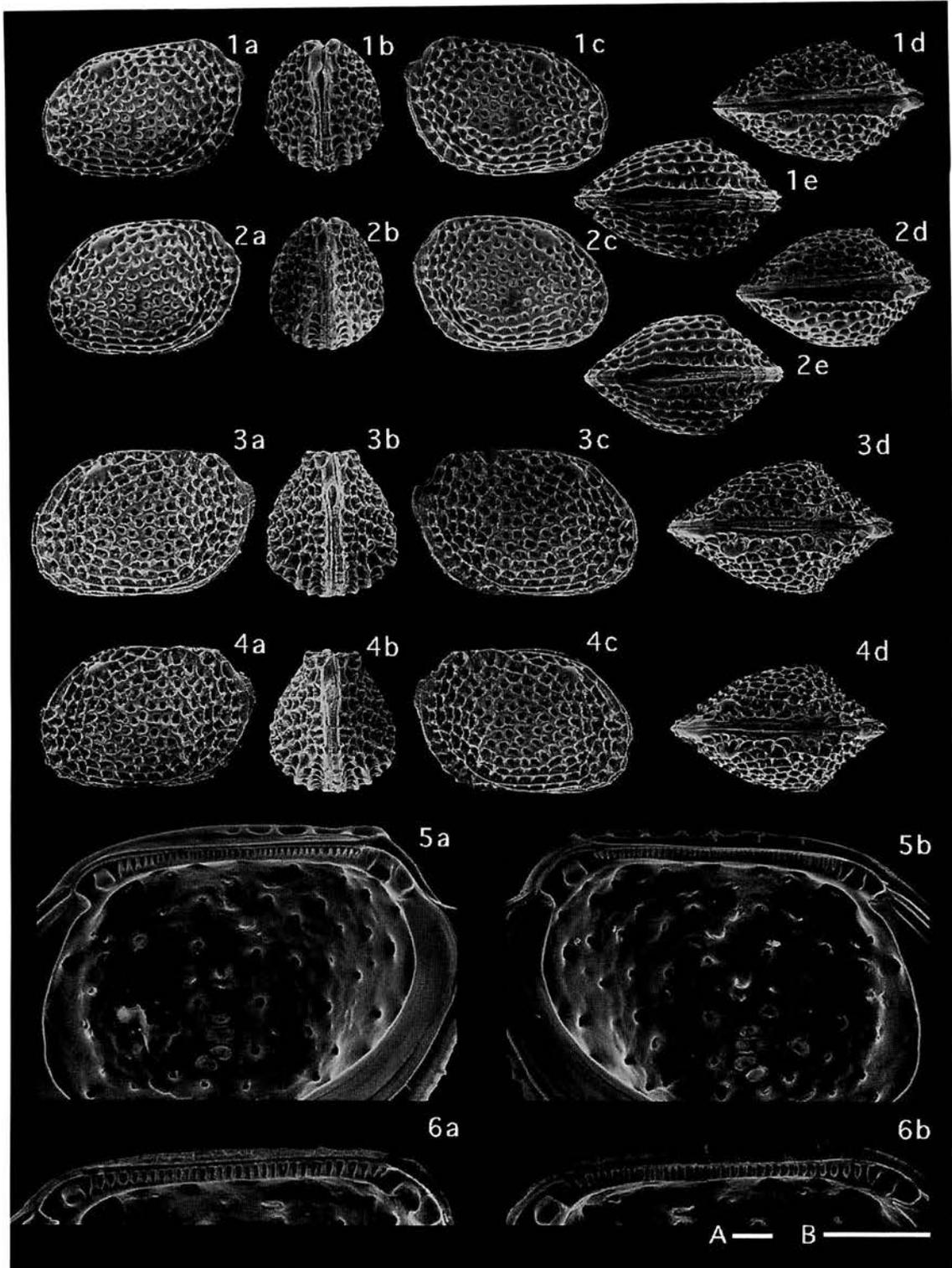
Figure 4. **1, 2, 5.** *Loxoconcha shanhaiensis* Hu, 1981.   **3, 4, 6.** *Loxoconcha tumulosa* (Hu, 1979).   **1.** A male carapace of the same specimen in external left lateral view (**a**), posterior view (**b**), right lateral view (**c**), dorsal view (**d**) and ventral view (**e**) from sample no. 17 (SUM-CO-1284). **2.** A female carapace of the same specimen in external view (**a–e**) from sample no. 17 (SUM-CO-1285).   **3.** A male carapace of the same specimen in external view (**a–d**) from sample no. 23 (SUM-CO-1294).   **4.** A female carapace of the same specimen in external view (**a–d**) from sample no. 23 (SUM-CO-1295).   **5.** Hingement and muscle scars of female right (**a**) (SUM-CO-1286) and left (**b**) (SUM-CO-1287) valves from sample no. 20h.   **6.** Hingement of female right (a) (SUM-CO-1296) and left (b) (SUM-CO-1297) valves from sample no. 23.   Scale bars = 100 μm (A for 1–4; B for 5, 6).

a down-turned claw, median element with 25–51 teeth, and posterior element is ball-shaped.
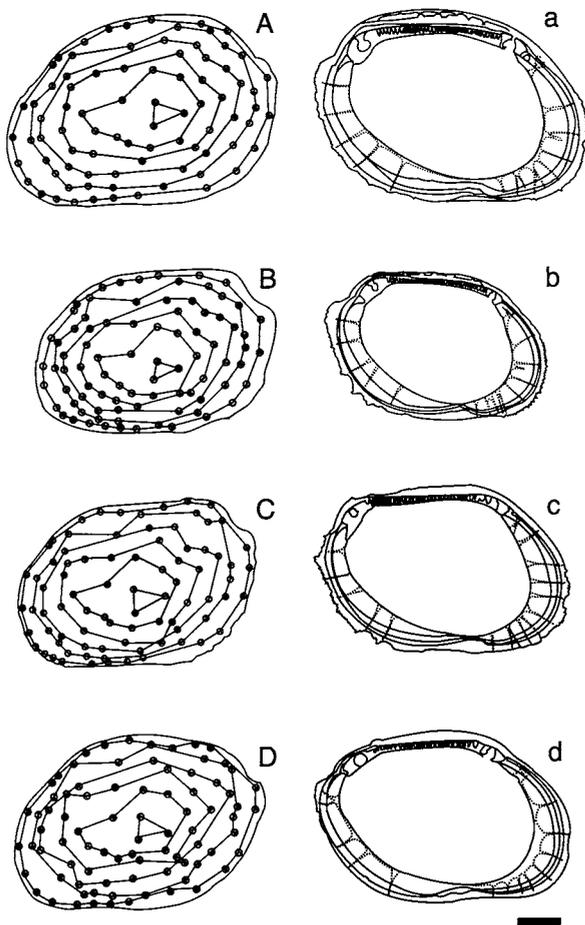
Ocular sinus.—In all four species, nipple-like projection develops at the dorsoposterior portion in internal view.

Muscle scars.—Four adductor muscle scars in an arcuate row, concave anterior. The upper of the two middle ones is larger than the rest. A bean-shaped frontal scar of occurs in front of the lower two adductor muscle scars. Two mandibular scars in front and below the lowest adductor muscle scar. Fulcral point absent.

Pore system.—In all species, 83 sieve-type pores are distributed in each adult valve, and each pore opening location resembles among four species (left side of Figure 5). Distribution of radial pores falls into two patterns (right side of Figure 5), depending on numbers of pores extending to marginal area: a), 11 in anterior area and 5 in posterior area: *L. japonica*, *L. shanhaiensis* and *L. tumulosa*; b), 10 and 5, respectively: *L. lilljeborgii*. Moreover, *L. lilljeborgii* is differentiated from the other three species, in that

Figure 5. The pattern of distribution pores in external view (A–D) and the radiation of radial pores in internal view (a–d) on four species of the *Loxoconcha japonica* species group (all specimens are female left valves). A, a. *Loxoconcha japonica* Ishizaki, 1968 (A, SUM-CO-1262; a, SUM-CO-1263). B, b. *Loxoconcha shanhaiensis* Hu, 1981 (B, SUM-CO-1274; b, SUM-CO-1275). C, c. *Loxoconcha tumulosa* (Hu, 1979) (C, SUM-CO-1288; c, SUM-CO-1289). D, d. *Loxoconcha lilljeborgii* Brady, 1868 (D, SUM-CO-1298; d, SUM-CO-1299). Scale bar = 100 μm.
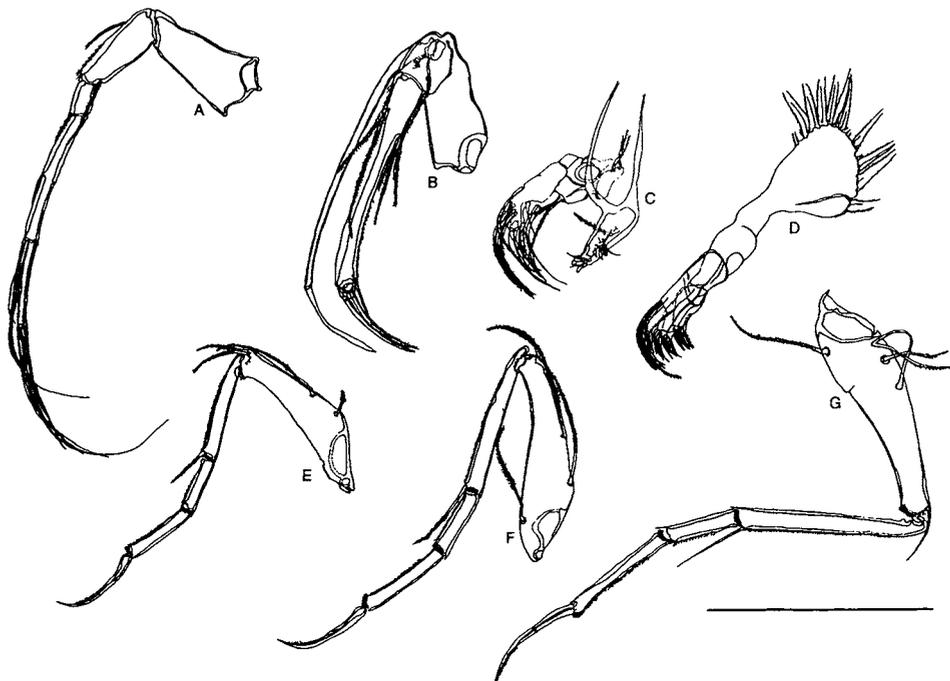

Figure 6. Chitinous parts of *Loxoconcha shanhaiensis* Hu, 1981 from sample no. 20f. A, antennule; B, antenna (SUM-CO-1277); C, mandible; D, maxilla (SUM-CO-1278); E, first thoracic leg; F, second thoracic leg; G, third thoracic leg (SUM-CO-1279). Scale bar = 50 μm.
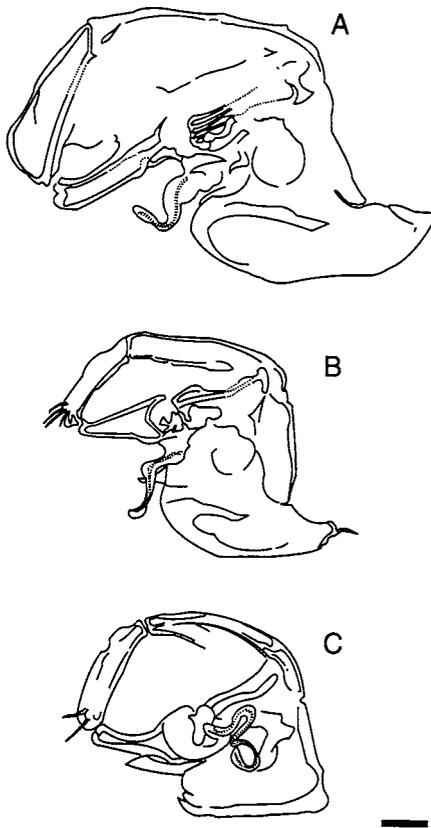
Figure 7. Male copulatory organs of three species of *Loxoconcha japonica* species group. **A.** *Loxoconcha japonica* Ishizaki, 1968 from sample no. 8 (SUM-CO-1264). **B.** *Loxoconcha shanhaiensis* Hu, 1981 from sample no. 20f (SUM-CO-1276). **C.** *Loxoconcha lilljeborgii* Brady, 1868 from sample no. 19 (SUM-CO-1300). Scale bar = 50 μm.

the upper two pores of at the posterior margin branch in the middle of the marginal infoldment.

Appendages.—No significant differences are observed among the four species.

Male copulatory organ.—Except for *L. tumulosa*, outline of the basal capsule is trapezoidal and costa are developed in three species. In detail, however, several differences are observed among the three species in morphology of the copulatory organ. Distal corner rounded in *L. lilljeborgii* but tapered in *L. japonica* and *L. shanhaiensis*; ductus ejaculatorius curved in *L. lilljeborgii* but shoehorn-shaped in *L. japonica* and *L. shanhaiensis*; clasping apparatus absent in *L. japonica*, triangular in *L. shanhaiensis* and square in *L. lilljeborgii*.

Ontogenetic differentiation in carapace morphology

For the carapace morphologies of the four species, the ontogenetic differentiation from the A-2 instar to the adult were compared.

Carapace outline (Figure 8).—The position of the maximum height shifts toward the posterior from the A-2 instar to the adult. The time of shift is at the A-1 instar for *L. japonica* and *L. lilljeborgii* and at the adult for *L. shanhaiensis* and *L. tumulosa*.

The position of the maximum width is stationary from the A-2 instar to the adult (*L. shanhaiensis* and *L. tumulosa*) or shifts to the anterior at the adult (*L. lilljeborgii* and the male of *L. japonica*).

Carapace ornamentation (Figure 8).—The concentric arrangement of reticulation or pits is fixed from the A-2 instar to the adult. From the A-2 instar to the adult, the developmental state of reticulation or pits, however, differs from species to species. Namely, *L. japonica* already has adult-like coarse reticulation in the A-2 instar, but *L. shanhaiensis* and *L. tumulosa* only attain coarse reticulation in the A-1 instar. *L. lilljeborgii* has pits in the A-2 and A-1 instars, and is smoothly reticulate in the adult.

The posteroventral alate ridge is well developed in the A-2 and A-1 instars of all four species. In the adult, this character is retained in *L. shanhaiensis* and *L. tumulosa*, but disappears in *L. lilljeborgii* and the male of *L. japonica*. In the female of *L. japonica*, however, some specimens keep and others lose this character.

The posterodorsal protuberance does not appear during ontogenetic development in *L. japonica* and *L. shanhaiensis*, whereas, it appears from the A-1 instar onward in *L. tumulosa* and *L. lilljeborgii*.

Hinge (Figure 9).—Although development of the anterior element of the hinge is weak in the A-2 instar, these species clearly possess a gongylodont hinge after the A-1 instar. The number of teeth in the median element could not be counted in the A-2 instar, since it is smooth, however, from the A-1 instar onward the number of teeth is: 42–51 in *L. japonica*, 39–40 in *L. shanhaiensis*, 31–40 in *L. tumulosa*, and 25–31 in *L. lilljeborgii*.

Ocular sinus (Figure 9).—The nipple-like projection in the dorsoposterior area on the internal side appears after the A-2 instar for *L. japonica*, *L. shanhaiensis* and *L. tumulosa* and after the A-1 instar for *L. lilljeborgii*.

Muscle scars (Figure 4).—After the A-2 instar, the four species have four adductor muscle scars in an arcuate row; with no morphological variation in this feature among the species.

Pore system (Figure 8).—The total number of sieve-type pores per valve is the same in all four species: 54 in the A-2 instar, 73 in the A-1 instar and 83 in the adult.

From the carapace characters described above, it is thought that *L. japonica*, *L. lilljeborgii* and an ancestor of *L. shanhaiensis-L. tumulosa* differentiated at the A-2 instar, and that *L. shanhaiensis* and *L. tumulosa* differentiated in the A-1 instar (Figure 10).
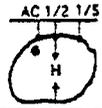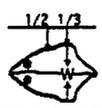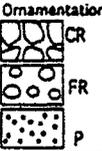
Carapace outline			Carapace ornamentation			Pore system	
Lateral Max. height AC 1/2 1/5	Dorsal Max. width 1/2 1/3	Posterior Max. width 1/2 1/4	Ornamentation CR FR P	Alate ridge AR	Protuberance PT	Numbers/valve	
A-2							
AC	1/3	1/4	CR	AR	Non	54	*L. japonica*
AC	1/3	1/4	P	AR	Non	54	*L. shanhaiensis*
AC	1/3	1/4	P	AR	Non	54	*L. tumulosa*
AC	1/3	1/4	P	AR	Non	54	*L. lillieborgii*
A-1							
1/2	1/3	1/4	CR	AR	Non	73	*L. japonica*
AC	1/3	1/4	CR	AR	Non	73	*L. shanhaiensis*
AC	1/3	1/4	CR	AR	PT	73	*L. tumulosa*
1/2	1/3	1/4	P	AR	PT	73	*L. lillieborgii*
Adult ♀							
1/2	1/3~1/2	1/4~1/2	CR	AR or Non	Non	83	*L. japonica*
1/3	1/3	1/4	CR	AR	Non	83	*L. shanhaiensis*
1/2	1/3	1/4	CR	AR	PT	83	*L. tumulosa*
1/2	1/2	1/2	FR	Non	PT	83	*L. lillieborgii*
Adult ♂							
1/5	1/2	1/2	CR	Non	Non	83	*L. japonica*
1/5	1/3	1/4	CR	AR	Non	83	*L. shanhaiensis*
1/2	1/3	1/4	CR	AR	PT	83	*L. tumulosa*
1/5	1/2	1/2	FR	Non	PT	83	*L. lillieborgii*

Figure 8. Schematic diagram of ontogenetic differentiation of carapace morphology. Abbreviations: AC = anterior cardinal angle, H = maximum height, W = maximum width on dorsal view, W' = maximum width on posterior view, CR = coarse reticulation, FR = fine reticulation, P = pit, AR = alate ridge, PT = protuberance.

Paleobiogeography

On the basis of our materials and published reports, we considered the paleobiogeographic distributions of the four species.

Fossil distribution (Figure 11).—The oldest specimens of *L. lilljeborgii* and *L. tumulosa* occur in the Late Miocene Round Chalk and Silt Formation from the Andaman Islands of the Indian Ocean (Loc. A: Guha, 1968). Two species are also reported from the Pliocene Guiter Formation from the same region (Loc. A': Guha, 1968). These two species, however, occur also in the Late Pleistocene in the West Pacific region. Namely, *L. lilljeborgii* occurs from the Late Pleistocene Hengchun Limestone from Taiwan (Loc. E: Figure 2, 11) and in the Late Pleistocene Gundurimba Clay from Australia (Loc. C: McKenzie and Pickett, 1984), and *L. tumulosa* occurs from the Late Pleistocene Hengchun Limestone from Taiwan (Loc. D: Figure 2, loc. 12).

The oldest specimen of *L. japonica* comes from the Early Pliocene Maja Formation from Kume Island of the Ryukyus (Loc. G: Figure 2, loc. i). This species also occurs in thirteen post-Pliocene formations ranging from Taiwan to the northern part of Honshu (Locs. D, H and J–S) and in Holocene sediments from Hong Kong (Loc. B: Cao, 1998).

The oldest fossil occurrence of *L. shanhaiensis* is known
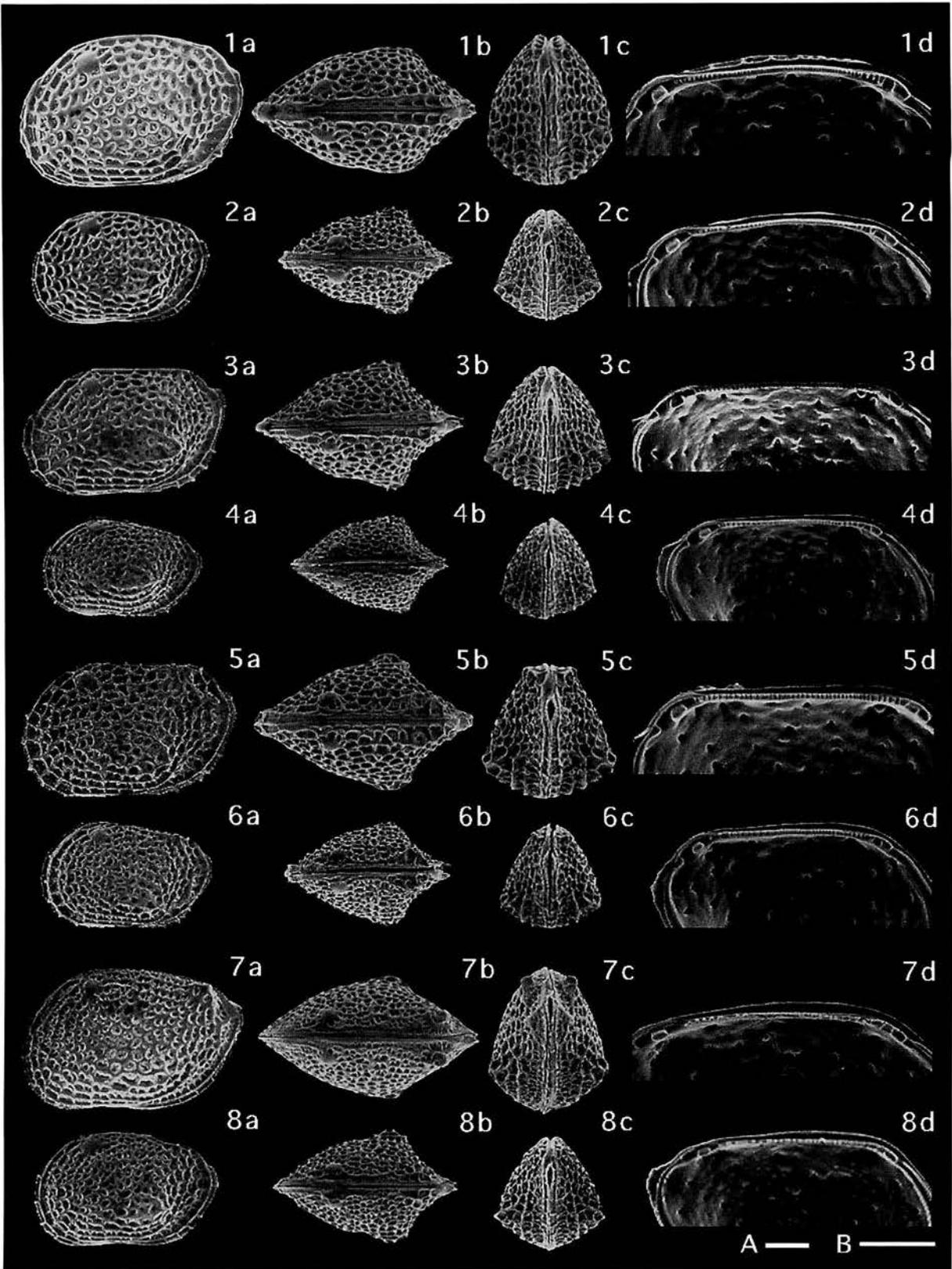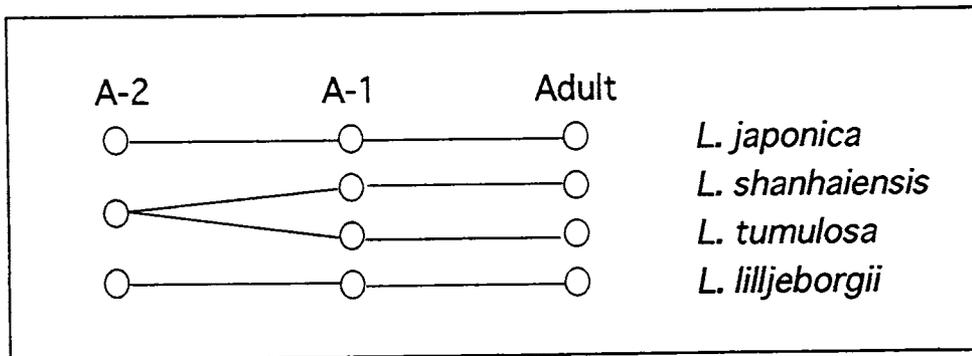
Figure 10. Ontogenetic differentiation of four species based on carapace characters.
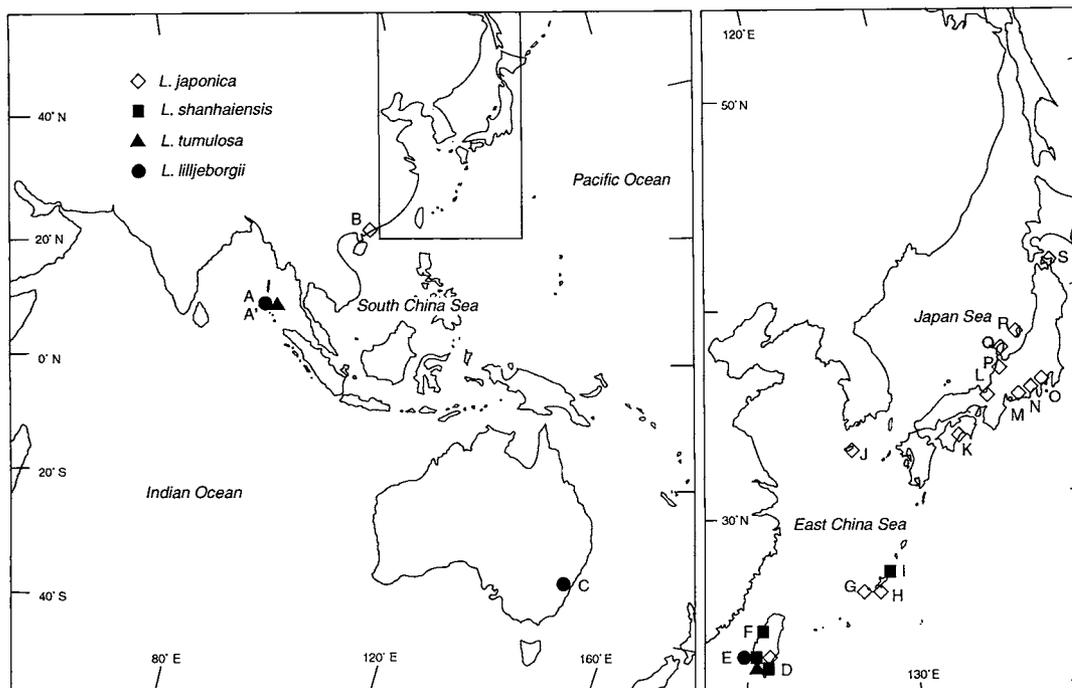
Figure 11. Geographic distribution of four species of *Loxoconcha japonica* species group (fossil). A and A' (Late Miocene Round Chalk and Silt Formation and Pliocene Guiter Formation; Guha, 1968); B (Holocene Hang Hau Formation; Cao, 1998); C (Late Pleistocene Gundurimba Clay; McKenzie and Pickett, 1984); D (Late Pleistocene Hengchun Limestone; Hu, 1979); E (Late Pleistocene Hengchun Limestone; Hu, 1981); F (Late Pleistocene Tungshiao Formation; Hu, 1986); G (Early Pliocene Maja Formation); H (Early Pleistocene Chinen Sand); I (Middle Pleistocene Shimo-jiro Formation); J (Early Pleistocene Sogwipo Formation and Middle Pleistocene Shinyangri Formation; Lee, 1990); K (Plio-Pleistocene Ananai Formation); L (Holocene Takahama shell bed); M (Holocene Hamamatsu Formation); O (Holocene bore hole core samples; Irizuki *et al.*, 1998); P (Plio-Pleistocene Omma Formation; Ozawa, 1996); Q (Late Pleistocene Miyainu and Numashiro formations); R (Pliocene Sawane Formation); S (Late Pleistocene Hamada Formation).

◀ **Figure 9.** Juvenile specimens of *Loxoconcha japonica* species group. 1, 2. *Loxoconcha japonica* Ishizaki, 1968. 3, 4. *Loxoconcha shanhaiensis* Hu, 1981. 5, 6. *Loxoconcha tumulosa* (Hu, 1979). 7, 8. *Loxoconcha lilljeborgii* Brady, 1868. 1. A-1 stage carapace of same specimen in external left lateral view (a), dorsal view (b) and posterior view (c) from sample no. 8 (SUM-CO-1265), and hingement of the same stage of left valve (d) from sample no. 8 (SUM-CO-1266). 2. A-2 stage carapace of same specimen in external view (a-c) from sample no. 8 (SUM-CO-1267), and hingement of the same stage of left valve (d) from sample no. 8 (SUM-CO-1268). 3. A-1 stage carapace of same specimen in external view (a-c) from sample no. 20h (SUM-CO-1280), and hingement of the same stage of left valve (d) from sample no. 20h (SUM-CO-1281). 4. A-2 stage carapace of same specimen in external view (a-c) from sample no. 20h (SUM-CO-1282), and hingement of the same stage of left valve (d) from sample no.20h (SUM-CO-1283). 5. A-1 stage carapace of same specimen in external view (a-c) from sample no. 23 (SUM-CO-1290), and hingement of the same stage of left valve (d) from sample no. 23 (SUM-CO-1291). 6. A-2 stage carapace of same specimen in external view (a-c) from sample no. 23 (SUM-CO-1292), and hingement of the same stage of left valve (d) from sample no. 23 (SUM-CO-1293). 7. A-1 stage carapace of same specimen in external view (a-c) from sample no. 19 (SUM-CO-1301), and hingement of the same stage of left valve (d) from sample no. 19 (SUM-CO-1302). 8. A-2 stage carapace of same specimen in external view (a-c) from sample no. 19 (SUM-CO-1303), and hingement of the same stage of left valve (d) from sample no. 19 (SUM-CO-1304). Scale bars = 100 μm. (A for a-c; B for d)
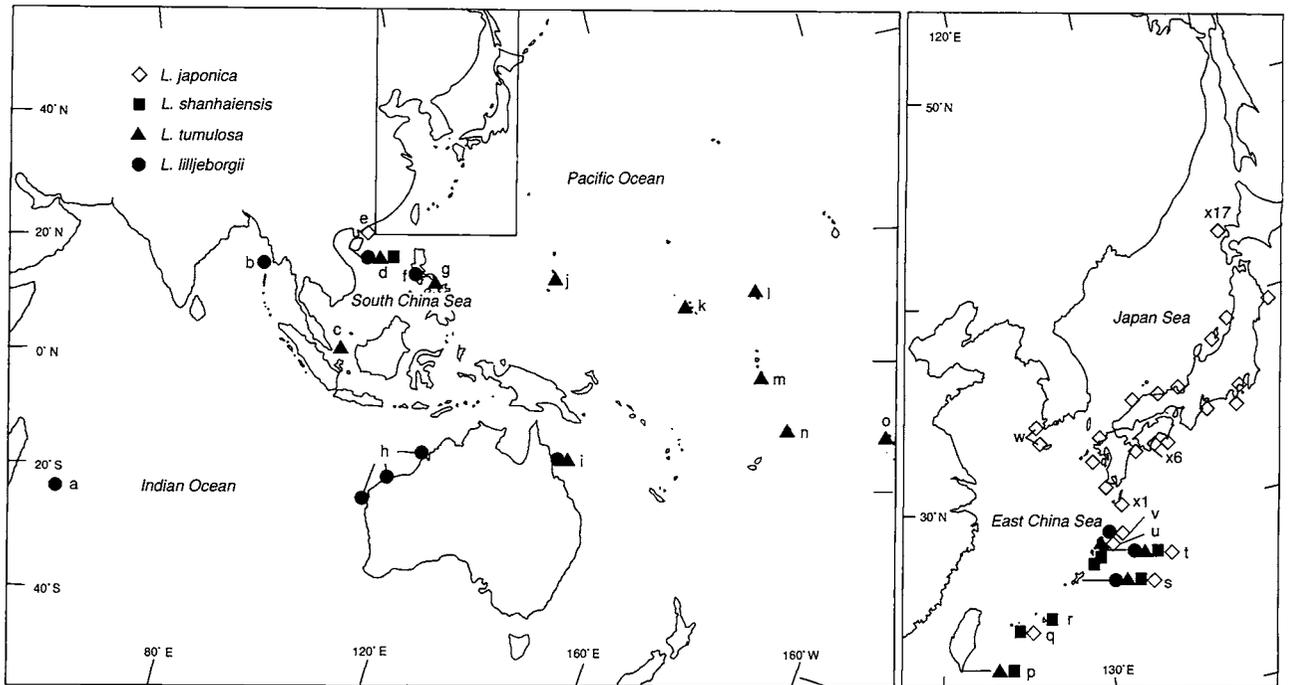
Figure 12. Geographic distributions of four species of *Loxoconcha japonica* species group (Recent). a (Mauritius; Brady, 1868); b (Burma; Gramann, 1975); c (Sunda Shelf; Mostafawi, 1992); d (Hainan Island; Gou, 1990); e (Hong Kong); f (Manila Bay; Keij, 1954); g (Cebu Island); h (West Australian Coast; Hartmann and Hartmann, 1978); i (Lizard Island; Behrens, 1991); j (Guam); k (Truk); l (Marshall Islands); m (Gilbert Islands); n (Samoa); o (Tuamotu Islands; Hartmann, 1984); p (South Taiwan); q (Sekisei-sho); r (Miyako Island); s (Okinawa); t (Yoron Island); u (Tokuno-shima Island); v (Amami-o-shima Island); w (southern part of Korean Peninsula; Choe, 1984MS); x 1–17 (Japan coast; x6 = Uranouchi Bay; Ishizaki, 1968). e, g, and j-n (R. Ross, pers. comm., 2002).

from the Middle Pleistocene Shimo-jiro Formation from the Okino-erabu Island of the Ryukyus (Loc. I: Figure 2, loc. h). This species also occurs in two Late Pleistocene formations from Taiwan, the Hengchun Limestone (Locs. D and E: Figure 2, locs. 11 and 12) and the Tungshiao Formation (Loc. F: Figure 2, loc. k).

Recent distribution (Figure 12).—*L. lilljeborgii* is widely distributed over lower latitude coastal regions of the Indian Ocean (Locs. a and b), the South China Sea (Locs. d and f), the northern part of Australia (Locs. h and i) and the Ryukyus (Locs. s, t and v: Figure 2, locs. 17, 19 and 20). *L. tumulosa* is distributed over lower latitudes in the West Pacific coastal regions of the South China Sea (Locs. c, d and g), the northeastern part of Australia (Loc. i), many islands of the West Pacific (Locs. j-o), Taiwan (Loc. p: Figure 2, loc. 23), and the Ryukyus (Locs. s-u: Figure 2, locs. 18–20). *L. japonica* is distributed over lower-to middle latitude coastal regions from Hong Kong to Japan (Locs. e, q, s, t, u, v, w and x1-17: Figure 2, locs. 1-20 and 22). *L. shanhaiensis* is only distributed over the lower latitude coastal regions of Hainan Island (Loc. d), Taiwan (Loc. p: Figure 2, loc. 23) and the Ryukyus (Locs. q-t: Figure 2, locs. 17 and 19-22).

The dispersal and evolution of the four species can be in-

ferred from these data (Figure 13). Firstly, *L. lilljeborgii* and *L. tumulosa* were distributed over the Indian Ocean in the Late Miocene. Secondly, these species migrated from the Indian Ocean to the West Pacific Ocean during the Early Pliocene. Based on morphological and ontogenetic information, together with biogeographic data, *L. japonica* evolved from the northern population of *L. tumulosa*. Finally, *L. shanhaiensis* evolved from the southern population of *L. japonica* in the Middle Pleistocene. These inferences are discussed in greater detail below.

Discussion

Paleobiogeographic and ontogenetic changes in the carapace morphology of the *L. japonica* species group from East Asia are the key to interpreting the phylogeny of the group. In the preceding section, we deduced that *L. japonica* evolved from *L. tumulosa* in the Early Pliocene. In *L. japonica*, the lateral outline and the surface ornamentation change in the A-1 instar and the A-2 instar, respectively. In contrast, in *L. tumulosa*, the lateral outline and the surface ornamentation change in the adult and the A-1 instar, respectively. Futhermore, in *L. japonica*, the alate ridge, which is a common character among the juvenile stages of
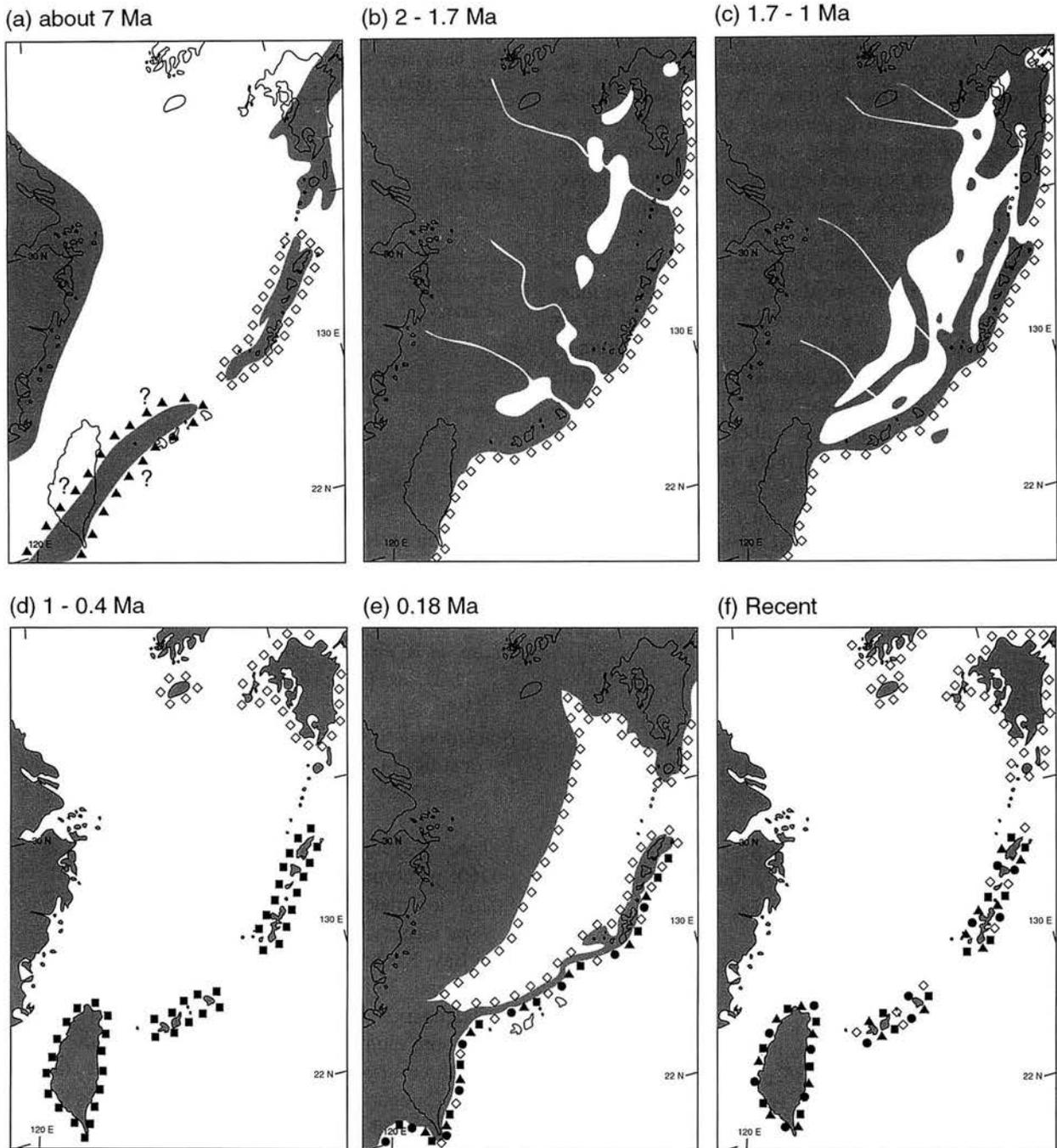
Figure 13. Paleobiogeographic distribution of *Loxoconcha japonica* species group around the Ryukyus. Shaded zones are land areas. *Loxoconcha japonica* Ishizaki, 1968 (open diamond shapes), *Loxoconcha shanhaiensis* Hu, 1981 (solid squares), *L. tumulosa* (Hu, 1979) (solid triangles) and *L. lilljeborgii* (solid circles). Paleogeographic reconstructions are after (a), Ujiié (1986); (b)–(d), Kimura (1996); (e), Ujiié and Nakamura (1996).

all four species, disappears in most adult specimens. From this evidence, the carapace characters of *L. japonica* are considered to have developed by peramorphosis. Moreover, it was deduced that *L. shanhaiensis* differentiated from *L. japonica* in the Middle Pleistocene. In *L. shanhaiensis*, ontogenetic changes of the lateral outline and the surface ornamentation are delayed by one stage, and the adult stage retains the alate ridge. These data indicate that the carapace characters of *L. shanhaiensis* are derived from *L. japonica* by paedomorphosis.

A heterochronic process results from the modification of the relationships among three parameters-age, size and

shape-which are assumed to be independent (Gould, 1977). Peramorphosis and paedomorphosis are each subdivided into three processes, and heterochronic evolution is described by one or more of these six processes (Kluge, 1988). In many taxa, it is generally assumed that age is equivalent to size when dealing with fossils, but in fact the relationship between age and size is not always correlative. In the case of ostracods, each instar can be compared in relative age, but relative age does not always correspond to absolute age. If it is assumed that the relative age equals the absolute age, we can consider age and size to be independent of each other. We cannot decide which of the six processes can be applied to the heterochronic evolution of the *L. japonica* species group, because we lack information on the earliest ontogenetic stage of each species. Nonetheless, we can state that either peramorphosis or paedomorphosis has occurred. If the number of moltings is the same among the four species, then it is likely that *L. japonica* became differentiated from *L. tumulosa* by pre-displacement and *L. shanhaiensis* was derived from *L. japonica* by post-displacement. To solve these phylogenetic problems, it is essential to clarify the life history of the species in culturing experiments (Ikeya and Kato, 2000).

Systematic descriptions

Order Podocopida G. W. Müller, 1894
Suborder Podocopina Sars, 1866
Superfamily Cytheracea Baird, 1850
Family Loxoconchidae Sars, 1925
Subfamily Loxoconchinae Sars, 1925
Genus *Loxoconcha* Sars, 1866

Loxoconcha japonica Ishizaki, 1968

Figures 3.1-3.3, 3.6; 5A, 5a; 7A; 9.1, 9.2

Loxoconcha japonica Ishizaki, 1968, p. 28, 29, pl. 2, fig. 1, pl. 6, figs. 10-12; Ishizaki, 1971, p. 86, pl. 3, fig. 21; Okubo, 1980, p. 416-418, figs. 12, 13, 18a-d; Hu, 1981, p. 77, pl. 3, fig. 7; Kamiya, 1988a, pl. 1, figs. 1-7, text-figs. 4, 5, 7, 8, 10, 11, 13; Kamiya, 1988b, pl. 1, figs. 1-6; Kamiya, 1988c, pl. 1, figs. 9-16; Kamiya, 1989a, pl. 1, figs. 1-8, 13, 14, 17, pl. 2, figs. 1-3, 10, text-figs. 1-8; Kamiya, 1989b, figs. 3, 4, 6, 7, 9, 11, 12; Ruan and Hao, 1988, p. 323, pl. 57, figs. 11-13; Lee, 1990, p. 358, pl. 34, figs. 3, 4; Ikeya and Suzuki, 1992, pl. 5, fig. 9; Kamiya and Hazel, 1992, figs. 1, 3, 4, pl. 1; Kamiya and Nakagawa, 1993, pl. 5, figs. 11, 12; Ozawa, 1996, pl. 6, fig. 5; Cao, 1998, pl. 3, figs. 16-19; Irizuki *et al.*, 1998, fig. 3-5; Yamane, 1998, pl. 6, fig. 2; Yasuhara and Irizuki, 2001, pl. 6, fig. 12.
Loxoconcha impressa (Baird). Kajiyama, 1913, p. 9, pl. 1, figs. 50, 51.

Table 2. Measurements of valve of *Loxoconcha japonica* Ishizaki, 1969 from sample nos. 1, 6, 8 and 17. Abbreviations: Av = average; OR = observation range; N = number of specimens; M = male; F = female; R = right; L = left.

Sample (No.)	Sex	Valve	Length (mm)		Height (mm)		N
			Av.	OR	Av.	OR	
Suttu Bay (1)	M	R	0.65	0.63-0.67	0.45	0.43-0.46	15
	M	L	0.66	0.64-0.69	0.44	0.41-0.46	14
	F	R	0.58	0.55-0.62	0.42	0.40-0.45	27
	F	L	0.59	0.55-0.64	0.43	0.40-0.45	29
Kagoshima (6)	F	L	0.54	0.49-0.60	0.40	0.38-0.44	24
Misaki (8)	M	R	0.59	0.56-0.64	0.40	0.38-0.43	30
	M	L	0.60	0.57-0.64	0.40	0.37-0.44	36
	F	R	0.54	0.51-0.61	0.39	0.36-0.43	42
	F	L	0.55	0.52-0.61	0.40	0.37-0.44	46
Amami Is. (17)	M	R	0.59	0.55-0.64	0.40	0.37-0.43	30
	M	L	0.59	0.56-0.64	0.41	0.37-0.43	29
	F	R	0.54	0.49-0.58	0.38	0.35-0.41	58
	F	L	0.54	0.50-0.59	0.39	0.35-0.43	64

Loxoconcha sp. Hanai, 1961, p. 371, text-fig. 12, figs. 4a, b; Igo and Ikeya, 1971, p. 204, fig. 13.
Loxoconcha sp. A. Ishizaki, 1968, p. 34, pl. 7, figs. 4, 5; Ishizaki, 1971, p. 88, pl. 3, fig. 16.
? *Loxoconcha japonica* Ishizaki. Hu, 1979, p. 69-70, pl. 2, figs. 32-37, text-fig. 8; Hu, 1984, pl. 4, figs. 24-26; Cai, 1982, pl. 3, fig. 21.
Non *Loxoconcha japonica* Ishizaki. Hu, 1981, pl. 3, figs. 1-4, 8, text-fig. 14; Hu, 1983, pl. 2, figs. 3, 4, 6; Hu, 1986, pl. 4, figs. 22, 28, 30, 31; Nohara and Ohshiro, 1992, fig. 6.

Types.—Holotype, a male left valve, IGPS coll. cat. no. 90260; paratypes, a male right valve, IGPS coll. cat. no. 90261, a female left valve, IGPS coll. cat. no. 90262.

Type locality.—St. 303 (33°24.6′N. 133°26.5′E), Uranouchi Bay, Kochi Prefecture, Shikoku, Japan, Recent, coarse sand, depth 25 m (×6 in Figure 12).

Diagnosis.—Large sexual dimorphism; in lateral view, male more elongate and highest more posteriorly than the other three species described here from the *L. japonica* group. Carapace subrhomboidal in lateral view. Dorsal margin straight and sloped toward anterior in male, arched dorsally in female; anterior margin with an oblique infracurvature; ventral margin concave at mid-anterior portion; posterior margin broadly rounded at posteroventral portion. No prominent caudal process. In dorsal view, carapace diamond-shaped, often wedge-shaped in some females. In posterior view, carapace generally elliptical, often egg-shaped in female. Ornamentation consists of concentrically arranged reticulation. Boot-shaped male copulatory organ has trapezoidal basal capsule, triangular distal lobe and basally inflated L-shaped ductus ejaculatorius.

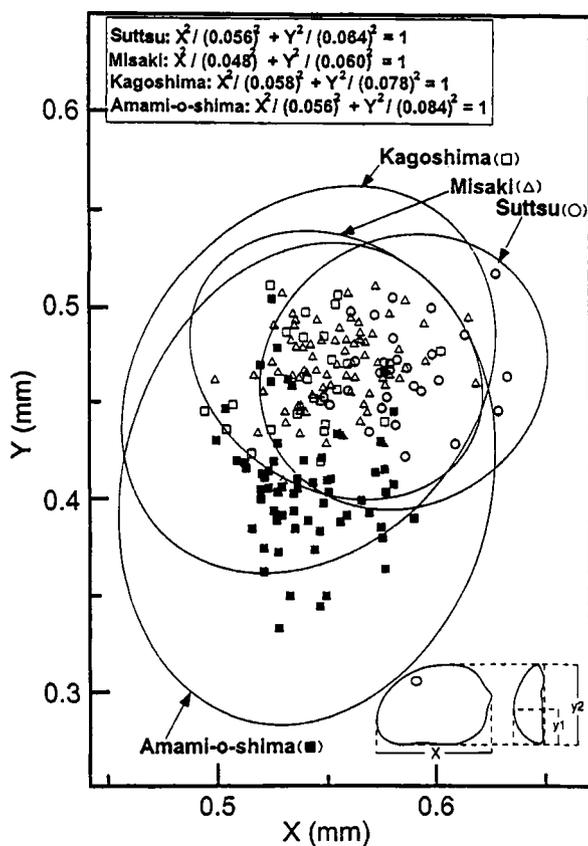*Dimensions.*—Length and height of adult males and fe-

Figure 14. Geographic variation in posterior view of females of *Loxoconcha japonica* Ishizaki, 1968. Symbols refer to Suttsu population (open circles; n = 29), Misaki population (open triangles; n = 76), Kagoshima population (open squares; n = 24) and Amami-o-shima population (solid squares; n = 63). Plot of the distance from the base of ventral margin to the point on the marginal line of the maximum width (y1)/height (y2) on the posterior view of left valve (Y = y1/y2) versus length in the lateral view (X), with series of rejection ellipses with 95% confidence intervals.

males from the sample nos. 1, 6, 8 and 17 are listed in Table 2.

Occurrences.—Fossil (Figure 11): Early Pliocene Maja Formation from Kume Island; Pliocene Sawane Formation from Sado Island; Late Pliocene Yonabaru Formation from Okinawa Island; Pleistocene formations and Holocene deposits and boring core samples from Honshu to Cheju Island, southern Taiwan and Hong Kong. Recent (Figure 12): Japan (Hokkaido-Iriomote Island), southern coast of Korean Peninsula and Hong Kong.

Remarks.—Some specimens from Recent material from the Ryukyus and fossils from the Ryukyus to Taiwan, have an alate ridge on the posteroventral area (see Ruan and Hao, 1988, pl. 57, fig. 13). The alate ridge is especially developed in southern female specimens with an egg-shaped outline in posterior view (Figure 14); this ridge is not developed in males. *L. impressa* reported by Kajiyama (1913) belongs to this species, based on carapace outline,

surface ornamentation and the shape of the male copulatory organ. In the illustration of the male copulatory organ by Okubo (1980) it appears that the distal part of the ductus ejaculatorius extends beyond from the illustrated figure. However, we think that his specimen has been crushed and modified in shape.

Loxoconcha shanhaiensis Hu, 1981

Figures 4.1, 4.2, 4.5; 5B, 5b; 6; 7B; 9.3, 9.4

Loxoconcha shanhaiensis Hu, 1981, p. 76, 77, pl. 3, figs. 5, 9, 11, text-figs. 13a, b; Hu, 1982, p. 180, 182, pl. 2, fig. 23; Hu, 1984, pl. 4, figs. 21-23, 27.

Loxoconcha japonica Ishizaki. Hu, 1981, pl. 3, figs. 1-4, 8, text-fig. 14; Hu, 1983, pl. 2, figs. 3, 4, 6; Hu, 1986, pl. 4, figs. 22, 28, 30, 31; Nohara and Ohshiro, 1992, fig. 6.

Types.—Holotype, TNUM. 4148; paratypes, TNUM. 4151, 4153 and 4150.

Type locality.—The west margin of the Hengchun Table land, near Shanhai-li, 80-90 m above sea level, about 3 km west of Hengchun City, southern Taiwan (E in Figure 11).

Diagnosis.—In lateral view, carapace subtrapezoidal and ornamented by concentric coarse reticulations. Boot-shaped male copulatory organ has trapezoidal basal capsule, subtriangular distal lobe, a shoehorn-shaped ductus ejaculatorius and a triangular clasping apparatus.

Description. — **Carapace:** Strong sexual dimorphism. Carapace subtrapezoidal, highest at posterior cardinal angle in lateral view. Dorsal margin straight and sloped toward anterior; anterior margin with an oblique curvature and well developed denticulations; ventral margin straight; posterior margin with broad flat zone, broadly rounded in posteroventral area, with several strong spines. Short but prominent caudal process. In dorsal view, carapace wedge-shaped with maximum width about one-third of length from posterior end. Ornamentation consists of concentrically arranged coarse reticulation. Prominent alate ridge developed in posteroventral area extended toward posterior. **Pore system:** (a) Lateral (sieve-type) pore system. 67 pores distributed on each valve in adult specimens. (b) Marginal pore system includes 16 pores (Figure 5b). **Hinge** (Figure 4.5a, b): Gongylodont. Hinge-line nearly straight. In left valve, anterior element is a downturned claw, median element has 39-42 teeth, and posterior element is a ball-like knob. The hinge of the right valve is complementary. **Muscle scars** (Figure 4.5a, b): Row of 4 adductor muscle scars curved anteriorly at inside of median to slightly anterior of ventromedian of carapace. The upper of the two middle ones elliptical with hollows at middle, the other three scars bean-shaped. Elliptical frontal scar inclines anteroventrally in front of middle two scars. Two divided mandibular scars in front

of lowest adductor muscle scars. Fulcral point absent.
Marginal infoldment (Figure 5b): Widest in anteroventral
region, twisted in middle of ventral region and narrowed
posterodorsally. **Appendages**: Antennule (Figure 6A).
Five segments (there are six segments, but 4th and 5th are
fused). Length ratio between distal segments is
26:19:8:29:19. Costae well developed in 2nd, 3rd and 4th
segments. Second segment has numerous short hairs on
the anterior margin and a short seta on the posterior margin.
Third segment has a short seta on the anterior distal end.
Fourth segment has two short and three long setae. Fifth
segment with four long setae on the distal end. **Antenna**
(Figure 6B): Four articulated segments (there are five seg-
ments actually, but the 3rd and 4th are fused). Length
ratio between distal segments is 26:11:46:4. Costae well
developed, especially broad in the anterior margin of 3rd
segment. Second segment has a long two-segmented
exopodite and a seta on the posterior margin. Third seg-
ment has a pair of unequal long setae and numerous hairs
on the anterior margin one-sixth of the distance from the
proximal end. Along the posterior margin of the 3rd seg-
ment, three unequal-sized long setae and numerous hairs
are developed in the middle of the ledge and one-third of
the distance from the distal end. Furthermore, the third
segment bears a seta on the posterior distal end. Fourth
segment has two very well developed terminal claws with
numerous serrations. **Mandible** (Figure 6C): Five-
segmented. Length ratio between two propodite segments
and three endopodite segments is 25+: 16:8:12:5. Basal
segment (coxa) with eight teeth and a seta on anterior distal
margin. Second segment of protopodite (basis) bears an
exopodite reduced to a seta. First and 2nd segments of
endopodite almost fused. First segment of endopodite
with two long setae on the ventral distal end. Second seg-
ment of endopodite with a pair of setae on the proximal and
ventral distal ends, respectively. Furthermore, the 2nd
segment has two setae on the anterior dorsal margin and a
seta on the anterior distal margin. Third segment of
endopodite with three pairs of setae on the distal end.
Maxilla (Figure 6D): Extremely thin branchial plate
(exopodite) with 16 setae. Basal segment bears a palp and
three masticatory processes. Palp indistinctly two-
segmented. The proximal segment bears 4 setae on its an-
terior distal end. Distal segment with three setae on the
distal end and one seta on the ledge in the posterior proxi-
mal end. Outer, middle and inner masticatory processes
bear 5, 4 and 5 setae, respectively, on each distal end.
Thoracic legs (Figure 6E, F and G): All three legs are 4-
segmented, similar in shape. Length ratio between distal
segments is 24:20:8:13 in 3rd thoracic leg. Costae devel-
oped on both margins. First segment having a seta on the
anterior proximal end and two setae on the anterior proxi-
mal end. The segment has a seta on the posterior proximal

Table 3. Measurements of valve of *Loxoconcha shanhaiensis* Hu,
1981 from sample nos. 17 and 20. Abbreviations same as Table 2.

Sample (No.)	Sex	Valve	Length (mm)		Height (mm)		N
			Av.	OR	Av.	OR	
Amami Is. (17)	M	R	0.48	0.45–0.51	0.33	0.31–0.37	29
	M	L	0.49	0.46–0.54	0.33	0.31–0.36	27
	F	R	0.48	0.46–0.52	0.34	0.32–0.36	26
	F	L	0.48	0.44–0.53	0.34	0.31–0.37	42
Okinawa Is. (20)	M	L	0.50	0.44–0.52	0.33	0.32–0.34	12
	F	L	0.49	0.46–0.53	0.34	0.32–0.38	40

end. Second segment bearing numerous hairs along the
anterior margin and a seta on the anterior distal end. Third
and 4th segments bearing numerous hairs along the anterior
margin. **Copulatory organ** (Figure 7B): The basal cap-
sule, with costae in the margin, is trapezoidal. A large
subtriangular distal lobe and a small clasping apparatus are
developed on the distal end of the basal capsule. Small
shoehorn-shaped ductus ejaculatorius.

Dimensions.—Length and height of adult males and fe-
males from the sample nos. 17 and 20 are given in Table 3.

Occurrences.—Fossil (Figure 11): Middle Pleistocene
Shimo-jiro Formation from Okino-erabu Island; Late
Pleistocene Tungshiao Formation and Hengchun Limestone
from Taiwan. Recent (Figure 12): Ryukyus (Amami
Island to Iriomote Island), Taiwan and Hainan Island.

Remarks. — Specimens reported by Hu (1981, 1983,
1986) and Nohara and Ohshiro (1992) as *L. japonica* have
coarse reticulation, straight dorsal margin sloped toward the
anterior, posterior margin with broad flat zone and several
strongly developed spines, so these specimens are identi-
fied as *L. shanhaiensis.*

Loxoconcha tumulosa (Hu, 1979)

Figures 4.3, 4.4, 4.6; 5C, 5c; 9.5, 9.6

Loxocorniculum tumulosum Hu, 1979, p. 71, 72, pl. 2, figs. 17,
  21, 22, 26, 27, 30, 31, text-fig. 10.
Loxoconcha tumulosa (Hu). Hu, 1981, p. 78, pl. 3, figs. 6, 7; Hu,
  1984, pl. 4, figs. 17, 18, 20; Zhao *et al.*, 1985, pl. 20, fig. 11;
  Gou, 1990, p. 25, pl. 3, figs. 45–47.
Loxoconcha alata Brady. Guha, 1968, p. 61, pl. 4, figs. 5, 13.
Loxoconcha heronislandensis Hartmann. Hartmann, 1984, p. 128,
  pl. 7, figs. 1–6, text-figs. 47, 48; Whatley and Zhao, 1987, p.
  350, pl. 5, fig. 12; Behrens, 1991, pl. 5, figs. 5, 6.
Loxoconcha sp. Hartmann and Hartmann, 1978, pl. 10, fig. 6.
Non *Loxoconcha tumulosa* (Hu). Zhao and Wang, 1988, pl. 2,
  fig. 27.

Types.—Holotype, TUM. 4033; paratypes, TUM. 4034–
4036, 4065, 4066.

Type locality.—A road cut from Hengchun to Oluanpi,
15–20 m above sea level, about 1 km east of Nanwan,

Table 4. Measurements of valve of *Loxoconcha tumulosa* (Hu, 1979) from sample no. 23. Abbreviations same as Table 2.

Sample (No.)	Sex	Valve	Length (mm)		Height (mm)		N
			Av.	OR	Av.	OR	
Taiwan (23)	F	R	0.51	0.50–0.53	0.33	0.33–0.34	10
	F	L	0.52	0.50–0.54	0.35	0.34–0.36	7

Table 5. Measurements of valve of *Loxoconcha lilljeborgii* Brady, 1868 from sample no. 17. Abbreviations same as Table 2.

Sample (No.)	Sex	Valve	Length (mm)		Height (mm)		N
			Av.	OR	Av.	OR	
Amami Is. (17)	M	R	0.51	0.47–0.54	0.34	0.32–0.36	78
	M	L	0.52	0.49–0.55	0.34	0.32–0.36	69
	F	R	0.50	0.46–0.54	0.34	0.32–0.39	95
	F	L	0.50	0.45–0.54	0.35	0.31–0.37	97

Pingtung Prefecture, southern Taiwan (D in Figure 11).

Diagnosis.—Large sexual dimorphism; in lateral view, male more elongate. Carapace rhomboidal in lateral view. Dorsal and ventral margins nearly parallel; anterior margin with an oblique infracurvature, and developed denticulations; posterior margin broadly rounded in posteroventral area. Prominent caudal process. In dorsal view, carapace wedge-shaped. In posterior view, carapace egg-shaped. Ornamentation consists of very coarse oncentrically arranged reticulation. Prominent alate ridge developed at postero-ventral area, and protuberance developed in posterodorsal area.

Dimensions.—Length and height of adult males and females from the locality sample no. 23 is listed in Table 4.

Occurrences.—Fossil (Figure 11): Late Miocene Round Chalk and Silt Formation, Pliocene Guiter Formation from the Andaman Islands of the Indian Ocean and Late Pleistocene Hengchun Limestone from Taiwan. Recent (Figure 12): Ryukyus (Tokuno-shima to Okinawa), Taiwan, Hainan, Cebu Island, Lizard Island, Guam, Truk, Marshall Islands, Gilbert Islands, Samoa and Tuamotu Islands from Southwest Pacific.

Remarks.—Specimens reported by Guha (1968) from the Late Miocene and the Pliocene sediments of Interview Island and Guiter Island as *L. alata* are identified as *L. tumulosa*. *L. heronislandensis* reported by Behrens (1991) also belongs to this species. A specimen reported by Zhao and Wang (1988) as *L. tumulosa* differs from this species, because it has a protruded anterior margin and does not have a posterodorsal protuberance.

Loxoconcha lilljeborgii Brady, 1868

Figures 3.4, 3.5, 3.7; 5D, 5d; 7C; 9.7, 9.8

Loxoconcha lilljeborgii Brady, 1868, p. 183, pl. 13, figs. 11–15; Mostafawi, 1992, p. 151, pl. 5, fig. 102.
Loxoconcha lilljeborgii Brady? Whatley and Zhao, 1987, p. 351, pl. 5, fig. 13.
Loxoconcha lilljeborchi Brady. Keij, 1954, p. 358, pl. 3, fig. 4; Guha, 1968, p. 61, pl. 4, fig. 20; Gramann, 1975, pl. 5, figs. 6–8; Zhao et al., 1985, pl. 20, fig. 12; Zhao and Wang, 1988, pl. 2, fig. 26.
Loxoconcha georgei Hartmann and Hartmann, 1978, p. 105, pl. 9, figs. 15, 16, text-figs. 259–268, (non) pl. 9, figs. 13, 14; Howe and Mckenzie, 1989, p. 24, figs. 8, 84, 85, 154;

Behrens, 1991, p. 116, 117, pl. 4, figs. 6–9.
Loxoconcha broomensis Hartmann and Hartmann, 1978, p. 106, pl. 10, fig. 1, text-figs. 272, 279, (non) pl. 10, figs. 2–4, text-figs. 269, 280.
Loxocorniculum sp. 1, Tabuki et al., 1987, pl. 2, fig. 11; Tabuki and Nohara, 1990, pl. 2, fig. 11; Tabuki, 1992, pl. 1, fig. 15.
Loxocorniculum sp. A. Tabuki and Nohara, 1988, pl. 1, figs. 13, 14.
Loxocorniculum cf. (*Loxoconcha*) *georgei* Hartmann. Tabuki and Nohara, 1995, fig. 4–8.
Loxocorniculum georgei (Hartmann). Gou, 1990, p. 26, pl. 3, figs. 43, 44.

Types.—Not defined.

Type locality.—Mauritius, Indian Ocean (a in Figure 12).

Diagnosis.—Strong sexual dimorphism; in lateral view, male more elongate. Carapace subrhomboidal in lateral view. Dorsal margin nearly straight in male, arched dorsally in female; anterior margin with an oblique infracurvature; ventral margin concaved in mid-anterior area; posterior margin broadly rounded in posteroventral area. Caudal process not prominent. In dorsal view, carapace elongate arrowhead-shaped. In posterior view, egg-shaped. Ornamentation consists of concentrically arranged oblong pits. Prominent protuberance developed in posterodorsal area. Pear-shaped male copulatory organ has inflated trapezoidal basal capsule, subtriangular distal lobe, a leaf-shaped clasping apparatus and elongate ductus ejaculatorius.

Dimensions.—Length and height of adult males and females from the sample No. 17 is given in Table 5.

Occurrences.—Fossil (Figure 11): Late Miocene Round Chalk and Silt Formation, Pliocene Guiter Formation from the Andaman Islands of the Indian Ocean, and Late Pleistocene Hengchun Limestone from Taiwan. Recent (Figure 12): Ryukyus (Tokuno-shima to Okinawa), Taiwan, Hainan, and Lizard Island from Southwest Pacific.

Remarks. — Specimens reported from the Ryukyus as *Loxocorniculum* sp. 1 (by Tabuki et al., 1987; Tabuki and Nohara, 1990; Tabuki, 1992), *Loxocorniculum* sp. A (by Tabuki and Nohara, 1988) and *Loxocorniculum* cf. (*Loxoconcha*) *georgei* (Tabuki and Nohara, 1995) are identified as *L. lilljeborgii*, with its carapace outline, concentri-

cally arranged oblong pits and postero-dorsal alate ridge. Hartmann and Hartmann (1978) described *Loxoconcha georgei* as a new species, and figured carapaces of both sexes and male soft parts, but a type specimen was not designated. Judging from the carapace ornamentation, we think the figured male and female specimens belong to different species. The male specimens we identify as *L. lilljeborgii*, with its concentrically arranged oblong pits, nearly straight dorsal margin, developed posterodorsal alate ridge and identically shaped of male copulatory organ. On the other hand, the female specimens are *Loxoconcha broomensis*, which was described in the same paper. This specimen has two strong anterior ridges. Carapaces of both sexes and the male soft parts of *L. broomensis* were also figured by Hartmann and Hartmann (1978), but a type specimen was not designated. Judging from the carapace outline and ornamentation, the female specimen should be identified as *L. lilljeborgii*.

Acknowledgements

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Note added in proof.—After the acceptance of the manuscript, T. Kase (National Science Museum, Tokyo) kindly provided us specimens of *Loxoconcha lilljeborgii* from the Tartaro Formation (Late Miocene) of Luzon Island, Philippines. The fossil record of *L. lilljeborgii* in East Asia, therefore, dates back from the Pleistocene to the Late Miocene.

Middle Permian (Guadalupian) brachiopods from the Xiujimqinqi area, Inner Mongolia, northeast China, and their palaeobiogeographical and palaeogeographical significance

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Abstract. A small brachiopod fauna is described from the lower part of the Xiujimqinqi Formation of the Xiujimqinqi area in central-east Inner Mongolia, northeast China. The age of this fauna is regarded as Wordian (Middle Guadalupian, Middle Permian) by comparison with a similar brachiopod fauna from the Zhesi area of central Inner Mongolia, and by constraints from fusulinaceans associated with the Zhesi fauna. The Xiujimqinqi fauna is typical of mixed Boreal/Palaeoequatorial Middle Permian brachiopod faunas of East Asia. The mixed nature of these faunas is interpreted to have resulted from the combined effects of a middle palaeolatitudinal position, intensified plate convergence between Sino-Korea and Mongolia, and sea surface current connections with both the Arctic Sea in the north and eastern Palaeo-Tethys to the south. Possible *Kaninospirifer* is reported for the first time from China.

Key words: brachiopods, Middle Permian, northeast China, palaeobiogeography, transitional fauna, Xiujimqinqi

Introduction

Permian marine sedimentary rocks are common in Inner Mongolia and contain abundant and varied marine invertebrate faunas. Generally, these faunas show a consistent palaeobiogeographical pattern, in that those from northern Inner Mongolia appear to be dominated by elements characteristic of the cool- to cold-water Boreal Realm, while faunas in central and southern Inner Mongolia tend to be more characteristic of the warm-water Palaeoequatorial Realm, but at the same time contain some taxa common to, or characteristic of, the Boreal or Gondwanan Realms (Tazawa, 1991; Shi et al, 1995; Shi and Zhan, 1996). As such, the Permian marine faunas of central and southern Inner Mongolia typify a transitional biogeographical zone between the Boreal Realm to the north and the Palaeoequatorial Realm to the south, as defined and discussed by Shi et al. (1995).

Despite their ubiquity and abundance in the Permian marine sediments in Inner Mongolia and hence great significance for dating and correlation, only a few brachiopod faunas have been systematically described in detail. One of the better studied areas is the Xiujimqinqi area in central-eastern Inner Mongolia (Figure 1), where Permian brachiopods are common throughout the entire Lower and Middle Permian marine volcaniclastic, bioclastic and terrigenous sediments, well over 4,000 m in total thickness (Figure 2). Permian brachiopod faunas from various localities of this area have been studied by Lee et al. (1982, 1983, 1985) and Liu and Waterhouse (1985), and have furnished the basic premise for the Permian biostratigraphical zonation schemes of this area (Lee et al., 1982, 1983; Liu and Waterhouse, 1985; BGMNG, 1991).

However, with the exception of Liu and Waterhouse's (1985) work, which described five brachiopod assemblages but did not give specific details on the exact location of
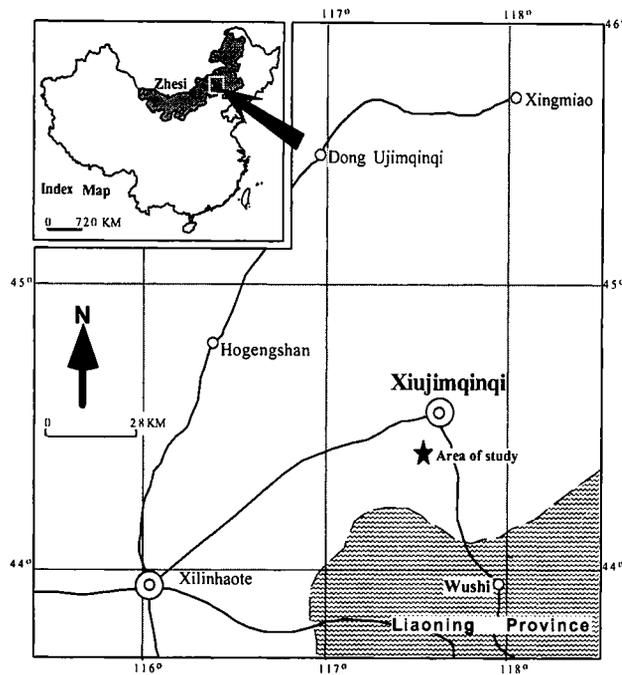
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Figure 1. Map showing the study area, as well as the Zhesi area also referred to in the text. The enlarged map shows the detailed location of the area of study (Yuejin Coal Mine) in the Xiujimqinqi area. The shaded area in the index map is the Nei Mongol (Inner Mongolia) Autonomous Region.

their measured sections other than the general Xiujimqinqi area, the other earlier studies (Lee *et al.*, 1982, 1983, 1985) dealt only with certain taxa instead of the entire faunas. These latter investigations demonstrate that there are at least 10 relatively well exposed sections/localities in the general Xiujimqinqi area where Permian marine sequences with abundant brachiopods crop out. Lee *et al.* (1982) provided a detailed list of all the Permian brachiopod species then known to occur in this area, which they used as the basis for the erection of their brachiopod-based stratigraphical assemblages.

The present study is based on a small collection from the Yuejin Coal Mine, about 10 km southwest of Xiujimqinqi Township (Figure 1). This collection was originally made by the officers of the Bureau of Geology and Mineral Resources of Nei Mongol (Inner Mongolia) during the 1950s-1970s and was entrusted to Zhan Li-Pei, Chinese Academy of Geological Sciences (Beijing), for age determination. Zhan Li-Pei subsequently fulfilled this request by providing a list of his identified species and a broad age indication ["Early Permian", which, in terms of Jin's *et al.* (1997) proposed Permian timescale, includes both Early and Middle Permian]. Up to the present, this collection has not yet been systematically described. As will be documented below, this collection provides additional and

new records to what is currently known about the Middle Permian brachiopod faunas of the Xiujimqinqi area. Moreover, this collection also affords important material to document *Kaninospirifer* from China for the first time.

Specimens described and illustrated in this paper are housed in the Museum of Victoria, Melbourne, Australia, with registration numbers prefixed with NMVP.
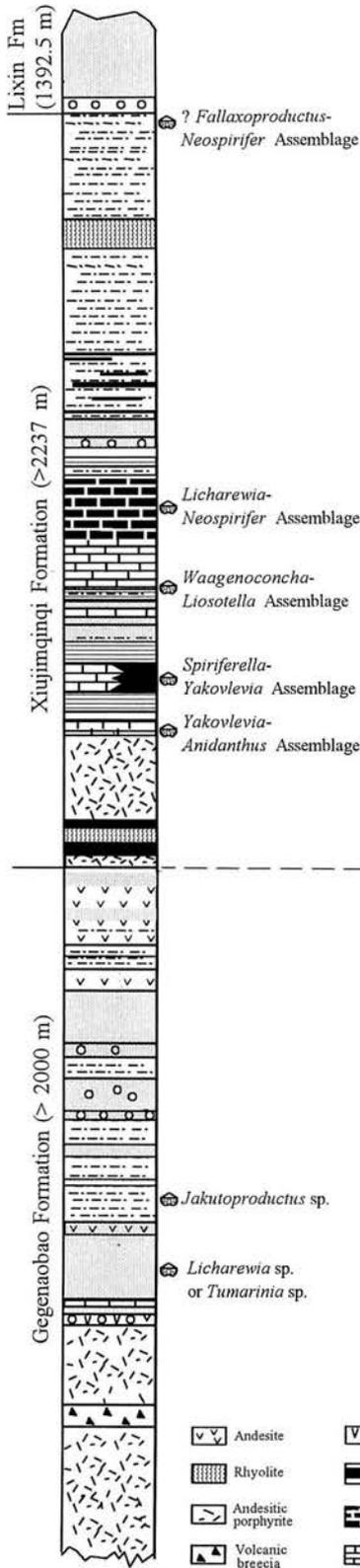
Stratigraphy

Over the last 2 decades, there has been a significant increase of lithostratigraphical names applied to the Permian rocks of the Xiujimqinqi area. In the two latest attempts to rationalize the stratigraphical nomenclature for the Permian System for the broad Inner Mongolian province (BGMNM, 1991; Jin *et al.*, 2000), many of the previously used names have been abandoned or treated as synonyms of others. In this study, we follow the stratigraphical framework recommended by BGMNM (1991) for the Xiujimqinqi area, which was also adopted in Jin *et al.* (2000). According to this scheme, the Permian sequence in the Xiujimqinqi area comprises, in ascending order, the Gegenaobao, Xiujimqinqi and Linxi formations (Figure 2). The Gegenaobao Formation is a sequence of acidic to intermediate volcanics, volcaniclastics and a minor amount of carbonate rocks. Both shallow marine and nonmarine fossils occur in this formation, indicating a volcanically active continental marginal marine setting. Among the marine fossils, brachiopods are most common and notably include species of *Jakutoproductus* and *Licharewia* (or *Tumarinia*). The cooccurrence of these two genera in this formation would indicate a relatively broad age range for the formation, from probably Artinskian (Early Permian) to as high as Roadian (early Middle Permian).
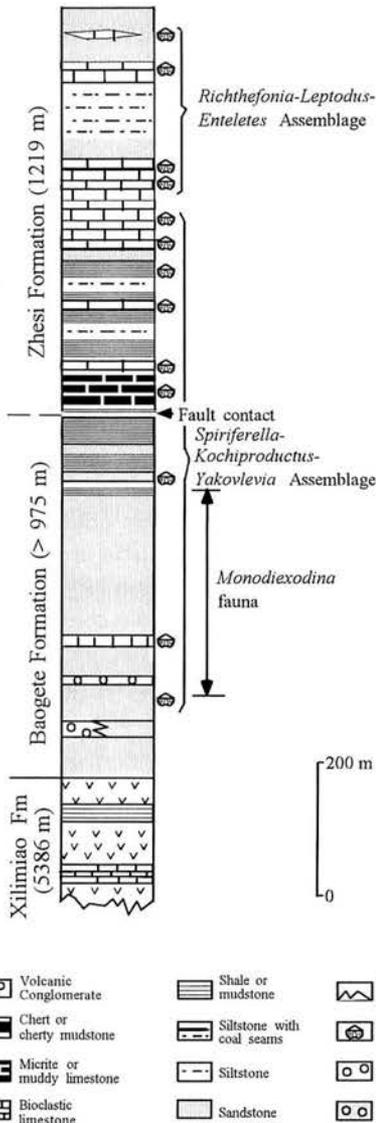
The Gegenaobao Formation in the Xiujimqinqi area is conformably overlain by the Xiujimqinqi Formation. The latter is dominated by andesite in the lower part, limestone and mudstone in the middle part, and siltstone in the upper part (Figure 2). Brachiopods occur throughout the formation but are mainly concentrated in several major horizons, each of which appears to form a distinct assemblage (Figure 2). By reference to the lithology and overall species composition, the brachiopod collection described below is considered to have come from the lower portion of the middle part of the formation. Plant fossils have also been reported from the siltstone beds in the upper part (BGMNM, 1991). As will be detailed below, the age of this formation is regarded as Wordian by correlation with faunas elsewhere.

Upwards, the Xiujimqinqi Formation grades to sandstone and conglomerate of the Linxi Formation without distinct disconcordance. The latter contains abundant Late Permian (Lopingian) mixed Cathaysia/Angara type flora

Xiujimqinqi area

Lixin Fm (1392.5 m)

? *Fallaxoproductus-Neospirifer* Assemblage

Xiujimqinqi Formation (>2237 m)

Zhesi area

Licharewia-Neospirifer Assemblage

Richthefonia-Leptodus-Enteletes Assemblage

Zhesi Formation (1219 m)

Waagenoconcha-Liosotella Assemblage

Spiriferella-Yakovlevia Assemblage

Yakovlevia-Anidanthus Assemblage

Fault contact

Spiriferella-Kochiproductus-Yakovlevia Assemblage

Baogete Formation (> 975 m)

Monodiexodina fauna

Gegenaobao Formation (> 2000 m)

Jakutoproductus sp.

Licharewia sp. or *Tumarinia* sp.

Xilimiao Fm (5386 m)

200 m

0

Andesite	Volcanic Conglomerate	Shale or mudstone	Top or base not complete
Rhyolite	Chert or cherty mudstone	Siltstone with coal seams	Brachiopod horizons
Andesitic porphynite	Micrite or muddy limestone	Siltstone	Conglomerate
Volcanic breccia	Bioclastic limestone	Sandstone	Sandstone with conglomerate

Figure 2. Permian stratigraphical sequences of the Xiujimqinqi and Zhesi areas, Inner Mongolia, northeast China. The stratigraphic columns and biozones are based on data from BGMNM (1991).

(Zhang, 1988).

Correlation and age

The present collection comprises 10 species, of which several are species indeterminate and two genera and species indeterminate. At first glance, the assemblage cannot be readily correlated with any of the five assemblages originally established by Lee *et al.* (1982, 1983, 1985) and elaborated by BGMNM (1991) (see Figure 2) because of the lack of key zonal species in our collection; neither can it be matched with certainty with any of the five Early and Middle Permian brachiopod assemblages recognized by Liu and Waterhouse (1985). The closest assemblage among the established schemes is the *Spiriferella-Yakovlevia* assemblage of Lee *et al.* (1982), which occurs in the lower portion of the middle part of the Xiujimqinqi Formation (Figure 2). This assemblage was originally recognized based on the brachiopod fauna from a limestone quarry about 7 km northwest of the present Yuejin Coal Mine (Lee *et al.*, 1982), and is characterized by abundant occurrence of *Spiriferella* and *Yakovlevia*, the former being represented by two species and the latter by four (Lee *et al.*, 1982). Other characteristic species of this assemblage include *Liosotella septentrionalis* (Tschernyshew), *Marginifera gobiensis* Chao, *Paramarginifera zhesiensis* Lee and Gu, *Waagenoconcha permocarbonica* Ustritskiy, *W. xiuqiensis* Lee, Gu and Li, *Strophalosia paradoxa* Fredericks, *S. pulchra* Lee, Gu and Li, *Linoproductus cora* (d'Orbigny), *Leptodus* sp., *Neospirifer xiujumqinqiensis* Lee, Gu and Li, *N. ravana* (Diener), *N. moosakhailensis* (Davidson), and *Paeckelmanella laevis* Lee and Gu. Although lacking many of these species, the present collection nevertheless contains relatively abundant *Spiriferella* and neospiriferids (*Neospirifer* and *Kaninospirifer*), hence suggesting a significant degree of correlation. On the other hand, we note that some other factors, for example, insufficient sampling in the present collection and/or localized specialization of biofacies, may have also contributed to the apparent difference in species composition between the present collection and the *Spiriferella-Yakovlevia* assemblage.

The age of the above *Spiriferella-Yakovlevia* assemblage has been considered to be either late Early Permian (Lee *et al.*, 1982) or middle Early Permian (BGMNM, 1991) in the traditional twofold Permian chronostratigraphical timescale of China (e.g., Zhan and Li, 1984). A more specific age determination for the *Spiriferella-Yakovlevia* assemblage is possible by correlation with the classic Permian brachiopod faunas of the Zhesi area in central Mongolia (see index map in Figure 1 for location), where brachiopods are associated with fusulinaceans. Here, the Permian is divided into three formations: the Xilimiao Formation, Baogete Formation and Zhesi Formation, in as-

cending order (BGMNM, 1991) (Figure 2). The brachiopod-bearing horizons that are comparable with those of the Xiujimqinqi area lie in the Baogete and Zhesi formations. Permian brachiopods are very rich in this area and have been the subject of two major monographical studies (Grabau, 1931; Duan and Li, 1985). According to them, the Permian brachiopods in this section can be divided into two broad assemblages: the *Spiriferella-Kochiproductus-Yakovlevia* assemblage (or SKY assemblage, as called by Duan and Li, 1985), followed by the *Richthofenia-Leptodus-Enteletes* assemblage (or RLE assemblage). Of these, the SKY assemblage is well correlated with the *Spiriferella-Yakovlevia* assemblage of the Xiujimqinqi area as both assemblages contain abundant Boreal-type genera such as *Neospirifer*, *Spiriferella* and *Yakovlevia*, and are similarly characterized by an admixture of Boreal and Palaeoequatorial taxa. The RLE assemblage of the Zhesi area, on the other hand, is dominated by Palaeoequatorial or Cathaysian-type genera and bears no significant similarities with any of the Xiujimqinqi assemblages.

The age of the SKY assemblage of the Zhesi section is well constrained by the associated fusulinaceans of the *Monodiexodina sutchanica* Zone in its lower part, and the fusulinaceans of the *Codonofusiella* Zone and corals of the *Waggenophyllum-Wentzella* Zone that directly and conformably overly the SKY assemblage and are associated with the brachiopods of the RLE assemblage (Duan and Li, 1985; BGMNM, 1991) (Figure 2). The *Monodiexodina sutchanica* Zone is generally regarded as of early Midian or Wordian age (Kotlyar *et al.*, 1999; Shi and Tazawa, 2001), and the *Codonofusiella* and *Waagenophyllum-Wentzella* zones of Capitanian age (Jin *et al.*, 1997). Thus, the SKY assemblage can be safely assigned to the Wordian in age. This implies that the *Spiriferella-Yakovlevia* assemblage, and hence, by correlation, the present collection from the Yuejin Coal Mine under discussion, is also Wordian in age.

Palaeobiogeographical and palaeogeographical implications

In spite of its small species composition, the present collection demonstrates aspects of a mixed Boreal/Cathaysian palaeobiogeographical fauna. The cool-water Boreal aspect of the fauna is represented by two characteristic northern Eurasian genera: *Anemonaria* and *Kaninospirifer*. *Anemonaria* is primarily restricted to the Arctic region (Arctic Russia, Spitsbergen, Greenland, and Arctic Canada) (Sarytcheva, 1977), although some occurrences from Australia (Briggs, 1998) and middle-latitudinal regions are also known, such as Japan (Tazawa and Niigata Pre-Tertiary Research Group, 1999; Tazawa, 2001) and the Russian Far East (Likharev and Kotlyar, 1978). The only exception to this essentially high-to middle-palaeolatitu-
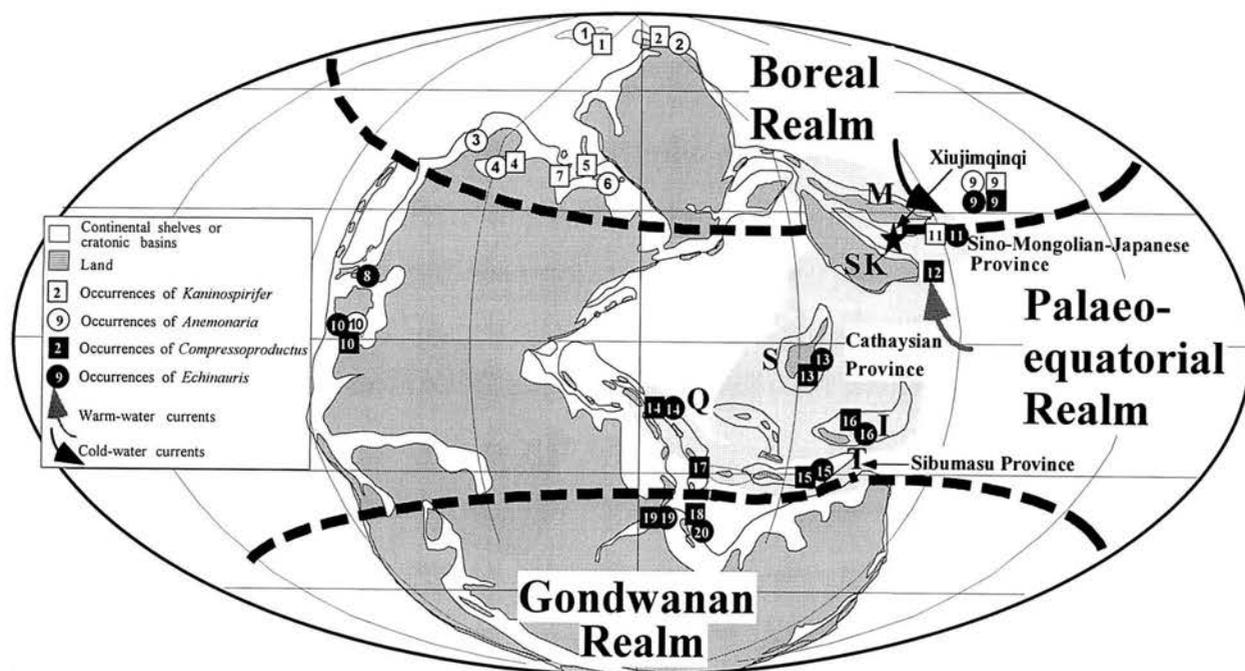
Figure 3. A Permian reconstruction map showing the distribution *of Anemonaria, Compressoproductus, Echinauris,* and *Kaninospirifer,* and the inferred palaeo-position (indicated by star) of Xiujimqinqi during the Middle Permian (base map from Ziegler *et al.*, 1998). Locations of the occurrences of *Anemonaria, Compressoproductus, Echinauris,* and *Kaninospirifer* are as follows: **1**, Kolyma Block, Russia; **2**, northern Verkhoyansk, Russia; **3**, Yukon Territory, Canada; **4** Sverdrup Basin, Canada; **5**, Kanin Peninsula, Russia; **6**, Pechora Basin, Russia; **8**, Phosphoria Basin, western USA; **9**, Xiujimqinqi and adjacent areas in northeast China; **10**, Texas, USA and central America; **11**, SW Japan and South Primorye of Far Eastern Russia; **12**, South Kitakami, northeast Japan; **12**, South China **14**, northwest Iran and Armenia; **15**, Shan-Thai (Sibumasu) block; **16**, Indochina; **17**, southeast Pamir, Karakorum and central Afghanistan; **18**, southern Tibet; **19** northwest Nepal, **20**, Salt Range, Pakistan. Explanations of main tectonic blocks: Q, Qiangtang Block; I, Indochina Block; M, Mongolia Block; S, South China Block; SK, Sino-Korea Block; T, Shan-Thai (Sibumasu) Block.

dinal distributional pattern is a record of the genus from Texas, southern U.S.A. (Cooper and Grant, 1969, 1975) and Venezuela (Hoover, 1981). These two "outlying" occurrences may be explained by the possible effect of a California-type cold current that might have intermittently operated off the western coast of northern Pangea during the Permian, bringing cold-water Boreal faunal elements to palaeoequatorial Texas and South America (Shi, 1995; Shi and Tazawa, 2001).

By contrast, the palaeogeographical distribution of *Kaninospirifer* is much more restricted, with occurrences known only from the northern part of the Russian Platform, Arctic Canada, Greenland, and Spitsbergen (Kalashnikov, 1996), Mongolia (Pavlova, 1991), northeast China (this report) and Japan (Tazawa, 2000; see discussion below) (Figure 3).

The warm-water palaeoequatorial aspect of the Xiujimqinqi brachiopod fauna is signaled by *Compressoproductus* and *Echinauris*. These two genera have essentially concordant palaeogeographical distributions, with occurrences restricted to the Tethys and southwest U.S.A. and have never been recorded from either the

Gondwanan Realm or the Boreal Realm proper (Figure 3).

In addition to the four genera noted above, the palaeogeographical distribution of *Spiriferella* is also of great interest. Unlike *Anemonaria, Kaninospirifer, Echinauris* and *Compressoproductus,* which, as noted above, have either restricted high palaeolatitudinal Boreal occurrences or low palaeolatitudinal Tethyan occurrences, the palaeogeographical distribution of *Spiriferella* is typically bipolar and bitemperate (terms as defined in Shi and Grunt, 2000), in that it occurred only in the middle and high palaeolatitudinal regions of both hemispheres (Shi and Grunt, 2000).

The mixed nature of the Xiujimqinqi brachiopod assemblage, as outlined above, is consistent with several other Middle Permian brachiopod faunas reported from northeast China, southeast Mongolia, South Primorye of the Russian Far East, and Japan, as already summarized and discussed by Tazawa (1991), Shi *et al.* (1995) and Shi and Zhan (1996). A refined scenario to interpret the origin of these mixed Middle Permian brachiopod faunas has recently been put forth by Shi and Tazawa (2001). In this interpretation, it is suggested that all the mixed Middle Permian
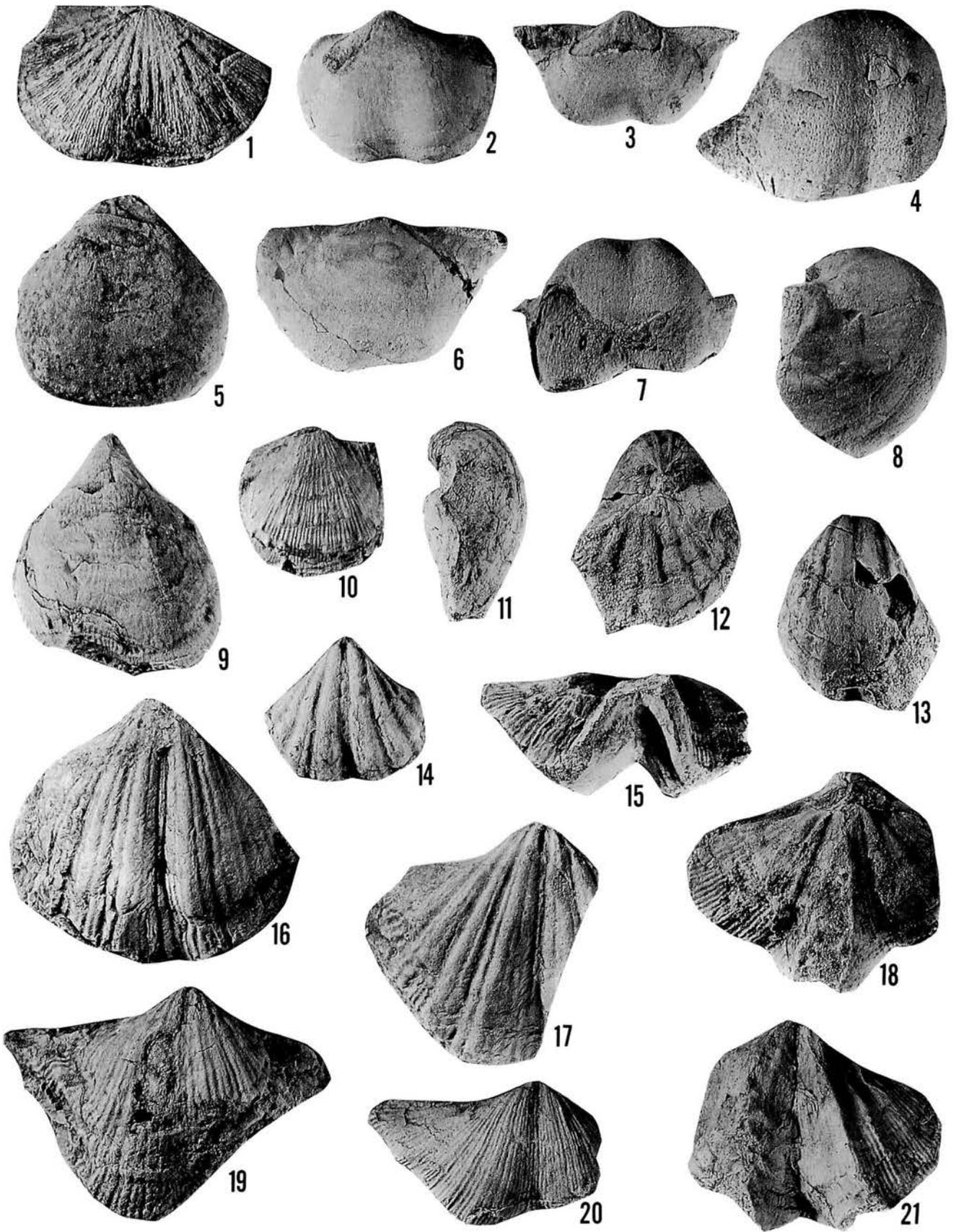
faunas in eastern Asia (NE China, parts of Japan, Mongolia, and South Primorye of the Russian Far East) are referable to characterize the same single palaeobiogeographical unit, the Sino-Mongolian-Japanese Province (= Inner Mongolia-Japanese Transitional Zone of Tazawa, 1991). This province has a distinct transitional biogeographical nature characterized by intermingling genera typical of both the palaeoequatorial Cathaysian Province in the south and the Boreal Realm to the north. The origin of this biogeographical mixing, apparently limited to the Wordian interval, is thought to have resulted from the interplay of three main factors: (1) a middle palaeolatitudinal position for the Sino-Mongolian-Japanese Province; (2) intensified plate convergence between the Sino-Korea and Mongolia blocks during the Permian; and (3) sea surface current connections with both the warm-water eastern Palaeo-Tethys to the south and the temperate to polar Arctic sea to the north (Figure 3). A middle palaeolatitudinal position for the Sino-Mongolian-Japanese Province, estimated to be 25°–40° N, is suggested by the mixed nature of the faunas which, in analogy to modern latitude-dependent biogeographical zonation patterns (see Yin, 1989), would indicate a mesothermal setting comparable to a middle-latitudinal position or temperate zone. A phase of intensified plate convergence between Sino-Korea and Mongolia through the Permian, especially the Early and Middle Permian is assumed because this would have resulted in the shrinking and progressive shallowing of the Sino-Mongolian seaway that harbored the Sino-Mongolian-Japanese Province. This in turn would have facilitated and enhanced the intermingling of Boreal faunas that originally prevailed on the shelves of the Mongolian block and the eastern Palaeo-Tethyan faunas that dominated the northern shelves of the Sino-Korea block. The inferred sea surface current connections of the Sino-Mongolian-Japanese Province to both the Boreal Realm and the eastern Palaeo-Tethys is important because these currents would have brought their prospective faunal elements to the Sino-Mongolian seaway where they were eventually intermingled. Therefore, in light of these considerations we propose that the Xiujimqinqi area was probably located within the eastern end of the Sino-Mongolian seaway, in an intermediate position between Sino-Korea and Mongolia

(Figure 3).

Systematic palaeontology

Order Chonetida Nalivkin, 1979
Suborder Chonetidina Muir-Wood, 1955
Superfamily Chonetoidea Bronn, 1862
Family Rugosochonetidae Muir-Wood, 1962

Rugosochonetidae gen. and sp. indet.

Figure 4.1

Remarks. — An incomplete internal mould of a dorsal valve (NMV P308012) represents a species most likely of Rugosochonetidae in view of its prominent fold, finely papillose inner surface and about 20 coarse costellae each with scores of capillae. The specimen is badly worn, therefore the internal structures are not preserved, rendering even its generic status open.

Order Productida Waagen, 1883
Suborder Productidina Waagen, 1883
Superfamily Productoidea Gray, 1840
Family Productellidae Schuchert in Schuchert and LeVene, 1929
Subfamily Marginiferinae Stehli, 1954
Genus *Echinauris* Muir-Wood and Cooper, 1960

Type species. — *Echinauris lateralis* Muir-Wood and Cooper, 1960.

Echinauris sp.

Figure 4.5

Remarks. — An incomplete ventral valve (NMV P308016) is referable to *Echinauris*. The ventral valve is more than 25 mm long, 29 mm wide, and more than 20 mm thick, has a moderately convex profile and is ornamented with numerous fine spine bases, but appears to have no evident internal ridge. This specimen is much larger than *E. jisuensis* (Chao, 1927; also described and figured by Duan and Li, 1985, p. 112, pl. 35, figs. 7–13) from the Zhesi Formation in the Zhesi area of Inner Mongolia.

← **Figure 4.** **1.** Rugosochonetidae gen. et sp. indet. Internal mold of a dorsal valve, NMV P308012, ×2.5. **2–4, 6–8.** *Anemonaria sublaevis* (King, 1931). **2.** Ventral view of a ventral valve, NMV P308020, ×2; **3, 7.** Posterior and anterior views of a ventral valve, NMV P308017, ×2; **4, 8.** Ventral and lateral views of a ventral valve, NMV P308018, ×2; **6.** Posterior view of a ventral valve, NMV P308019, ×2. **5.** *Echinauris* sp., ventral view of a ventral valve, NMV P308016, ×1.3. **9.** *Compressoproductus corniformis* (Chao, 1927), ventral view of a ventral valve, NMV P308026, ×1.6. **10.** *Cancrinella*? *cancrini* (de Verneuil, 1845), ventral view of a ventral valve, NMV P308024, ×2. **11–14.** *Spiriferella persaranae* (Grabau, 1931). **11–13.** Lateral, dorsal, and ventral views of a conjoined shell, NMV P308029; **14.** Ventral view of a ventral valve, NMV P308030, ×1.5. **15, 18, 21.** *Neospirifer* sp. Anterior, dorsal, and ventral views of a conjoined shell, NMV P308036. **16–17.** *Spiriferella keilhavii* (von Buch, 1846). **16.** Ventral view of a ventral valve, NMV P308033; **17.** Ventral view of a ventral valve, NMV P308034. **19.** Neospiriferinae gen. and sp. indet. Ventral view of a ventral valve, NMV P308037. **20.** *Kaninospirifer* sp. Ventral view of a ventral valve, NMV P308035. All figures are natural size unless otherwise indicated.

Subfamily Paucispiniferinae Muir-Wood and Cooper, 1960
Genus *Anemonaria* Cooper and Grant, 1969

Type species.—Marginifera sublaevis King, 1931.

Anemonaria sublaevis (King, 1931)

Figure 4.2-4.4, 4.6-4.8

Marginifera sublaevis King, 1931, p. 89, pl. 23, figs. 15a-c, ?16a, b, 19 (non figs. 13, 14).
Anemonaria inflata Cooper and Grant, 1969, p. 8, pl. 5, figs. 28, 29.
Anemonaria sublaevis (King). Cooper and Grant, 1975, p. 1103, pl. 408, figs. 1-26.

Material. — Three conjoined shells (NMV P308017-308019) and a nearly complete ventral valve (NMV P308020).
Description.—Shell of medium size, subrectangular outline, strongly concavo-convex in profile; widest at hinge; anterior margin slightly emarginated medially; ears alate and acute, triangular in shape, well demarcated from visceral region. Ventral valve strongly but unevenly convex, strongly geniculated; umbonal region swollen; umbonal slopes sharply inclined; sulcus shallow and broad, originating from anterior to umbo, becoming prominent on trail. Dorsal valve deeply concave; fold broad and round on trail. Surface of both valves largely smooth; occasionally with some inconspicuous costae near margin; halteroid spines in row overhanging usually smooth ears; spines rare on body and trail.
Remarks.—King (1931) first named this species, but the type was selected by Cooper and Grant (1975). This species is characterized by subrectangular outline, broad and shallow sulcus, and small triangular ears. This species differs from *A. pseudohorrida* (Wiman, 1914, p. 74, pl. 17, figs. 1-11) from the Kungurian to Guadalupian Kapp Starostin Formation of Spitsbergen and *A. auriculata* Shi and Waterhouse (1996, p. 68, pl. 6, figs. 10-28; text-figs. 22-24) from the Artinskian Jungle Creek Formation in the Yukon Territory of Canada by its deeper and broader sulcus. *A. pinegensis* (Likharev, 1931, p. 26, pl. 3, figs. 24, 25; Sarytcheva, 1977, p. 123, pl. 18, figs. 5-14) from the Kungurian strata in Kanin Peninsula, northwestern Russia, could be conspecific with the present species in terms of its outline, and shallow and broad sulcus, but appears to have more subquadrate ears.

Superfamily Linoproductoidea Stehli, 1954
Family Linoproductidae Stehli, 1954
Subfamily Linoproductidae Stehli, 1954
Genus *Cancrinella* Fredericks, 1928

Type species.—Productus cancrini de Verneuil, 1845.

Cancrinella? *cancrini* (de Verneuil, 1845)

Figure 4.10

Productus cancrini de Verneuil, 1845, p. 273, pl. 16, figs. 8a-c; pl. 18, fig. 7; Likharev, 1931, p. 319, pl. 1, figs. 11-13; Miloradovich, 1935, p. 131, pl. 5, figs. 4, 5.
Cancrinella cancrini (de Verneuil). Sarytcheva and Sokolskaja, 1952, p. 112, pl. 20; Grigorjeva, 1962, p. 50, pl. 11, figs. 1-10; pl. 15, fig. 1; pl. 16, figs. 1, 2; Grigorjeva *et al.*, 1977, p. 129, pl. 19, figs. 1-9, text-figs. 75, 76.

Material.—A complete ventral valve (NMV P308024) and an incomplete external mould of a dorsal valve (NMV P308025).
Description.—Shell small, subquadrate in outline, hinge slightly narrower than greatest width; with broadly rounded anterior and lateral margins; ventral visceral disc strongly convex, somewhat triangular; beak pointed; ears small; cardinal extremities obtuse; umbonal slopes sharply inclined; sulcus absent; surface marked by strong concentric wrinkles and fine costellae; costellae numbering 7 in 2 mm near the anterior margin; spines thin and delicate; spine bases elongated, widely scattered. Dorsal valve deeply concave; strongly geniculated; surface also with distinct wrinkles and fine costellae; spines unknown.
Remarks.—The small size, subquadrate outline and very fine costellae of the present specimens are generally identical with the type figured by de Verneuil (1845). However, the unknown dorsal spines renders the generic status of the present material open. Many previously recognized species of *Cancrinella* have been attributed to *Costatumulus* Waterhouse (see Archbold, 1993), which differs from *Cancrinella* in possessing dorsal spines. Therefore, it is also possible that the Xiujimqinqi specimens could belong to *Costatumulus*.

Genus *Compressoproductus* Sarytcheva in Sarytcheva, Likharev and Sokolskaja, 1960

Type species.—Productus compressus Waagen, 1884.

Compressoproductus corniformis (Chao, 1927)

Figure 4.9

Striatifera compressa var. *corniformis* Chao, 1927, p. 101, pl. 15, figs. 6-9.
Productus (Striatifera) var. *corniformis* Chao. Grabau, 1931, p. 291, pl. 29, figs. 6-9.
Compressoproductus compressa var. *corniformis* (Chao). Wang *et al.*, 1964, p. 334, pl. 53, figs. 12, 13.

Remarks. — The occurrence of this species in the Xiujimqinqi collection is shown by a single specimen (NMV P308026). This species has been documented from the Zhesi Formation in Zhesi, Inner Mongolia, by Grabau (1931). The characteristic elongate outline, finely costellate surface and strongly laterally compressed nature of the shell of the present specimen fit very well with the type from the Longtan Formation in Guangxi, South China, as figured by Chao (1927). This species differs from all other species in the genus by the laterally compressed nature of its shell, hence warranting the recognition of Chao's variety as a separate species.

Order Spiriferida Waagen, 1883
Suborder Spiriferidina Waagen, 1883
Superfamily Spiriferoidea King, 1846
Family Spiriferellidae Waterhouse, 1968
Genus *Spiriferella* Tschernyschew, 1902

Type species.—Spirifer saranae de Verneuil, 1845.

Spiriferella persaranae (Grabau, 1931)

Figure 4.11–4.14

Spirifer persaranae Grabau, 1931, p. 156, pl. 19, fig. 4.
Spiriferella persaranae Grabau. Wang *et al.*, 1964, p. 595, pl. 114, figs. 15, 16; Li and Gu, 1976, p. 295, pl. 172, figs. 1–6; Li *et al.*, 1980, p. 418, pl. 178, fig. 5; Duan and Li, 1985, p. 121, pl. 1, figs. 1–11, 17, 18.

Material.—A slightly crushed conjoined shell (NMV P308029) and three incomplete ventral valves (NMV P308030–308032).

Description.—Shell medium in size, elongate in outline, unequally biconvex in profile, hinge narrower than greatest width at slightly anterior to midvalve; ventral beak strongly incurved; interarea very high, strongly concave, delthyrium about one-third of the hinge line; beak ridges angular; ventral sulcus narrow and shallow, commencing from beak, with several inconspicuous costae; boundary costae coarser than other costae; each flank with 4–6 costae; costae commonly bifurcating 1–2 times, producing some small costae beside the main costa; dorsal valve less convex than ventral valve; fold low, with a prominent median groove; each flank with 4–5 costae.

Remarks.—S. saranae (de Verneuil, 1845, p. 169, pl. 6, fig. 15a, b) is closest to this species. The original description of *S. saranae* by de Verneuil (1845) from the upper Artinskian of the Ufa River mentioned that this species is characterized by a high interarea, five to six smaller, equally spaced costae in the sulcus and a prominent median groove in the fold. *S. persaranae* differs from *S. saranae* in its more simple costae and less conspicuous and proba-

bly fewer and smaller costae in the sulcus. *S. praesaranae* (Stepanov,1948, p. 43, pl. 10, figs. 3–8) is probably synonymous with the present species as indicated by their similar costation, size and outline, but it is from the Upper Carboniferous.

Spiriferella keilhavii (von Buch, 1846)

Figure 4.16, 4.17

Spirifer keilhavii von Buch, 1846, p. 74, pl. 1, figs. 2a, b: Frech, 1901, p. 499, pl. 57c, figs. 1b–c.
Spirifer draschei Toula, 1875, p. 239, pl. 7, figs. 4a–c.
Spirifer parryanus Toula, 1875, p. 232, pl. 7, figs. 8a–d.
Spiriferella keilhavii (von Buch). Tschernyschew, 1902, p. 527, pl. 40, figs. 1–4; Wiman, 1914, p. 36, pl. 2, figs. 25–30, pl. 3, fig. 1; Tschernyschew and Stepanov, 1916, p. 79, pl. 11, figs. 2a–c, 3a–c; Frebold, 1931, p. 28, pl. 5, figs. 7–9; 1937, p. 46, pl. 11, fig. 9; Dunbar, 1955, p. 139, pl. 25, figs. 1–9; pl. 26, figs. 1–11; pl. 27, figs. 1–14; Gobbett, 1964, p. 154, pl. 20, fig. 7; Nelson and Johnson, 1968, p. 736, pl. 96, figs. 7, 8, 12; text-figs. 3e, 8a, 9, 13b; Brabb and Grant, 1971, p. 17, pl. 2, figs. 26–28, 34, 35; Duan and Li, 1985, p. 122, pl. 2, figs. 1, 5, 8.
Spiriferella draschei (Toula). Wiman (partim), 1914, p. 38, pl. 3, fig. 2.
?Spiriferella keilhavii (von Buch). Waterhouse and Waddington, 1982, p. 28, pl. 4, fig. 15; pl. 6, figs. 3–14; text-figs. 16e, g–i, 19.

Remarks.—As noted by Likharev and Einor (1939, p. 218) and Dunbar (1955, p. 152), von Buch's original figure of *S. keilhavii* is a drawing constructed from a number of specimens, two of which (a dorsal and a ventral) were later figured by Frech (1901, pl. 57c, figs. 1b–c). Likharev and Einor (1939) selected the dorsal valve of Frech's figured material (Frech, 1901, pl. 57c, fig. 1b) as the 'holotype' (lectotype) of *S. keilhavii* on the ground that the features of the dorsal valve match better with von Buch's original description of the species. Since our material consists only of two ventral valves (NMV P308033, 308034), no comparison can be made with the lectotype of the species, but the observed features of the ventral valves, especially the large and wide valves with a hinge line nearly as wide as the greatest shell width and strongly fasciculated costae, are characteristic of the ventral valve of *S. keilhavii* as figured by Tschernyschew (1902), Dunbar (1955) and Gobbett (1963).

Spirifer parryanus Toula (1875) from Spitzbergen was erected based on several incomplete specimens, and has been referred to *S. keilhavii* (Dunbar, 1955, p. 145). Specimens figured by Waterhouse and Waddington (1982) from Yukon Territory of Canada have flat, coarse and unbranched costae and a relatively narrower hinge, suggest-

ing that they are probably different from the type material of *S. keilhavii* as described and figured by Dunbar (1955, pl. 27, figs. 8, 9).

Family Spiriferidae King, 1846
Subfamily Kaninospiriferinae Kalashnikov, 1996
Genus *Kaninospirifer* Kulikov and Stepanov
in Stepanov *et al.*, 1975

Types species.—*Spirifer kaninensis* Likharev, 1943.

Remarks.—When proposing Kaninospiriferinae, Kalashnikov (1996) included two genera in this new subfamily: *Kaninospirifer* and *Imperiospira* Archbold and Thomas, 1994. The former is distinguished from the latter by its transverse outline, ill-defined fasciculation if present at all, and lack of adminicula within the ventral interior. On the other hand, both genera are readily distinguished from members of the Neospiriferinae by fine and equidimensional costae, generally weak fasciculation and absent to weakly developed adminicula.

As already noted, *Kaninospirifer* has very limited stratigraphical and geographical distributions. Kalashnikov (1996) has listed the genus occurring mainly in the Arctic region (Arctic Canada, Greenland, Spitsbergen, Arctic Russia) and East Asia (South Primorye of Far East of Russia, southeast Mongolia, northeast China). Pavlova (1991, p. 130) also listed some previously reported species from Timor and the Salt Range as possible representatives of the genus, but the true identities of these species have not yet been confirmed. On the other hand, *Gypospirifer* sp. from the Middle Permian of the Hida Gaien Belt of central Japan (Tazawa, 2000, figs. 3.12, 3.13) appears referable to *Kaninospirifer* judging by its shape and costation pattern. In all of its confirmed occurrences, *Kaninospirifer* is known to be associated with Kazanian (or Wordian) faunas.

Kaninospirifer sp.

Figure 4.20

Remarks. — An incomplete ventral valve (NMV P308035) in the collection indicates *Kaninospirifer*. The specimen is characterized by a transverse outline, very weak fasciculation that is visible only on the umbo, fine and equidimensional costae numbering about 15 per cm at about 2 cm from the beak, and a broad and well defined sulcus. This specimen appears to be closest to *Kaninospirifer kaninensis* (Likharev, 1943, p. 279, figs. 1 - 4), type species of the genus, from the Kazanian (Wordian) of the Kanin Peninsula, Russia. The two forms share a transverse outline, weak fasciculations that do not form prominent bundles, fine and even costae, and a well developed sulcus, but further comparison is hampered because of insufficient material in our collection, especially

the total lack of knowledge of the interior.

Pavlova (1991) assigned several species from the Middle Permian of Mongolia, South Primorye of Russian Far East, and northeast China to *Kaninospirifer*. Both *K. incertiplicatus* Pavlova (1991, p. 131, pl. 29, figs 5, 6; see also Fredericks, 1925, p. 27, pl. 4, figs. 111, 112) and *K. adpressum* (Liu and Waterhouse, 1985, p. 36, pl. 12, figs. 5–10; see also Pavlova, 1991, p. 132, pl. 29, figs. 7, 8) are larger than the present specimen, less transverse and more subquadrate in outline, and possess variably developed plicae on the shell surfaces.

Gypospirifer sp., from the Middle Permian Moribu Formation of the Hida Gaien Belt of central Japan (Tazawa, 2000, figs. 3.12, 3.13), is likely a representative of *Kaninospirifer*, judging by its transverse outline, relatively fine and even costae and ill-defined fasciculation, but the ventral valve (Tazawa, 2000, fig. 3.12) seems to display slightly coarser costae than the present specimen.

Subfamily Neospiriferinae Waterhouse 1968
Genus *Neospirifer* Fredericks 1923

Type species.—*Spirifer fasciger* von Keyserling, 1846.

Neospirifer sp.

Figure 4.15, 4.18, 4.21

Remarks. — An incomplete conjoined shell (NMV P308036) has a deeply V-shaped sulcus in the ventral valve and a highly elevated fold in the dorsal valve. The crests of the plicae that bound the sulcus are sharp. Costae on flanks are fascicostellate and fine, numbering about 10 per cm near the anterior margin. Each fascicle consists of 6–8 costae. This species differs from any known species of *Neospirifer* by its fine costae on both valves and the deep, V-shaped sulcus. *N. fasciger* (von Keyserling, 1846) is somewhat similar to this species in terms of its outline and general fasciculation pattern, but differs by its shallower and U-shaped sulcus and coarser costae.

Neospiriferinae gen. and sp. indet.

Figure 4.19

Remarks. — An incomplete ventral valve (NMV P308037) indicates possibly another species of *Neospirifer* or a related genus. The specimen has a subquadrate outline, weak fasciculation, coarse and somewhat flattened costae which are grouped into bundles of two to four (generally three), and a relatively broad and shallow sulcus. No known species of *Neospirifer* seems to resemble this specimen very closely. On the other hand, *Cratispirifer nuraensis* Archbold and Thomas (1985, p. 280, figs. 8A–F)

from the Sakmarian of Western Australia appears comparable in general terms, especially on account of their coarse, flattened and equidimensional costae that are grouped into bundles of no more than four (usually three), but the latter species is clearly distinguishable by its transverse outline, a proportionally high ventral interarea, and flattened costae. *Spirifer*? sp. from the Kungurian Talatinsk Formation of the Kozhim River section of the Pechora Basin, Russia (Kalashnikov, 1998), shares a similar outline and costation pattern with the present specimen, but it has a deeper sulcus and a more convex umbonal region.

Acknowledgements

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The Recent rhynchonellide brachiopod
Parasphenarina cavernicola gen. et sp. nov.
from the submarine caves of Okinawa, Japan

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Abstract. A new micromorphic rhynchonellide brachiopod *Parasphenarina cavernicola* gen. et sp. nov. is described from submarine caves on the outer slopes of coral reefs in the Ryukyu Islands, Japan. Based on the presence of spinuliform crura, the new genus is included in the Family Frieleiidae Cooper, the diagnosis of which is emended. Detailed morphological observations of different-sized shells and intraspecific variability have shown that the morphology of the hinge plates changes considerably during ontogeny. It is suggested that the new genus *Parasphenarina* could have evolved from forms close to the extremely rare bathyal Pliocene genus *Sphenarina* Cooper. The diagnostic characteristics of *Parasphenarina* such as diminutive adult size and lack of septalium and median septum may represent paedomorphic evolution.

Key words: Brachiopoda, Japan, Okinawa, ontogenetic variability, paedomorphic process, *Parasphenarina cavernicola* gen. et sp. nov., Recent, submarine cave

Introduction

Studies on the benthic fauna from more than thirty submarine caves on the outer slopes of coral reefs in the Ryukyu Islands and adjacent areas have been conducted since 1989. Thanks to the SCUBA diving technique it was possible to explore in detail the caves and collect a large amount of sediment samples. The samples turned out to be rich in many interesting organisms characteristic of cryptic habitats, such as bivalves, gastropods, chitons, polychaetes, crustaceans, brachiopods, bryozoans, echinoids, ahermatypic corals, sponges and benthic foraminifers. A number of taxonomic studies have been subsequently published: on molluscs (Hayami and Kase, 1992, 1993, 1996; Kase and Hayami, 1992; Kase and Kinjo, 1996) and ostracodes (Tabuki and Hanai, 1999). They report many unusual characteristics of the fauna, such as reduced adult size, anachronistic shell forms and life styles, paedomorphic forms in comparison with supposed ancestors, and unique taxonomic assemblages including many typical bathyal and abyssal genera. Some apparent

'living fossils' inhabiting the sheltered environment of the submarine caves were also discovered. The fauna as a whole is almost entirely different from that found in adjacent seas outside the caves.

The brachiopods collected from the submarine caves of the Ryukyu Islands include several species as yet undescribed. Among the brachiopod assemblage, a single rhynchonellide species was found. This paper describes this new, micromorphic, thin, transparent-shelled rhynchonellide species. Initially the new species was assigned with a query to the Pliocene genus *Sphenarina* Cooper, 1959 (Saito *et al.*, 2000). Based on detailed morphological observations, study of the ontogeny, and comparison with the type species of the genus *Sphenarina*, we found enough evidence to propose a new genus for the rhynchonellides from the Okinawa submarine caves, herein named *Parasphenarina cavernicola* gen. et sp. nov. The closest taxon to the new species is *Sphenarina ezogremena* Zezina (Zezina, 1981) known from a single specimen from the Flores Sea. We include the species *S. ezogremena* in the new genus *Parasphenarina*. The new genus could
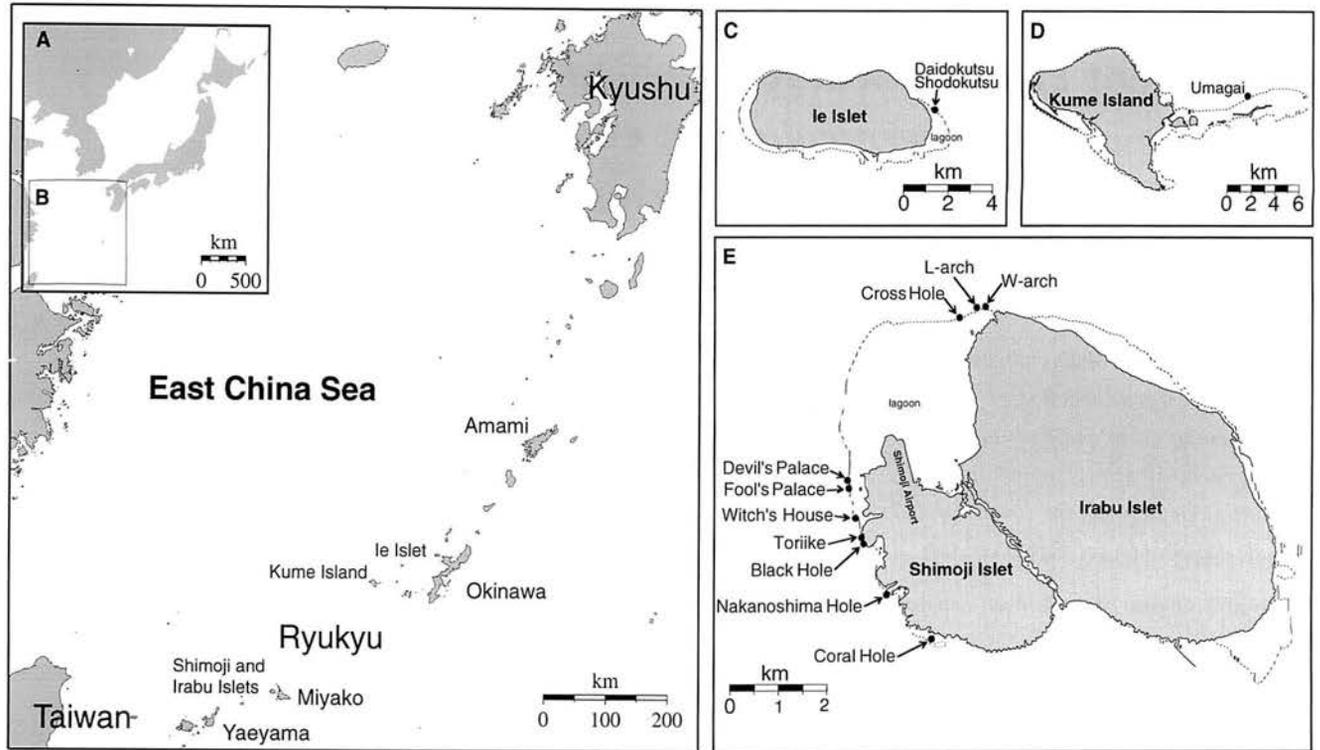
Figure 1. Locality maps (after Hayami and Kase, 1993). **A.** Index map. **B.** Detail of **A** showing Ie, Irabu and Shimoji Islands. **C.** Localities of submarine caves of Ie Islet. **D.** Localities of submarine cave of Kume Island. **E.** Submarine caves of Shimoji Islet and Irabu Islet in Miyako Islands.

have evolved from forms morphologically close to the extremely rare bathyal Pliocene genus *Sphenarina* from Sicily (cf. Cooper, 1959; Gaetani and Saccà, 1984). It is suggested that the diagnostic characteristics of *Parasphenarina* such as diminutive adult size and lack of septalium and median septum may have resulted from paedomorphic evolution.

Study area and methods of investigation

The submarine caves of Okinawa vary in size and topography, although they have many common characteristics. The caves are open to the forereef slopes, and their morphology is complicated, winding and bifurcating, with numerous crevices. The caves are in the Pleistocene Ryukyu Limestone, and generally have entrances at about 15 to 40 m water depth and horizontal lengths ranging from several meters to more than 70 m. Sediments on the cave floors are composed of calcareous mud and bioclasts. They are almost free of coarse terrigenous material (Hayami and Kase, 1996). The caves were probably formed by ground water during some lower sea level stages in the Pleistocene and finally drowned during the postglacial rise of sea level (Kase and Hayami, 1992; Hayami and Kase, 1993, 1996). Twelve submarine caves of the Ryukyu Islands (one is lo-

cated in Kume Island, two in Ie Islet, seven in Shimoji Islet, and two in Irabu Islet, Miyako Islands (Figure 1) yielded specimens of *Parasphenarina cavernicola* for this study. Sessile benthic biota were collected by brushing the surfaces of walls, ceilings and undersides of boulders or large shells of dead bivalves such as *Pycnodonte taniguchii*, with the assistance of divers. Boulders and dead bivalves that could be brought to the surface, as well as sediments in the caves, were also collected to look for live and dead individuals under the binocular microscope. The morphology of the specimens was examined both under the binocular and scanning electron microscopes (SEM). For observing the microstructure of the primary layer surface, selected shells of *Parasphenarina cavernicola* were treated with domestic-grade bleach (sodium hypochlorite: approximately 5% (v/w)) for 12 to 18 hours to remove surface debris and the periostracum, then washed, dried, and mounted on stubs for SEM. Other shells were dried and embedded in epoxy resin, transversely cut at the maximum shell width, polished with a set of diamond powders and subsequently etched with 5% (v/v) HCl for 5 seconds. Other specimens after drying were broken to observe the uneven natural fracture of the primary calcitic layer. All samples were then coated with Pt-Pd alloy, and photographed by a Hitachi S–2400S scanning electron microscope. The

Figure 2. Holotype of *Parasphenarina cavernicola* gen. et sp. nov., UMUT RB28220–MN01–a, 'Nakanoshima Hole', Shimoji Islet, Miyako Island.

measurements of *Parasphenarina cavernicola* were taken using the Nikon profile projector V–12BDC.

The specimens of *Sphenarina sicula* Davidson from the Pliocene of Messina, (Sicily, Italy), borrowed for comparison from the Smithsonian Institution, National Museum of Natural History (USNM 549381a, b; Cooper, 1959), were photographed with a Hitachi S–2250N natural SEM without coating. One of the borrowed specimens (USNM 549381b) was embedded in epoxy and transversely sectioned to compare with the sections of the new species *P. cavernicola*.

Systematic description

Class Rhynchonellata Williams *et al.*, 1996
Order Rhynchonellida Kuhn, 1949
Family Frieleiidae Cooper, 1959

Emended diagnosis.—Capillate to costellate or smooth rhynchonellides with subtriangular to teardrop outline and spinuliform crura.

Remarks. — The family Frieleiidae was created by Cooper (1959) for capillate to costellate rhynchonellide genera with triangular outline, strong dental plates and spinuliform crura, supported by short plates uniting with the septum of the dorsal valve to form a septalium. At the same time Cooper (1959) introduced the family Hispanirhynchiidae for rhynchonellides having spinuliform crura, low or no median ridge but no septalium in the dorsal valve. In the first edition of the brachiopod volumes of the Treatise on Invertebrate Paleontology (Ager, 1965) the hispanirhynchiids were included in the family Frieleiidae,

even though the hispanirhynchiid genera *Hispanirhynchia* Thomson and *Sphenarina* Cooper do not possess or have only a low median ridge in the dorsal valve and do not have a septalium by original diagnosis. However, according to our new observations (see below) on the type material of *Sphenarina*, this genus does possess an incipient septalium in the adult dorsal valve. This feature brings *Sphenarina* closer to the frieleiid genera with a septalium. Thus the separation of the hispanirhynchiid species into a family or subfamily seems not to be justifiable now, until a reappraisal of other genera like *Hispanirhynchia*, *Manithyris* Foster and *Abyssorhynchia* Zezina demonstrates the lack of a septalium in the adult forms. The new genus *Parasphenarina* lacks a septalium and a typical median septum. In the present state of knowledge we prefer to emend the diagnosis of the family Frieleiidae to exclude the presence of a septalium from the diagnosis and to include smooth-shelled genera like *Parasphenarina* into the family. Frieleiidae ranges from Pliocene to Recent.

Genus *Parasphenarina* gen. nov.

Type species. — *Parasphenarina cavernicola* sp. nov., Recent, Okinawa Islands, Japan.

Derivation of name.—From Greek *para* = near, close to, referring to the similarity to the genus *Sphenarina* and suggesting that *Parasphenarina* could have evolved from forms close to *Sphenarina*.

Diagnosis.—Diminutive smooth teardrop-shaped to triangularly oval rhynchonellides with smooth semitransparent shell; subequivalve, rectimarginate anterior commissure; suberect to straight beak, hypothyrid auriculate
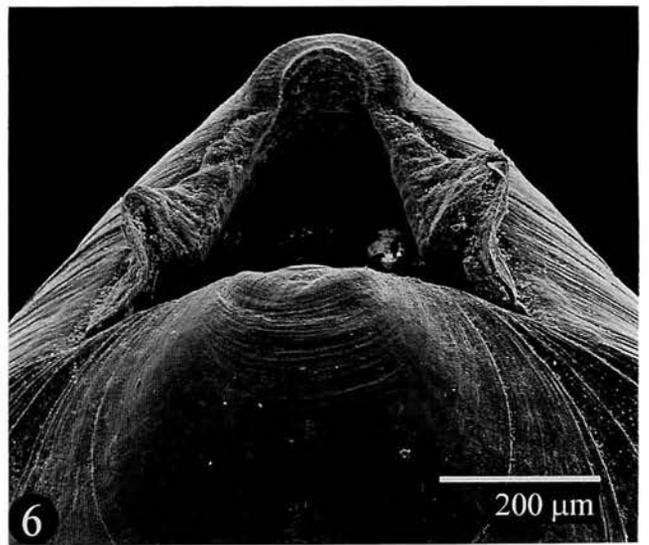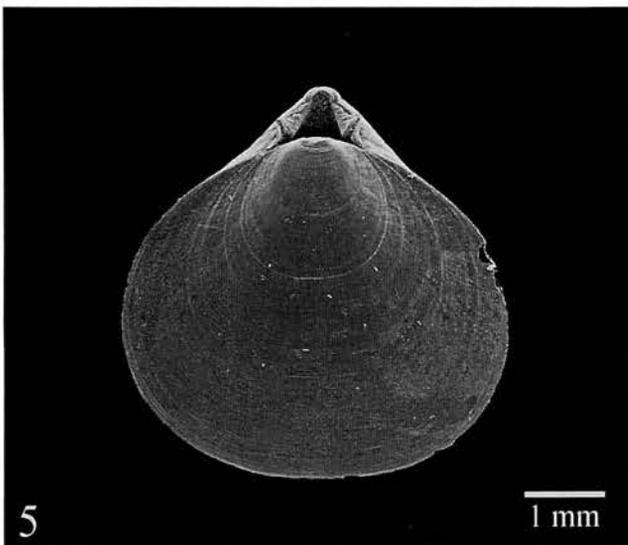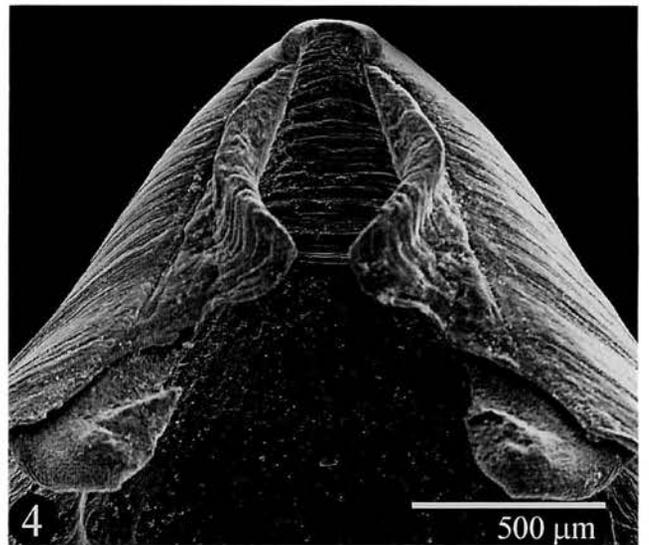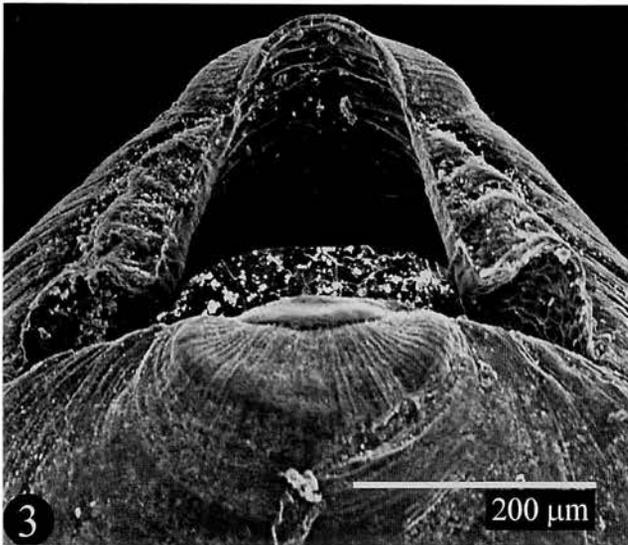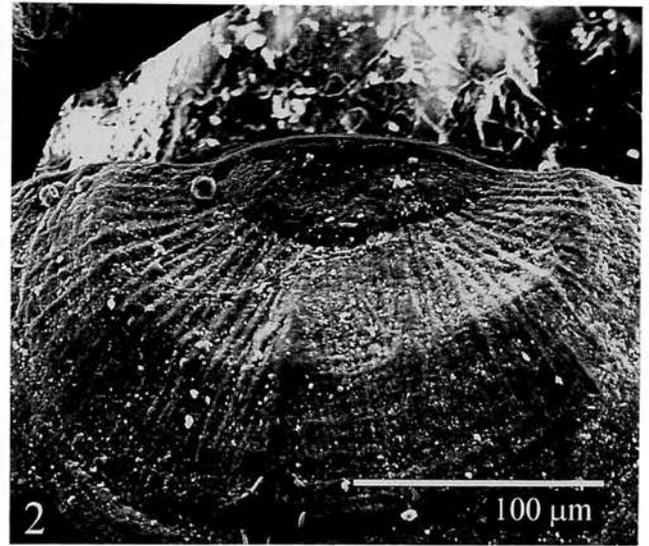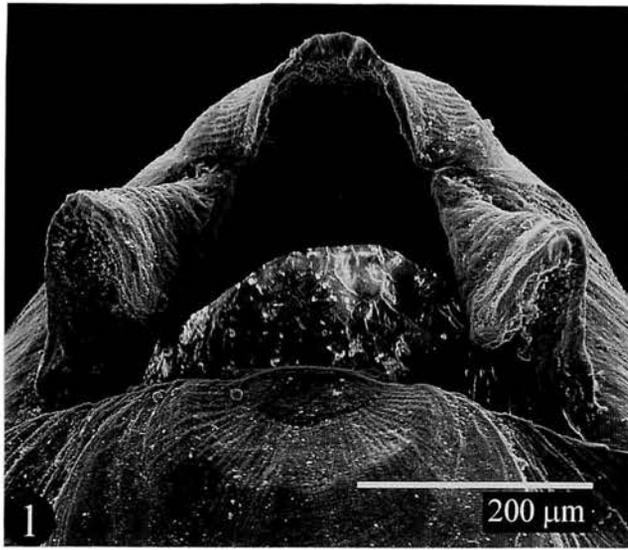
foramen, disjunct deltidial plates. Dorsal valve lacks a median ridge, though a shallow groove between two low ridges may be present instead. Crura spinuliform; cardinal process and septalium absent. Hinge plates and inner socket ridges do not meet together in posterior part of dorsal valve.

Species assigned.—Besides the type species *Parasphenarina cavernicola* sp. nov., only one more species based on a single specimen and referred previously to the genus *Sphenarina*, is here included in the new genus—the Recent *Sphenarina ezogremena* Zezina, found in the Flores Sea, north of Bali Island. Thus, the new combination *Parasphenarina ezogremena* (Zezina) is adopted below.

Remarks.—*Parasphenarina* is most similar to the genus *Sphenarina* Cooper, 1959 from the Pliocene of Sicily, Italy. Initially we tentatively assigned the new cave rhynchonellide species to the genus *Sphenarina* (Saito *et al.*, 2000) based on similar shape, spinuliform crura, rectimarginate anterior commissure, well developed hinge plates and lack of a median septum and septalium. According to the original diagnosis, *Sphenarina* does not possess a median septum. We examined the type material of *Sphenarina* used by Cooper, deposited at the National Museum of Natural History, Smithsonian Institution, Washington. Additionally we borrowed for comparison and serially sectioned one of the topotype specimens from the Pliocene of Messina (Sicily, Italy). In contrast to Cooper's diagnosis (1959, p. 63) we discovered a low median septum and a small incipient septalium in the umbonal part of the dorsal valve of the sectioned specimen of *Sphenarina sicula* (Davidson). The sectioned specimen with septalium (Figure 14.2) was larger (L = 15.60 mm, W = 15.10 mm, T = 8.40 mm) than the one figured by Cooper (1959, Pl. 8–A7) and in this paper on Figure 14.1 (L = 12.55 mm, W = 10.50 mm, T = 6.60 mm). It is possible that the septalium in *Sphenarina* develops in the late adult stage only and is not present in juvenile individuals. Since *Sphenarina* is an extremely rare genus (Gaetani and Saccà, 1984; personal communication, 2001) it is not possible to section further material to check the development of a septalium in other adult shells. However, a similar example of presence of a better developed septalium in a large specimen of *Burmirhynchia turgida* Buckman from the Bathonian of Laz, Yugoslavia is figured by Radulović (1991, figs 4, 5). From our data, we can assert that the new genus *Parasphenarina* differs from the Pliocene genus *Sphenarina* in the lack of a median septum and septalium in the adult stage. The hinge plates and the inner socket

ridges of the new genus do not meet at the top of the dorsal valve, and remain separated (Figures 5.1, 5.3, 5.5, 6.3). In contrast, the hinge plates and the inner socket ridges of *Sphenarina* meet together at the top of the dorsal valve. Additionally, an incipient cardinal process was noted in the specimen dissected by Cooper (Figure 14.1). *Parasphenarina* is micromorphic in size and has completely smooth shells, disjunct auriculate deltidial plates, poorly developed dental plates, delimiting narrow umbonal cavities and an elaborate pedicle collar, while *Sphenarina* is larger in size, finely capillate, with deltidial plates that can be conjunct (towards later ontogenetic stages), and has well developed dental plates and a shorter pedicle collar. The revision of the genus *Sphenarina* will be discussed elsewhere.

Parasphenarina is externally similar to *Cryptopora* Jeffreys and *Tethyrhynchia* Logan. However the three genera can be easily distinguished by their internal morphology, especially by the development of three different types of crura: spinuliform, maniculiform and luniform respectively, which places them in three different families.

## *Parasphenarina cavernicola* sp. nov.

Figures 2–12

Sphenarina? sp., Saito *et al.*, 2000, p. 77; Saito *et al.*, 2001, p. 131, 132.

Derivation of name.—From Latin *caverna* = cave plus the Latin suffix *-cola* = dweller, inhabitant, after its occurrence in submarine caves.

Holotype.—The holotype specimen (UMUT RB28220-MN01–a) (Figure 2) and 19 paratypes (UMUT RB28220-MN01–b) were collected at 27 m depth from the bottom of the cave 'Nakanoshima Hole', Shimoji Islet, Miyako Island. The holotype and all the paratypes are deposited at the University Museum, the University of Tokyo (UMUT).

Material and occurrence.—Twenty-one living specimens and more than 80 intact dead shells, many separated valves and fragments from 12 submarine caves in coral reefs of the Ryukyu Islands (Figure 1). The material is deposited at the University Museum, the University of Tokyo (UMUT RB28210–28222). One complete specimen, two ventral and two dorsal valves are housed at the National Museum of Natural History, Sofia (NMNHS 31068). Brief descriptions, the location of the caves and sample numbers are given below. The appended data on the geographical position, length, bottom depth and description of these caves are from Hayami and Kase (1993) with two ad-

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← **Figure 3.** *Parasphenarina cavernicola* gen. et sp. nov., Shimoji Islet, Miyako Island. **1.** Umbonal part of specimen UMUT RB28220–R1–7, 'Nakanoshima hole'. **2.** Detail of **1** showing the fine capillation anterior to the protegular node. **3.** Umbonal part of specimen UMUT RB28220–R1–6, 'Nakanoshima hole'. **4.** Ventral beak showing the teeth and disjunct deltidial plates UMUT RB28220–R5–8, 'Nakanoshima hole'. **5.** Subcircular juvenile specimen UMUT RB28219–R4–1, 'Coral hole'. **6.** Detail of **5** showing the umbonal part.
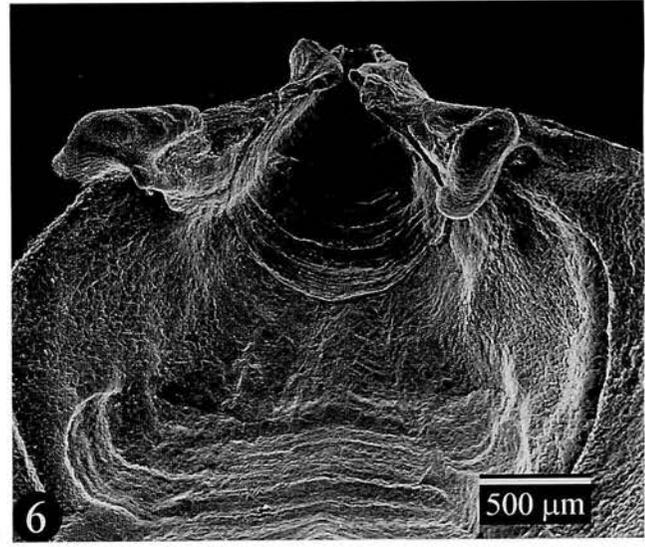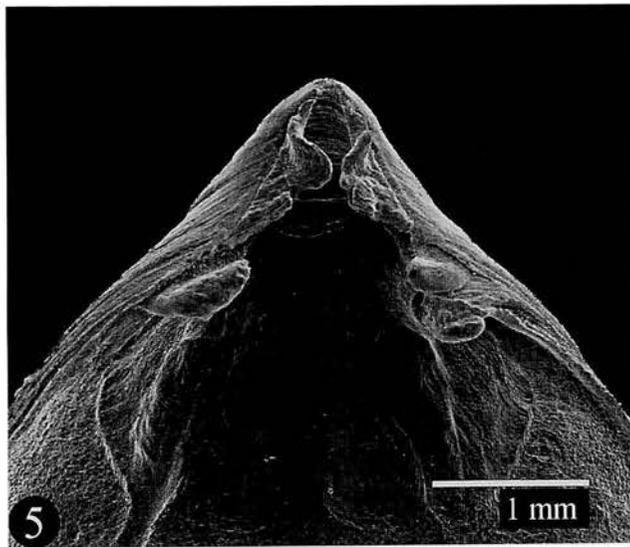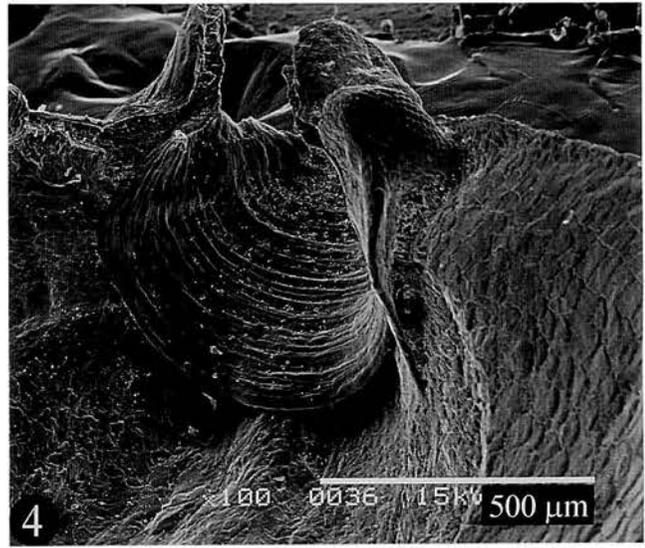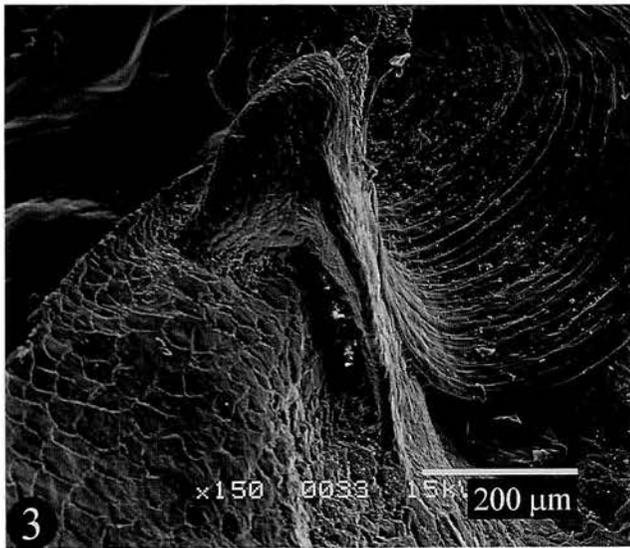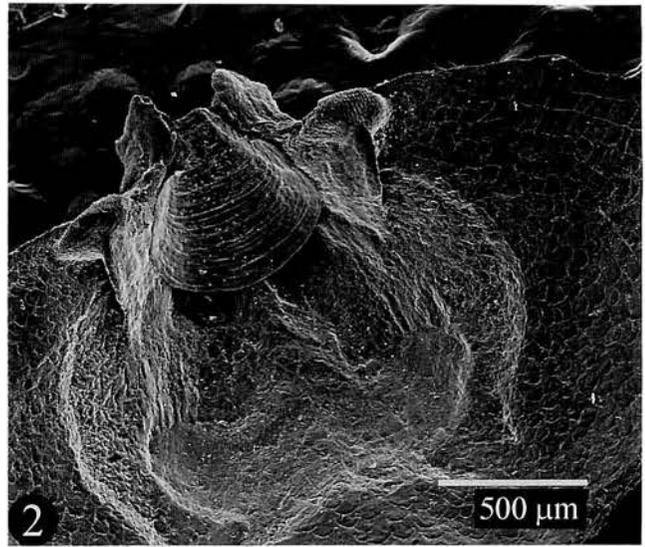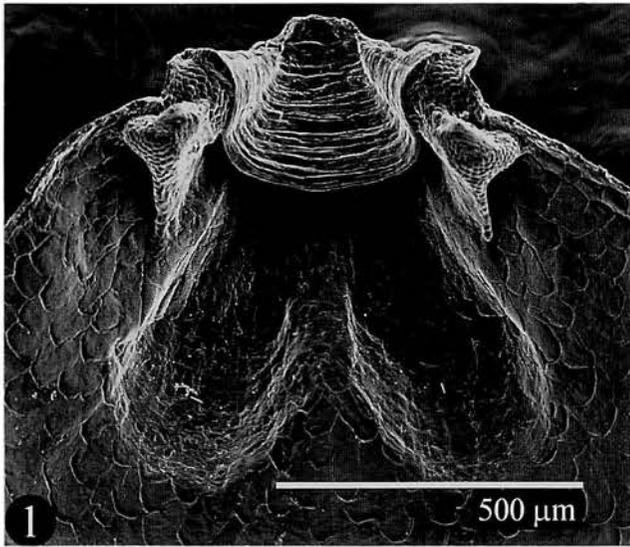
ditional caves ('Umagai' and 'Nakanoshima Hole') not mentioned by them. The bottom depth data are given for the entrances and the innermost parts of the caves: **Kume Island**: 1. 'Umagai' cave (26° 21.3′ N, 126° 53.3′ E), more than 25 m long, curved tunnel, innermost part is totally dark (-28.3 m to 26 m deep), UMUT RB28210-KU05. **Ie Island**: 2. 'Shodokutsu' (26° 42.9′ N, 127° 50.1′ E), more than 30 m long, totally dark, winding and branching tunnel (-20 to -7 m deep), UMUT RB28211-IS01, IS 02, IS05, IS23; 3. 'Daidokutsu' (26°42.9′ N, 127°50.1′ E), about 10 m long, very dark, cathedral-like wide cave (-20 m deep), UMUT RB28212-ID07, ID11, ID14, ID17, ID18; a mixed sample UMUT RB28213-ISD01 from 'Shodokutsu' and 'Daidokutsu' caves. **Shimoji Island**. 4. 'Devil's Palace' (24° 49.6′ N, 125° 08.2′ E), about 15 m long, dark tunnel (-25 m deep) with some narrow openings on the ceiling, UMUT RB28214-MD02, MD03; 5. 'Fool's Palace' (24° 49.6′ N, 125°08.2′ E), about 10 m long, almost totally dark tunnel (-35 to -32 m deep), #UMUT RB28215-MF01, MF02, MF04, MF05; 6. 'Witch's House' (24° 49.3′ N, 125° 08.3′ E), more than 10 m long, totally dark tunnel (-37 to -35 m deep), UMUT RB28216-MM06, MM07, MM09; 7. 'Toriike' (24° 49.1′ N, 125° 08.3′ E), a famous diving point, about 30 m long, large dark tunnel connected with two large side tunnels (-40 to -12 m deep), UMUT RB28217-MT06; 8. 'Black Hole' (24° 49.1′ N, 125° 08.3′ E), about 70 m long, totally dark stepwise tunnel with an air pocket in the innermost part (-35 to 0 m deep), UMUT RB28218-MB06; 9. 'Coral Hole' (24° 48.0′ N, 125° 09.0′ E), about 5 m long, dark hole and tunnel (-35 m deep), UMUT RB28219-MS01, MS02, MS03, MS05, MS06, MS07, MS08, MS09, MS10, MS12, MS13, MS16, MS17; 10. 'Nakanoshima Hole' (24° 48.47′ N, 125°08.65′ E), a submarine cave totally dark inside, entrance about 20 m deep, UMUT RB28220-MN01 (including the holotype and paratype), MN02, MN03. **Irabu Island**. 11. 'W-arch' (24° 51.7′ N, 125° 09.7′°E), double dark caves with an opening on the ceiling (-15 to -13 m deep), UMUT RB28221-MW01, MW05; 12. 'Cross Hole' (24° 51.67′ N, 125° 09.5′ E), 20 m long, dark hole with complicated morphology (-25 to -20 m deep), UMUT RB28222-MC13.

Ecology and associated brachiopods.—Live individuals of *Parasphenarina cavernicola* were mainly found attached to the undersides of hard substrates lying on the cave floor near the entrance, and were occasionally found on the cave wall at the middle of dark tunnels (such as 'Coral Hole') as a member of a cryptic brachiopod-sclerosponge community, but never found from the innermost part of the closed cave that does not have sufficient water movement. So far, fresh empty shells of *P. cavernicola* are limited to the sediments from within the caves and only a single fragmentary shell was collected from sediments outside the caves. Thus, *P. cavernicola* should be regarded as typically a cave-dweller. Brachiopods associated with *P. cavernicola* include: *Craniscus* cf. *japonicus*, *Terebratulina* sp., *Argyrotheca* sp.1, *Argyrotheca* sp.2, *Frenulina sanguinolenta*, '*Frenulina*' sp., '*Amphithyris*' sp., *Thecidellina* sp. and *Lacazella* sp. (Saito et al., 2000). Dead shells of *P. cavernicola* were most abundant in 'Nakanoshima Hole' cave, where the holotype was collected. In this cave *P. cavernicola* represents 11.2% of the total (N = 116) of the brachiopod dead shell assemblage. Corresponding figures for other brachiopods in the same cave are: *Craniscus* -11.2%, *Argyrotheca* sp.1 -14.7%, *Argyrotheca* sp.2 -0.9%, *Frenulina sanguinolenta* -1.7%, '*Frenulina*' sp. -47.4%, *Thecidellina* sp. -1.7% and *Lacazella* sp. -11.2%. All those cave brachiopods are characterized by a minute adult shell size, usually less than 5mm in length, which could have resulted from employment of the same adaptive strategy to the dark and oligotrophic environment as advocated for other cave-dwelling brachiopods, including the rhynchonellide *Tethyrhynchia* from the Mediterranean caves (Logan and Zibrowius, 1994; Simon and Willems, 1999), and cave molluscs (Kase and Hayami, 1992; Hayami and Kase, 1996).

Diagnosis.—*Parasphenarina* with abraded rounded ventral beak and poorly defined dental plates; teeth and dental sockets not corrugated. During ontogeny inner hinge plates appear in juveniles but are almost completely resorbed in adult individuals. Outer hinge plates appear in mid-sized specimens and develop gradually during ontogeny to reach their maximum size in adult and gerontic specimens.

Description.—Shell diminutive, impunctate, translucent, delicate, teardrop-shaped to rarely oval in outline, longer than wide, equibiconvex or dorsibiconvex. Maximum observed length (L) -6.20 mm, width (W) -5.51 mm, and thickness (T) -3.54 mm. Maximum width and thickness at midvalve; anterior commissure rectimarginate; lateral commissures straight. Surface smooth, with well defined growth lines; in adult specimens better developed anteriorly

← **Figure 4.** *Parasphenarina cavernicola* gen. et sp. nov. Shimoji Islet, Miyako Island. **1.** Interior of a ventral valve to show the sessile pedicle collar and heart-shaped muscle field, specimen UMUT RB28220-R5-11, 'Nakanoshima Hole'. **2.** Interior of a ventral valve showing the sessile pedicle collar, teeth and dental plates, specimen UMUT RB28219-R2-3, 'Coral Hole'. **3.** Detail of 2 showing the left tooth, dental plate and the narrow umbonal cavity. **4.** Detail of 2 showing the right tooth, dental plate and the narrow umbonal cavity. **5.** Umbonal part of a large ventral valve showing close disjunct deltidial plates, UMUT RB28220-R2-9. **6.** The same valve from 5, inclined to show the large teeth and pedicle collar lying on the valve floor.
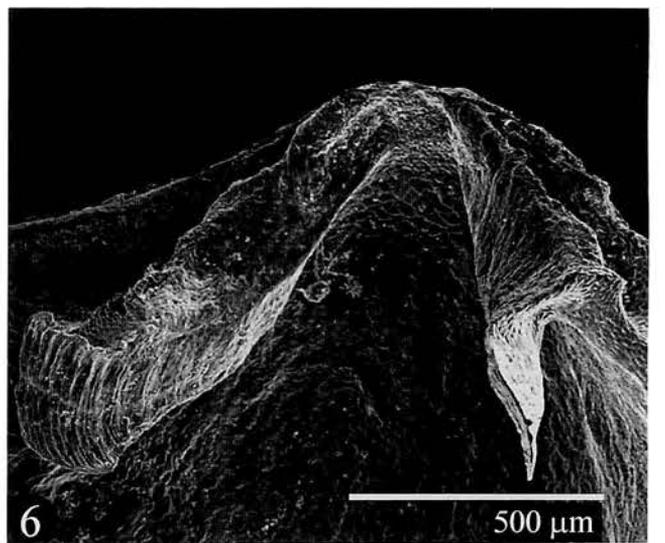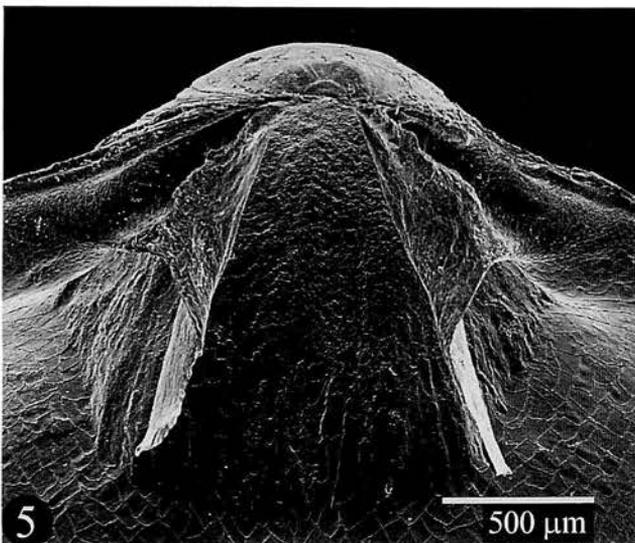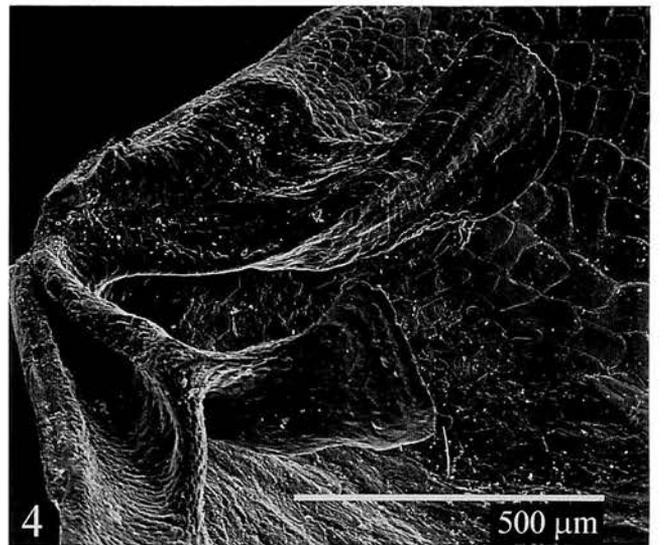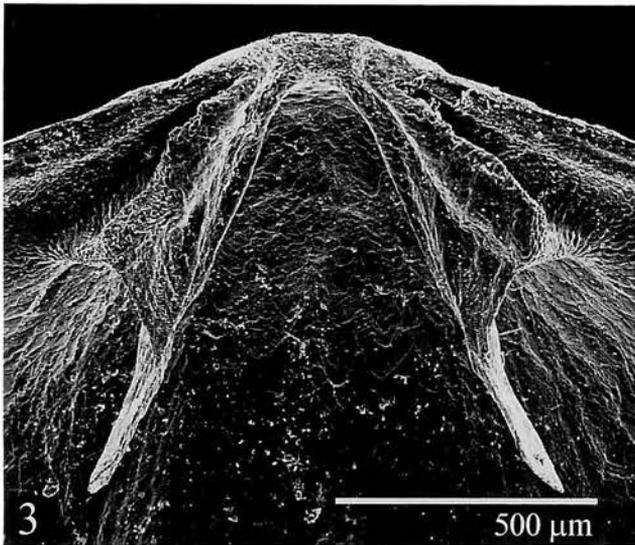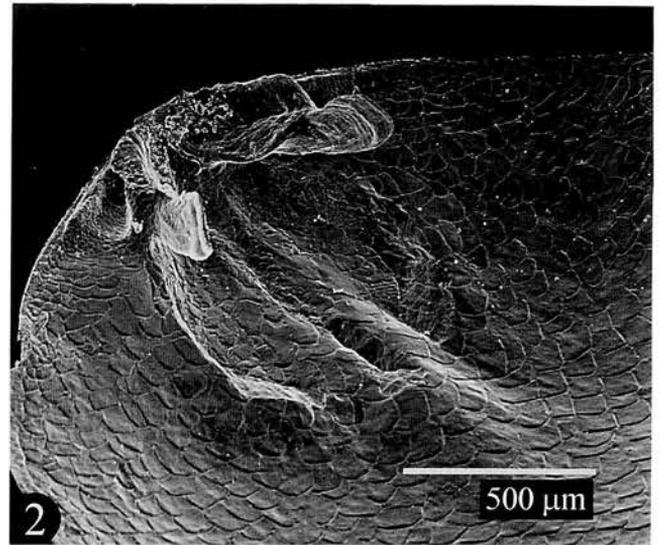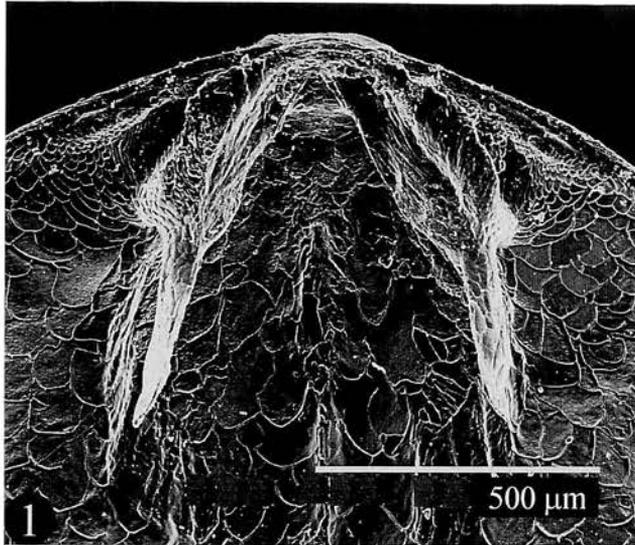
with slight imbrication laterally. In many specimens umbonal part of shell, just anterior to smooth protegular node, finely capillate (Figure 3.1 - 3.3). Beak almost straight, foramen hypothyrid, large, deltidial plates disjunct, auriculate (Figure 3.1, 3.4, 3.6). Ventral beak abraded, due to migration of pedicle towards ventral valve; foramen thus has a rounded tip (Figure 3.1, 3.3, 3.4, 3.6). Beak ridges not defined.

Ventral valve interior with short but elongate, uncorrugated, large teeth (Figure 3.4), supported by incipient, short, divergent dental plates, developed close to shell wall, forming shallow, narrow umbonal cavities (Figure 4.1, 4.3, 4.4). Pedicle collar large, elevated above valve floor forming a chamber beneath, with well defined growth lines (Figure 4.1-4.4). Muscle field large, heart-shaped (Figure 4.1, 4.2), occupying 1/4 to 1/3 of shell length. No pallial markings.

Dorsal valve interior with uncorrugated dental sockets, bounded by well developed socket ridges. Inner socket ridges thick; no cardinal process. Crura of spinuliform type, short blade-like (Figure 5.3–5.6), often widening like a spade at their distal ends (Figure 6.2, 6.4). Juvenile specimens have inner hinge plates (Figures 5.1, 11.1); adult specimens develop outer hinge plates, inclined dorsally to shell floor (Figure 5.3, 5.5). Relatively large circular muscle field defined by distinct slopes laterally. In this field there is a shallow median groove bounded by two low ridges from sides (Figure 5.2). No pallial markings visible. Compared to muscle field of other frieleiid genera musculature of this genus is feeble, correlating closely with reduced size.

Serial sections of an adult specimen embedded in epoxy show clearly divergent plates, narrow umbonal cavities, close to lateral wall and strong teeth (Figure 7). In dorsal valve, outer high plates dorsally inclined and spinuliform crura arise from dorsal side of hinge plates. Anteriorly, crura with weak crescent shape sections (convex outward). Median groove very weak and sinuated in centre between two low ridges in muscle field, outlined by lateral slopes.

Majority of living individuals juvenile. Lophophore rarely preserved, of a schizolophous type in a specimen 1.8 mm long with long setae present (Figure 8.1). Largest living specimen (L = 5.45 mm) with a spirolophous-type lophophore, but its shape, number of volutions and orientation unknown due to mechanical distortion. Mature gonads observed in posterior part of mantle in same specimen
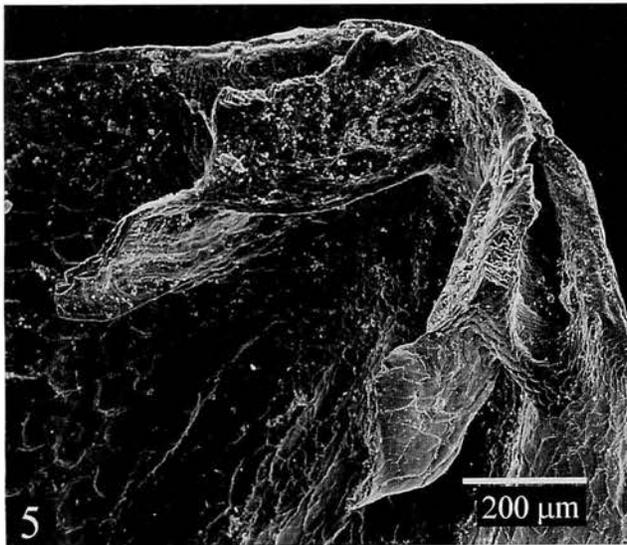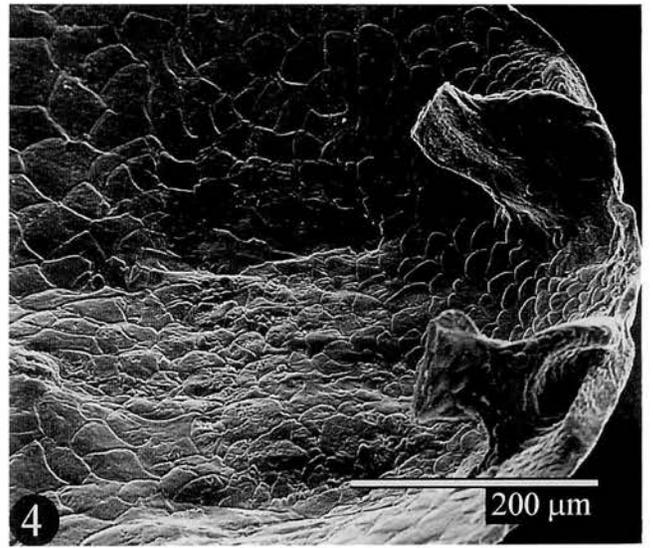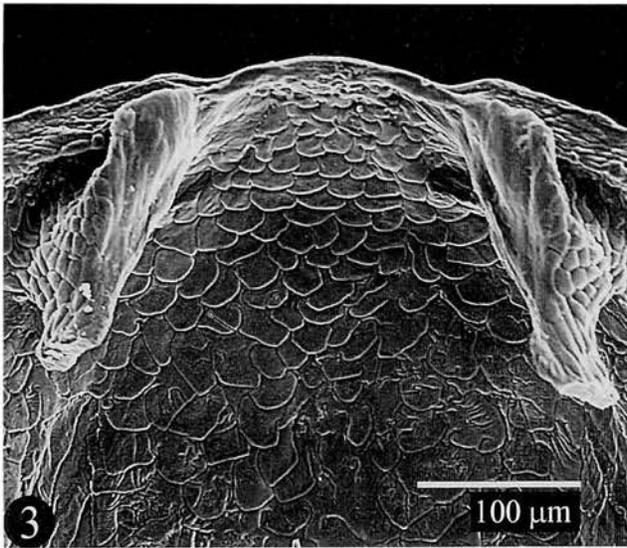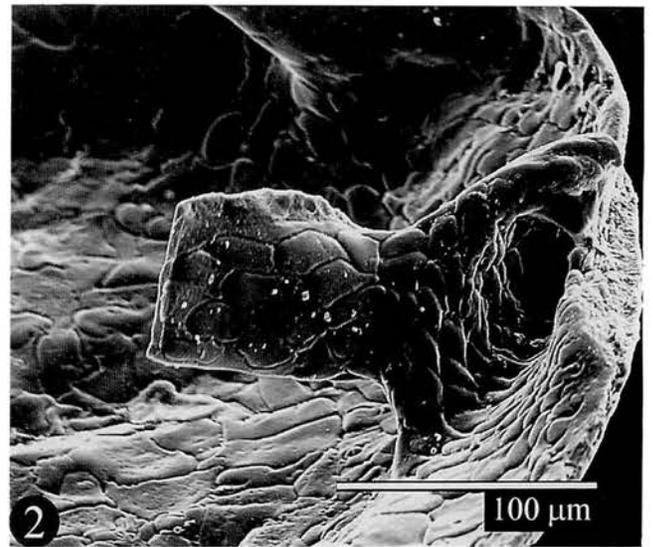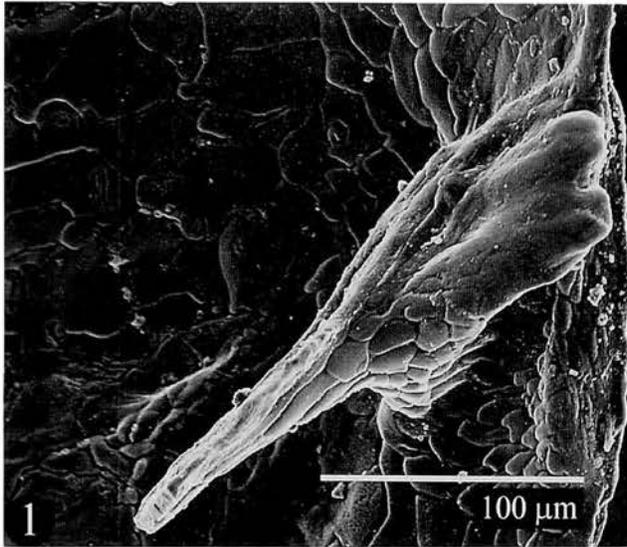
(Figure 8.2).

Measurements.—Length (L), width (W) and thickness (T) of all the intact specimens (except the living ones) were measured. The living individuals were measured for length and width only. Scatter graphs for L/W and L/T show more or less linear relationships (Figure 9A). Slopes of the regression lines for double-logarithmic scatter plots (Figure 9B) based on reduced major axis (Kermack and Haldane, 1950) were 0.99 and 1.12 for L/W (N = 126) and L/T (N = 70), respectively, and both were not significantly different from the slope of 1 (isometry) at the 95% confidence level.

Intraspecific variability. — The majority of the adult specimens have a teardrop outline (Figure 2), but some specimens are oval. The growth lines are well expressed in the majority of individuals, but some have weaker growth lines. Some individuals have well defined capillae just anterior to the smooth protegular node. This is better expressed in the dorsal valves (Figure 3.1-3.3). Some shells do not have well defined muscle fields in both valves, while others do. The cross sections of the crura are quite variable. Usually they represent straight thin vertical lamina or have slight crescent-shaped sections convex outward (Figures 5.1, 6.2, 7). In some specimens the crura are curved longitudinally, similar to falciform (Figure 6.5) or are gently sigmoidal anteriorly (Figure 5.6).

Ontogeny.—The smallest individual collected is 0.88 mm long and 0.73 mm wide. The variability of the cardinalia was studied in a sequence of 17 dorsal valves of different size, representing different ontogenetic stages (Table 1). The smallest dorsal valve is 0.92 mm long and 0.92 mm wide, and the largest one examined is 5.51 mm long and 5.37 mm wide. It was noticed that the smallest specimens (early juveniles) have slight or no inner hinge plates and no outer hinge plates (Figure 6.1, 6.3). The juvenile specimens between 1.4 and 2.7 mm length have well defined inner hinge plates but no outer hinge plates (Figures 5.1, 11.1), the crural bases being directly attached to the inner socket ridges. In juvenile and mid-sized specimens the inner socket ridges are swollen posteriorly. With increasing age the socket ridges decrease relatively in size and remain well defined, but not swollen. Dorsal valves, more than 3 mm in length, already have incipient outer hinge plates, inclined to the shell floor. The larger the valve is, the longer and better expressed the outer hinge plates are, and they become inclined to the shell floor

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← **Figure 5.** *Parasphenarina cavernicola* gen. et sp. nov. Shimoji Islet, Miyako Island, 'Nakanoshima hole'. Cardinalia of three different-sized dorsal valves. For dimensions of the valves see Table 1. **1.** Interior of middle-sized dorsal valve showing crura and well developed inner hinge plates, UMUT RB28220-R1-12. **2.** The same valve from 1 showing the median groove between two ridges. **3.** Cardinalia of a larger specimen showing well developed outer hinge plates, UMUT RB28220-R1-3. **4.** The same specimen as on 3 showing lateral view of the crura. **5.** Cardinalia of large specimen showing well developed outer hinge plates, UMUT RB28220-R1-8. **6.** The same specimen from 5 showing the crura anterolaterally.

0.1 0.3 0.4 0.5 0.6 0.65
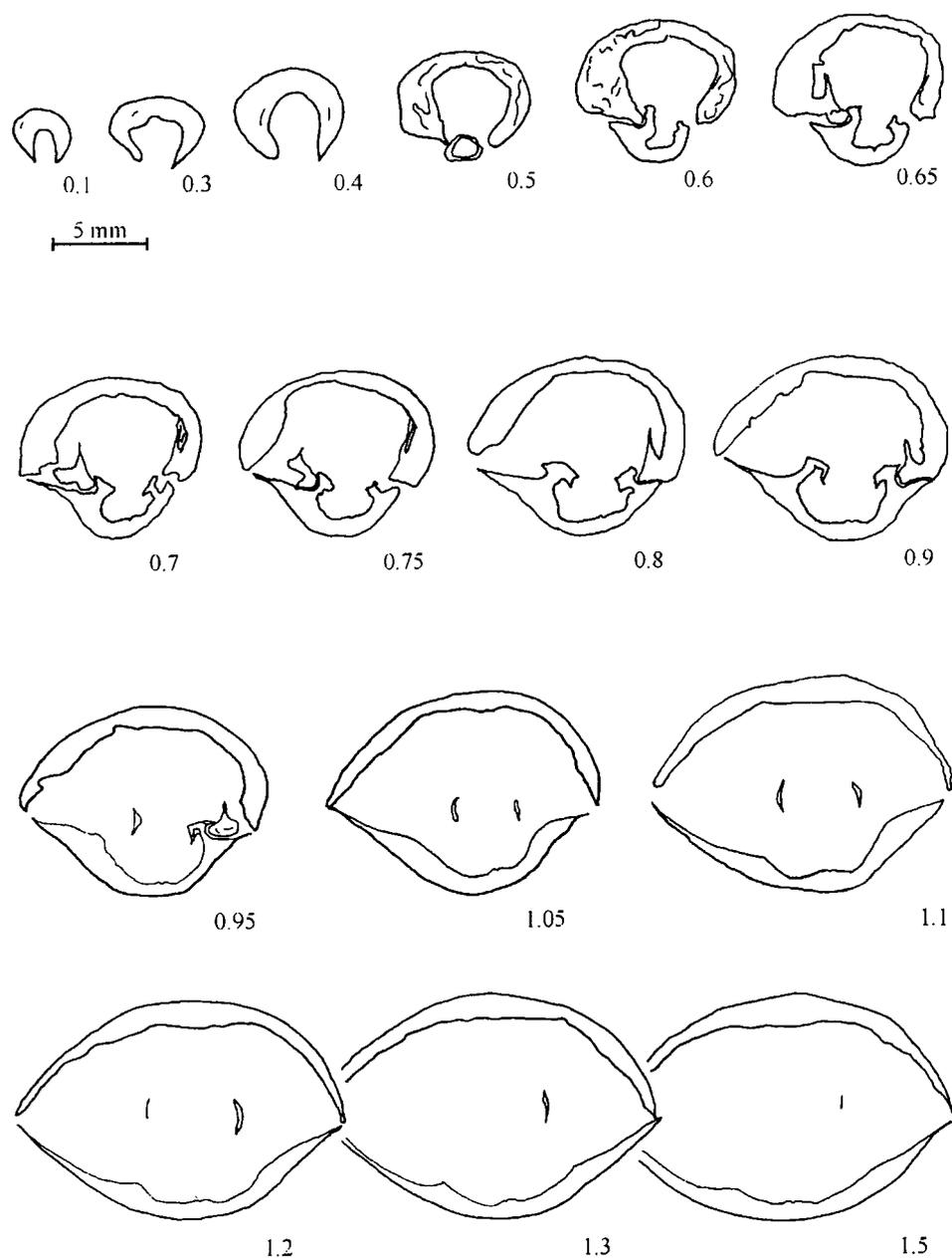
5 mm

0.7 0.75 0.8 0.9

0.95 1.05 1.1

1.2 1.3 1.5
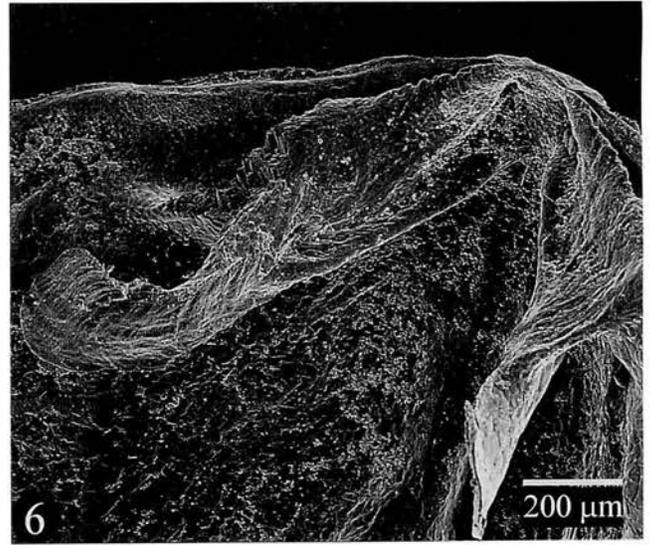
Figure 7. Sixteen quasitransverse serial sections through the umbo of *Parasphenarina cavernicola* gen. et sp. nov. Specimen UMUT RB28220-MN01-c, 'Nakanoshima hole' Shimoji Islet, Miyako Island. L = 4.5 mm, W = 4.1 mm; T = 2.3 mm. Distance from ventral umbo given in mm. The asymmetry of the sections is due to the slight lateral inclination of the minute shell during sectioning.

◄ Figure 6. *Parasphenarina cavernicola* gen. et sp. nov. For dimensions of the dorsal valves see Table 1. **1-5** Specimens from Shimoji Islet, Miyako Island, 'Nakanoshima hole". **1.** Juvenile crus, swollen inner socket ridge and incipient inner hinge plate seen in the commissural plane, UMUT RB28220-R5-4. **2.** The same crus as on **1**, seen laterally to show the spadelike shape. **3.** Cardinalia of juvenile specimen, UMUT RB28220-R5-9. **4.** The same valve from **3** seen laterally. **5.** Cardinalia of a middle-sized specimen with crescent-shaped crura and inner hinge plates, UMUT RB28220-R1-10. **6.** Cardinalia of adult or gerontic specimen showing the ventral curving of the distal ends of the crura, specimen from a mixed sample UMUT RB28213-R9 from 'Shodokutsu' and 'Daidokutsu' caves, Ie Islet, Okinawa Islands.
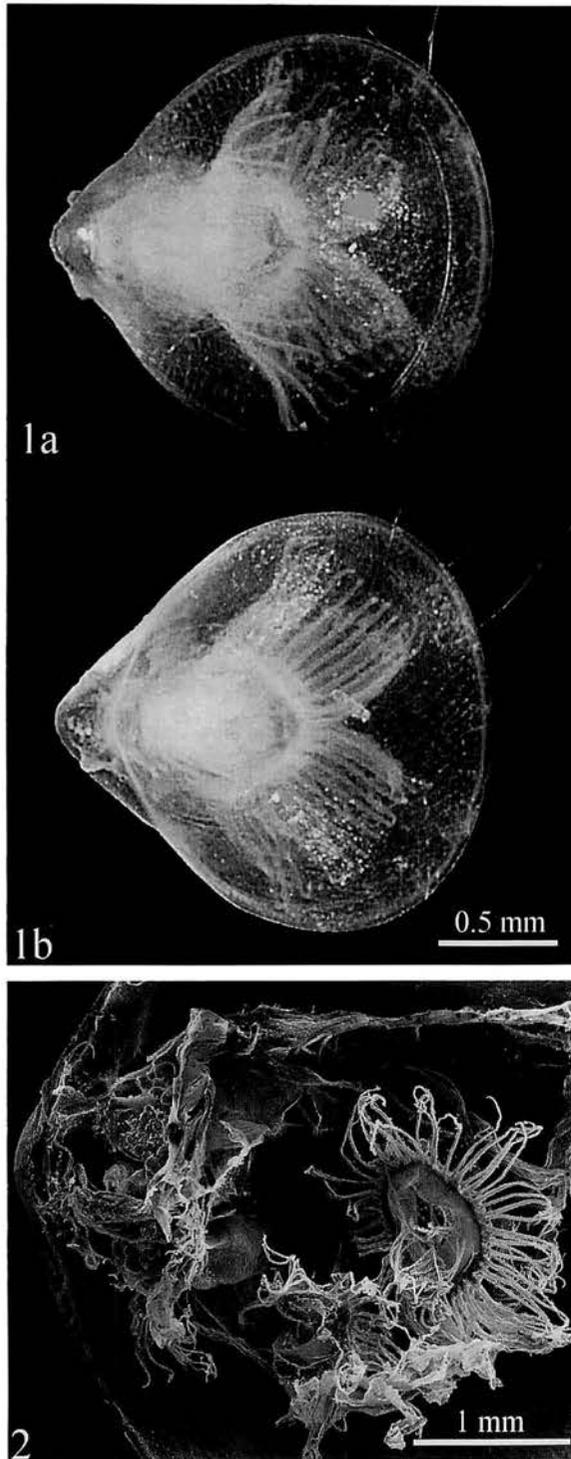
Figure 8. *Parasphenarina cavernicola* gen. et sp. nov. **1.** Setae and schizolophous lophophore in juvenile specimen seen through the transparent shell. **1a,** ventral side. **1b,** dorsal side. Specimen UMUT RB28214-MD03-a, "Devil's Palace', Shimoji Islet, Miyako Island. **2.** Distorted spirolophous lophophore in larger specimen. Mature gonads are seen in the posterior part of the mantle. Specimen UMUT RB28212-ID11-a, 'Daidokutsu' cave, Ie Islet, Okinawa Islands.

(Figures 5.3, 5.5, 7).

The crura in the juvenile specimens are shorter and slightly curved ventrally with spadelike anterior tips (Figure 6.2, 6.4). As pointed out by Dagys (1974), during ontogeny spinulifer crura simply increase in size. However, some larger specimens show characteristic stronger ventral bending of the distal ends of the crura (Figures 5.6, 6.6). The median dorsal groove between two low ridges is present in all stages except the early juvenile and with age it becomes better defined.

The juvenile ventral valves do not have dental plates detached from the shell wall, so the umbonal cavities are still not developed. The teeth are relatively large in juvenile specimens. During growth dental plates appear and start detaching from the lateral wall of the umbo. In adults they are well defined, but remain close to the wall, delimiting narrow umbonal chambers (Figure 4.1-4.4). With age the teeth become elongate in the commissural plane, but remain low perpendicular to this direction (Figure 4.5, 4.6). The juvenile individuals have well developed winglike deltidial plates (Figure 3.1, 3.6). In adults the deltidial plates are sometimes resorbed, but some specimens show excessive growth. In the largest ventral valve (L = 5.7 mm), the deltidial plates are very close to each other and the pedicle collar lies on the valve floor (Figure 4.5, 4.6).

Shell ultrastructure.—The shell ultrastructure of *Parasphenarina cavernicola* was observed using SEM by different preparation methods. The shell is very thin: maximum 300 μm in the centroanterior part. Laterally it is thinner and reaches 20 μm. It consists of two calcite layers, primary and secondary.

In some cases the periostracum was preserved on the shell surface, but for examining the microstructure of the external surface of the primary layer it was removed using domestic grade bleach as described in the previous section. Thus, its negative impressions on the external surface of the primary layer were revealed (Figure 10). They represent subparallel labyrinthine trenches normal to the growth lines of the shell. Such casts have been observed in different orders of brachiopods and were recently reappraised by Williams (1997, *in* Kaesler, 1997, p. 269–271).

The primary layer is 5 to 10 μm thick. It is built up of parallel rodlike calcite aggregates normal to the shell surface, which according to the method of treatment of the sample and the angle of observation can have different aspects, some of them illusory. The most typical texture of the primary layer observed is the vertical (normal to the bounding surfaces of the primary layer) (Figures 11.3, 11.4, 11.6, 12.2–12.4). It reflects the orientation of the parallel rodlike aggregates of calcite crystallites. The tips of the individual rodlike crystallites are better seen after etching the external surface of the layer (Figure 10.3, 10.4). The growth of the crystallites starts from the boundary between

Table 1. Ontogenetic variability of the cardinalia in *Parasphenarina cavernicola* gen. et sp. nov. Ld, length of the dorsal valve; Wd, width of the dorsal valve; Lcr, length of the crura = distance from the posteriormost point of attachment of the hinge plate to the anteriormost part of the crura tip, measured in the commissural plane; all in mm).

UMUT Specimen No.	Figure	Ld	Wd	Lcr	Inner hinge plates	Outer hinge plates
RB28220-R5-9	6.3, 6.4	0.92	0.92	0.18	?	no
RB28220-R5-1		0.97	0.95	0.26	slight	no
RB28215-R5-2		?	?	0.23	slight	no
RB28220-R5-4	6.1, 6.2	1.02	1.01	0.23	slight	no
RB28220-R5-6		1.03	1.05	0.22	slight	no
RB28215-R3-6		1.4	1.4	0.36	strong	no
RB28219-R2-2		1.47	1.82	0.41	strong	no
RB28220-R5-10	11.1, 11.2	1.9	1.85	0.47	strong	no
RB28219-R4-4		2.71	2.76	0.62	strong	no
RB28220-R1-12	5.1, 5.2	2.71	2.67	0.67	strong	no
RB28220-R1-10	6.5	2.89	2.88	0.61	strong	no
RB28215-R3-5		?	?	0.73	slight	yes
RB28215-R3-2		3.67	3.92	0.79	slight	yes
RB28220-R1-3	5.3, 5.4	3.74	4.34	0.84	??	well developed
RB28219-R2-1		?	?	0.97	slight	short
RB28220-R1-8	5.5, 5.6	4.59	4.69	1.22	?	well developed
RB28213-R9	6.6	5.51?	5.37	1.02	slight	well developed
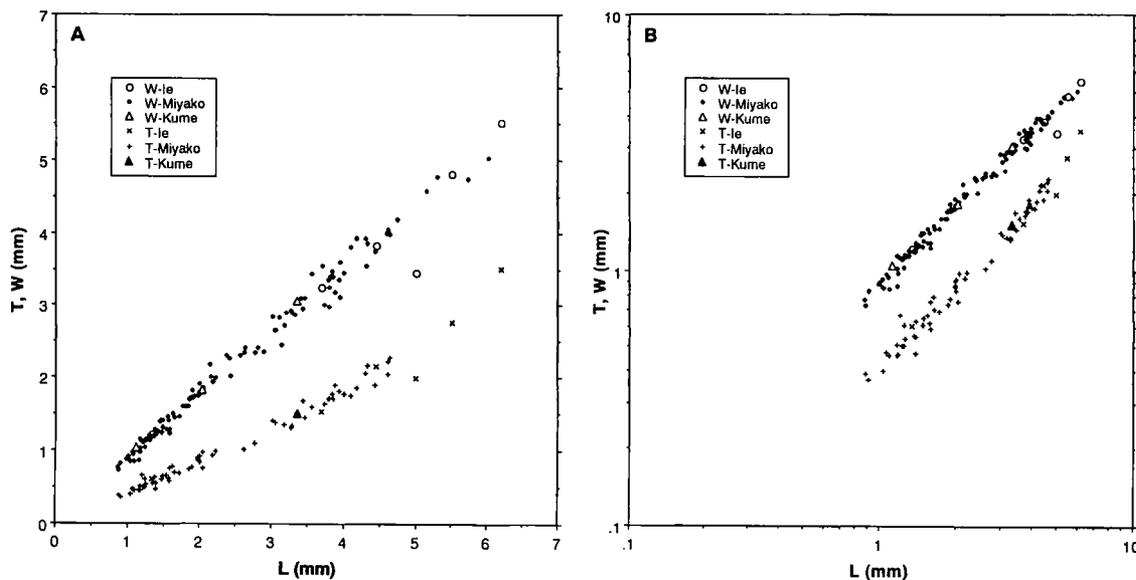
Figure 9. Shell measurements of *Parasphenarina cavernicola* gen. et sp. nov. Scatter plots (A) and double logarithmic scatter plots (B) of shell length (L) versus maximum shell width (W) and thickness (T). Specimens from Ie, Miyako (Irabu and Shimoji islands), and Kume Islands are indicated separately.

the periostracum and primary layer, where the crystallites are finer and not well defined, and advances towards the boundary between the primary and secondary layer. Some micrographs taken at different angles and higher magnification reveal a horizontal texture, which shows a fine lamination parallel to the shell surface and the boundary primary/secondary layer (Figures 11.4, 12.1, 12.2, 12.6). These are surfaces of synchronous growth of the crystal ag-

gregates (induction faces of common growth), which give a laminated aspect to the layer at high magnification. *Parasphenarina cavernicola* differs from *Notosaria nigricans* (Sowerby) in the parallel orientation of the synchronous growth surfaces. *Notosaria nigricans* develops its synchronous surfaces oblique to the two boundaries (Williams, 1971). An unusual pseudo-porcelain appearance, probably an artifact due to over coating with Pt-Pd
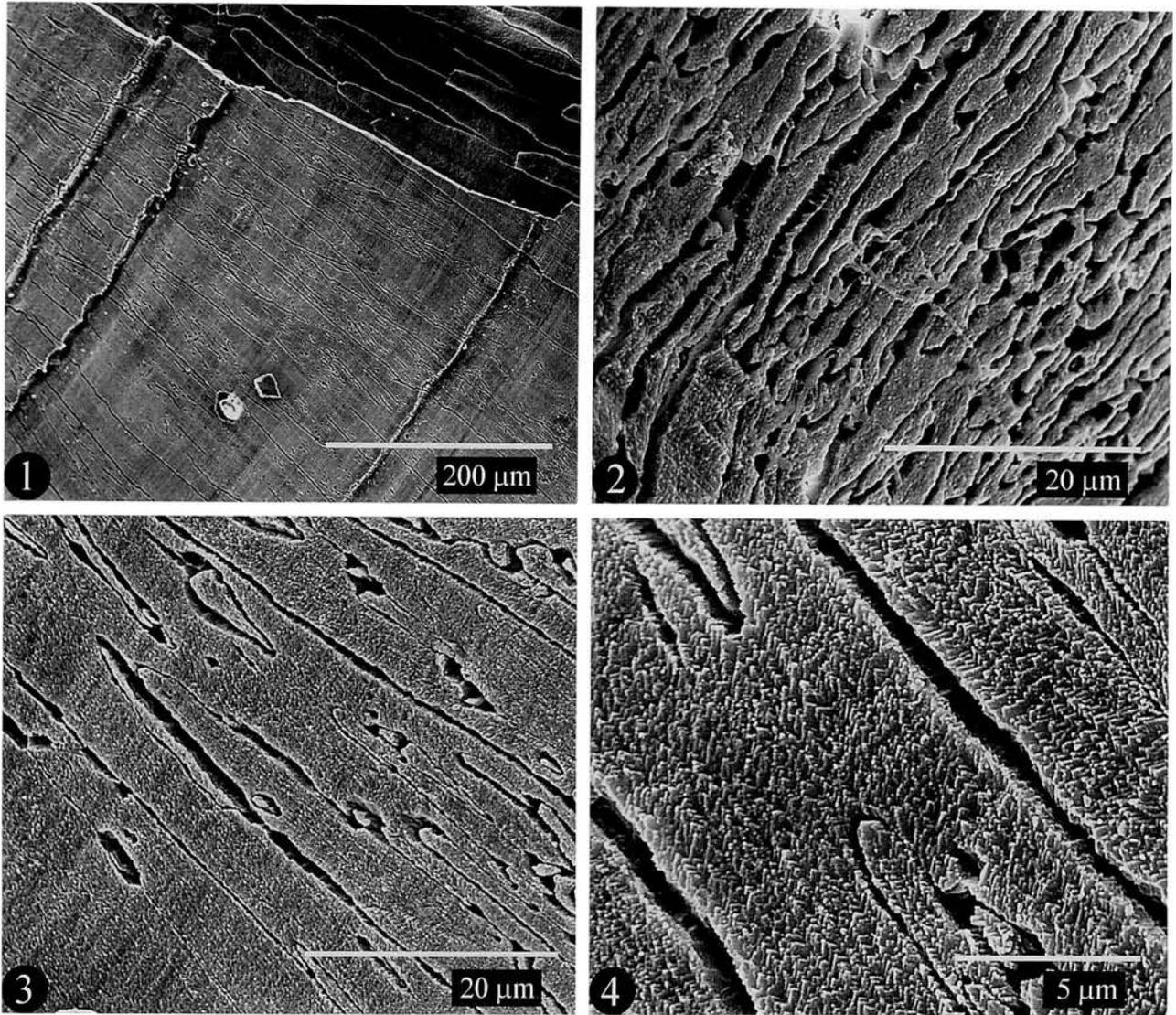
Figure 10. Views of the external surface of the primary layer of *Parasphenarina cavernicola* gen. et sp. nov., 'Nakanoshima Hole', Shimoji Islet, Miyako Island. **1, 3,** and **4** specimen UMUT RB28220-ss3-vv, fragment of a dorsal valve, treated with 5% v/w bleach for 13h and etched with 5% HCl for 5sec. **1.** General view of the external surface of the shell (respectively of the primary layer). Three growth lines are visible. In the top right corner the primary layer is broken off and the underlying fibres are visible. The trenches perpendicular to the growth lines represent negative casts of periostraca dissolved by bleach. **2.** Specimen UMUT RB28220-ss4-vv, fragment of a ventral valve, treated with 5% v/w bleach for about 3h and over etched with 5% HCl for longer period-15sec. Labyrinthine trenches are overetched impressions of periostraca casts in the primary layer. **3.** Detail of 1. **4.** Detail of 3. Tips of spiky calcite crystallites.

alloy, was observed on some spots of the primary layer (Figure 12.5).

The large fibres of the secondary shell, arranged in orthodox fashion, form a mosaic on the internal part of the valves (Figure 11.2). The fibres are usually rhombic in cross section. They are extraordinarily large: 50–100 μm in width and 20–40 μm in thickness. Near their origin (the boundary with the primary layer) the fibres are smaller (40–60 μm wide and 15–25 μm thick) and represent well

shaped rhombi. They expand rapidly towards the interior of the shell (80–140 μm wide and 30–40 μm thick), losing their regular rhombic shape and becoming irregular rhombi, polygons, or anvil-shaped and sometimes have rounded margins (Figure 11.3, 11.5, 11.6).

Among other genera with spinuliform crura, scanty data on the shell ultrastructure are illustrated on *Manithyris rosii* Foster, *Compsothyris racovitzae* (Joubin) and *Compsothyris ballenyi* Foster (Foster, 1974, pl. 9). The width of the

fibres on the internal surface of the ventral valve is 50 μm in *Manithyris rosii* and 40 μm in *Compsothyris*. Compared to the fibres of *Parasphenarina cavernicola*, the fibres in *Manithyris* and *Compsothyris* are narrower and the mosaic they form is different. Popov (1978) published 3 micrographs from different parts of the internal surface of the shell of *Frieleia halli* Dall showing fibres differing in size and morphology. Two of the micrographs show peculiar terminal faces of the fibres wrinkled parallel to the long axes (Popov, 1978, figs 1b–d).

A. Williams provided for comparative study five micrographs showing the shell ultrastructure of two fragments of *Frieleia halli*. In addition he commented (personal communication, 2000) on the peculiarities of the ultrastructure of this species: The external surface of the primary layer is sporadically pitted, probably by the imprints of the mucin-filled vesicles within the infrastructure of the periostracum (Figure 13.2). The primary layer seems finely laminated at high magnification (Figure 13.3), as described above for *Parasphenarina cavernicola*. At lower magnification the primary layer is crossed by nearly vertical planes, which are also comparable to the edges of the aggregates of parallel rodlike crystallites described above (Figure 13.2). The shell mosaic is somewhat different (Figure 13.1). The fibres are 40–50 μm wide, extremely flat and unusual in the way the apices of the terminal faces appear to be wrinkled parallel to the long axes of the faces (Figure 13.1), similar to that figured by Popov (1978).

Thus, the shell ultrastructure in the family Frieleiidae appears coarsely fibrous although more data are needed to draw conclusions about the taxonomic importance of ultrastructure in frieleiids in particular, and in the Norelloidea as a whole (cf. Manceñido and Owen, 2001 for a new rhynchonellid classification). It is noteworthy that a similar coarse-fibrous fabric has been already reported in Cretaceous Pugnacoidea, in contrast to the fine-fibrous ultrastructure in Cretaceous Rhynchonelloidea and Hemithyridoidea (Mochurova-Dekova, 2001). However, it should be noted that shell ultrastructure might be influenced by water temperature and other environmental factors as well. The coarseness of the mosaic and other ultrastructure features are probably largely genetically determined phenotypic changes favoured by natural selection in a particular environment over a long period of time but may also be evoked somatically (without change of genotype) by the same environmental conditions in the short term (M. Foster, personal communication, 2002). It is necessary to make quantitative studies of a large number of specimens of many different species from a wide variety of habitats to make sound observations and conclusions.

*DNA sequence data.* — Mitochondrial cytochrome c oxidase subunit I (cox1) gene sequence, DDBJ accession number AB053201 (Saito *et al.*, 2001).

Comparison. — *Parasphenarina cavernicola* closely resembles *P. ezogremena* (Zezina) in size, shape of the shell and crura and in having a shallow median groove bounded by low ridges in the dorsal valve instead of a typical median septum. *Parasphenarina ezogremena* differs from *P. cavernicola* in having a well defined larger triangular foramen with pointed acute beak. It lacks the characteristic abraded rounded ventral beak of *Parasphenarina cavernicola*. *P. ezogremena* has corrugated socket ridges and teeth, supported by stronger dental plates, while socket ridges and teeth are smooth and dental plates are poorly developed in *Parasphenarina cavernicola*. After examining several specimens of the new rhynchonellide from the Okinawa submarine caves, Zezina (personal communication, 2000) also suggested they be placed in a new species to distinguish them from *Parasphenarina ezogremena* (Zezina).

Parasphenarina cavernicola sp. nov. resembles *Sphenarina sicula* Davidson in the shape of the shell and crura (Figure 14.1) and the rectimarginate anterior commissures. The umbonal part of *P. cavernicola*, just anterior to the smooth protegular node, is finely capillate, which is reminiscent of the fine capillation of the entire shell of *S. sicula*. The main differences are given in the comparison between the two genera. *Parasphenarina cavernicola* differs from *Sphenarina sicula* in being smaller in size, completely smooth, with well developed growth lines, a larger foramen, consistently disjunct deltidial plates, relatively larger teeth, and very narrow umbonal chambers in the ventral valve, limited by slightly developed divergent dental plates. These are differences that could be also of specific importance. The most important difference between the two species (and genera) is in the cardinalia. The cardinalia of *Sphenarina sicula* are relatively more massive, have an incipient cardinal process, the hinge plates and inner socket ridges join together posteriorly (Figure 14.1), and a small septalium is present in the sectioned adult shell (Figure 14.2). In *Parasphenarina cavernicola* the hinge plates and socket ridges remain separate (Figures 5.1, 5.3, 5.5, 6.3) and touch the valve floor, which together with the lack of a median septum totally excludes the possible formation of a septalium. In *S. sicula* the crural bases project more ventrally than dorsally in adult shells (Figure 14.3), while in *Parasphenarina cavernicola* the crural bases project dorsally only (Figures 5.3–5.6, 7).

Discussion

The abundance of material, representing populations of *Parasphenarina cavernicola* inhabiting different caves, allows us to study in detail the intraspecific variability and the ontogeny of the shells. Such studies aid in preventing
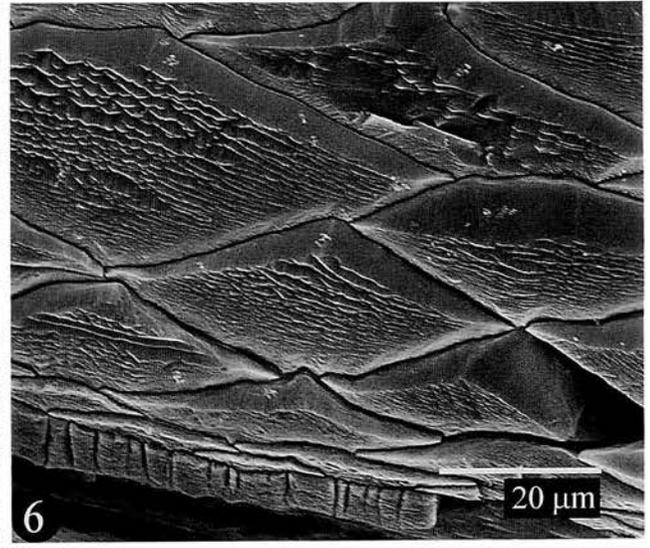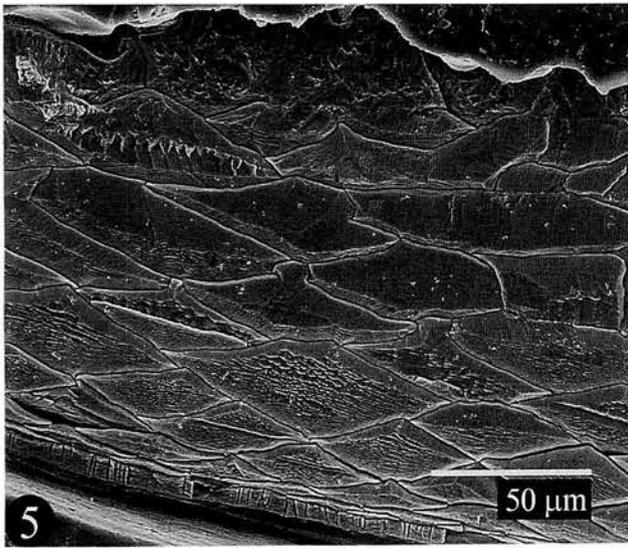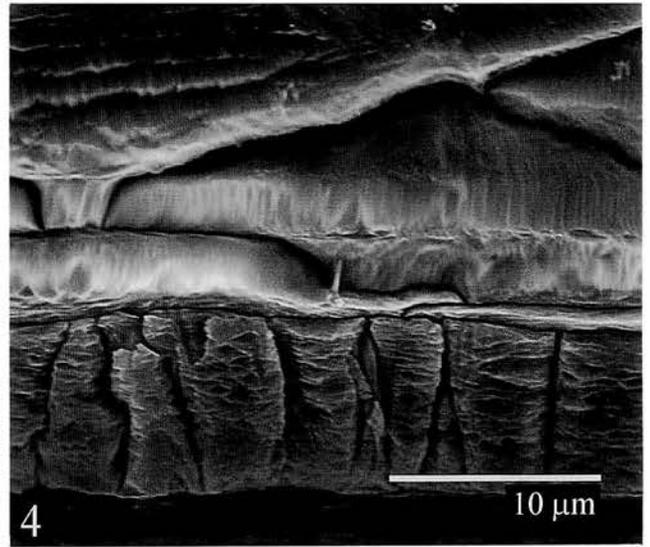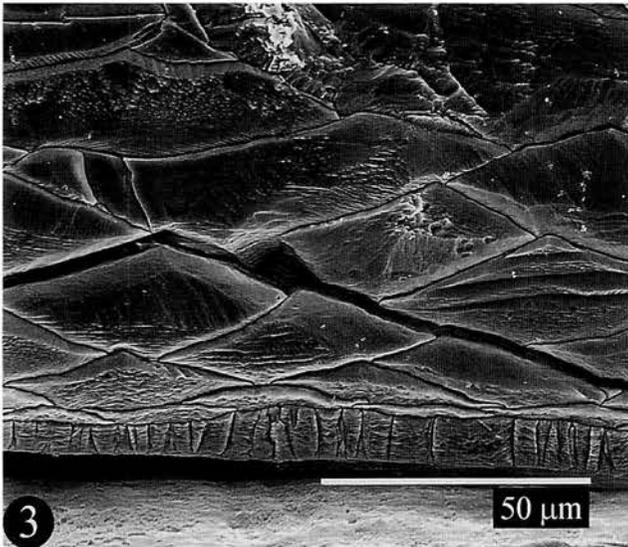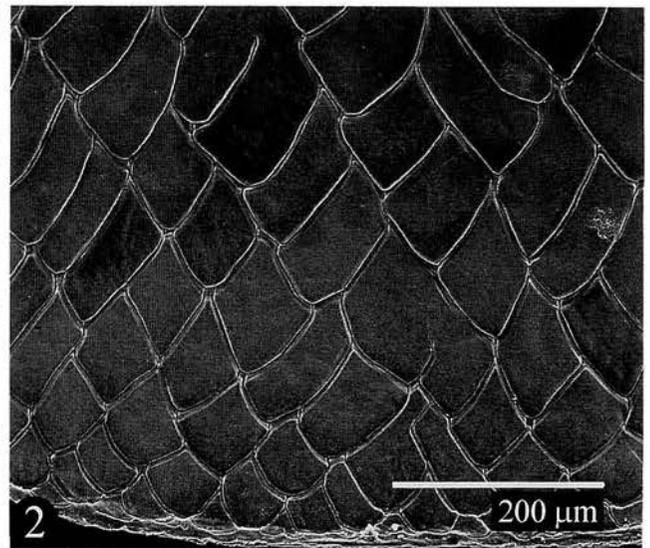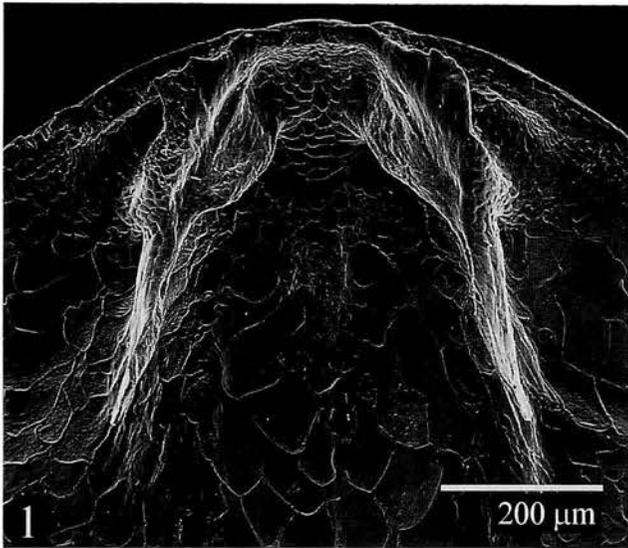
undue the taxonomical splitting that often arises when new species and genera are erected only on the basis of scarce material. As pointed out by Foster (1974), genera have customarily been too narrowly defined in the rhynchonellides. Some of the genera were monospecific when they were erected. Thus, their diagnoses coincided with the diagnoses of the type species. Including new species in such monospecific genera is always difficult. In the case of *Parasphenarina cavernicola* we have preferred to introduce a new genus rather than to emend the diagnosis of the closest genus *Sphenarina,* based on the absence of a septalium in the new genus. Another hampering factor was the lack of previous ontogenetic observations on the known species belonging to the Frieleiidae, except for Foster (1974), where he commented on the ontogeny of *Compsothyris racovitzae* (Joubin). As a whole, the rhynchonellides are considered as a group with primitive cardinalia and their possible ontogenetic changes were normally neglected.

Several authors in the past have drawn attention to the need to include in taxonomic descriptions detailed accounts of growth stages (Surlyk, 1972; Lee and Wilson, 1979). A detailed account of the growth stages in *Notosaria nigricans* was given by Lee and Wilson (1979). Manceñ ido and Walley (1979) point out the inadequacy of a classification based on the mere presence or absence of a morphological feature in the adult stage. They recommend erection of new taxa on the basis of both juvenile and adult morphology and inclusion of this in the diagnosis.

One important discovery resulting from this study was that the morphology of the hinge plates changes considerably during ontogeny. The morphology and the lack or presence of inner and outer hinge plates are often taken as a diagnostic generic character. After a careful examination of dorsal valves of different size of *Parasphenarina cavernicola,* it turned out that the inner hinge plates are present only in juvenile shells, later being resorbed or transformed. The outer hinge plates develop later and are well defined only in the adult shells. Thus, examining scarce material, not representing all the stages, may lead to misidentification or overestimation of some of the cardinalia features in rhynchonellides. In this instance we consider that too many genera were introduced on the basis of insufficient material. In this case we suggest that genera established on presence/absence of inner/outer hinge plates or
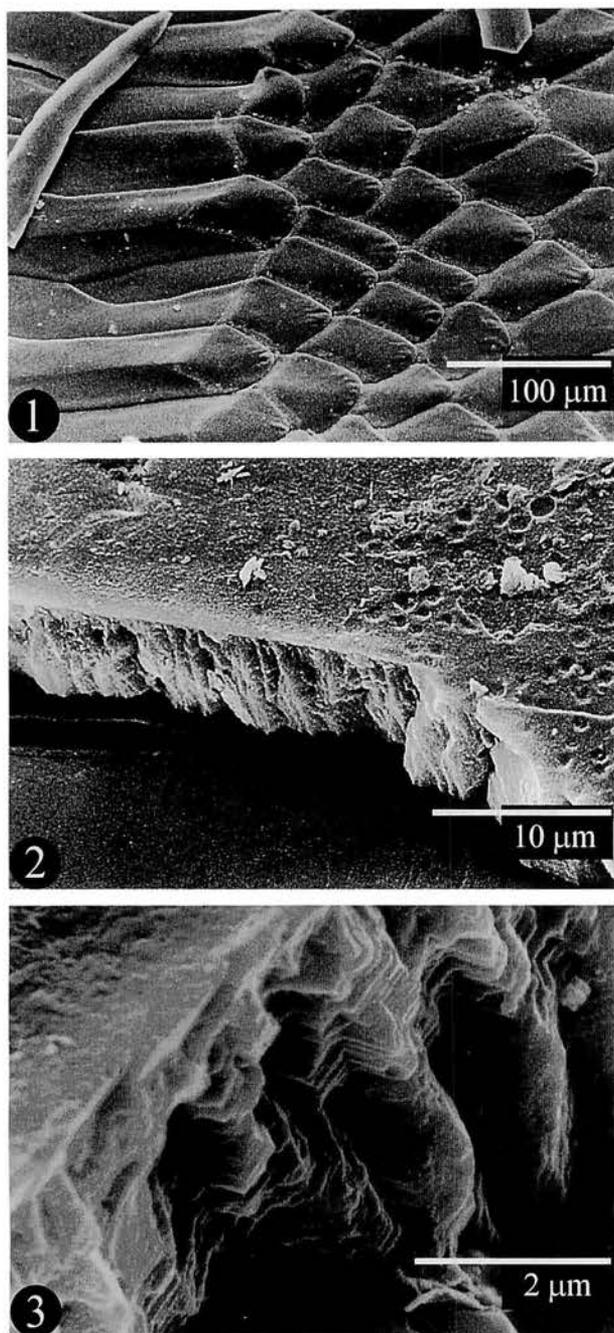
absence of septalium (for instance *Sphenarina*) should be carefully revised.

According to Dagys (1974) spinuliform crura appeared in different groups of rhynchonellides as a result of 'fetalization' (i.e. paedomorphosis). Genera having spinuliform crura retain some juvenile aspects in the adult stage. Dagys (1974) noted that such genera are characterised by a triangular outline, weak to moderate convexity, lack of a sinus, and unisulcate to rectimarginate anterior commissures, which are indicative of juvenile characters in rhynchonellides. Cooper (1959) also noted that the rectimarginate anterior commissure is a youthful character. The adult individuals of *Parasphenarina cavernicola* are micromorphic and bear all of the above-mentioned juvenile characters. On the other hand, *Parasphenarina* has one of the simplest arrangements of cardinalia among rhynchonellides, lacking a septalium and median septum. Thus the occurrence of *Parasphenarina cavernicola* supports Dagys' hypothesis about the paedomorphic nature of the spinuliform crura. *Parasphenarina* can reach sexual maturity at a length of 5.45 mm (Figure 8.2). All these data support the hypothesis that *Parasphenarina cavernicola* can be regarded as a paedomorphically developed form in the submarine caves of Okinawa. The rarity of the new genus in Recent seas is also noteworthy, the only other species, *Parasphenarina ezogremena,* being recorded from a single specimen in the Flores Sea on the upper continental slope (Zezina, 1981). Taking into account the morphologic similarities with the genus *Sphenarina* from Sicily it can be suggested that the new genus could have evolved from forms morphologically close to the extremely rare bathyal Pliocene genus *Sphenarina* through paedomorphosis. Heterochronic processes have probably played an important role in the origination of major new taxa and evolutionary novelties in post-Palaeozoic rhynchonellides. Frieleiids were interpreted as end-members of lineages, which become adaptively anachronistic in high-energy environments and eventually occupied refugia in deeper and darker low-energy habitats (Ma nceñido and Owen, 1996; Manceñido, 1997; Manceñido and Owen, 2001). Considering also the occurrence of associated taxa from other phyla, the new frieleiid *Parasphenarina cavernicola* may be cited as yet another example of an anachronistic taxon with closest bathyal ancestors, which has found refuge in the peculiar low-

← Figure 11. *Parasphenarina cavernicola* gen. et sp. nov, 'Nakanoshima Hole', Shimoji Islet, Miyako Islands. 1. Juvenile dorsal valve with well developed inner hinge plates and swollen inner socket ridges, specimen UMUT RB28220-R5-10. 2. Anterior of the dorsal valve of the same specimen as on 1 to show the study surface for the mosaic of the fibres (compare to Figure 13-1). 3-6. Transverse sections at 1.7 mm from the ventral umbo of a ventral valve of the same specimen as on Figure 7. Section thoroughly polished and subsequently etched with 5% HCl for 2-3 sec. 3. Secondary fibrous layer (above) and primary layer (below). 4. Detail of 3 to show the primary layer with the vertical edges of aggregates of calcite and fine horizontal lamination parallel to the shell surface. 5. The whole shell thickness showing the secondary fibrous layer and the primary layer below. 6. Detail of 5 showing the rhombic fibres and the primary layer.
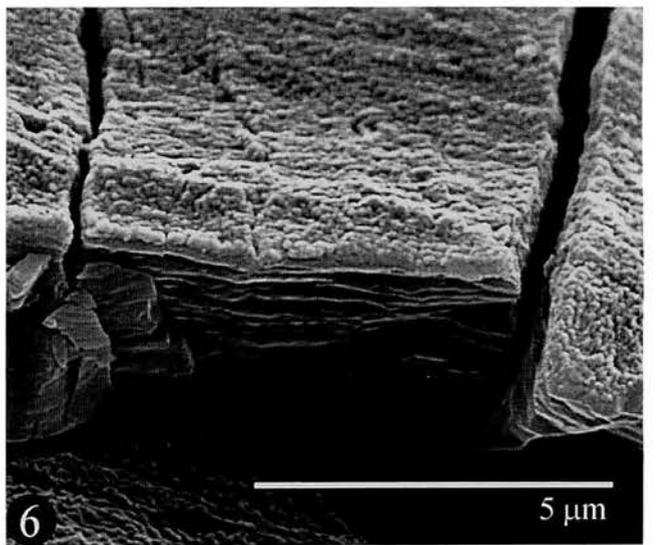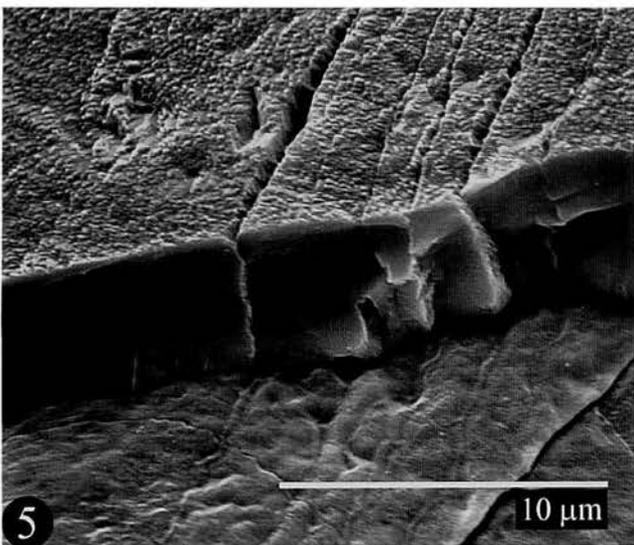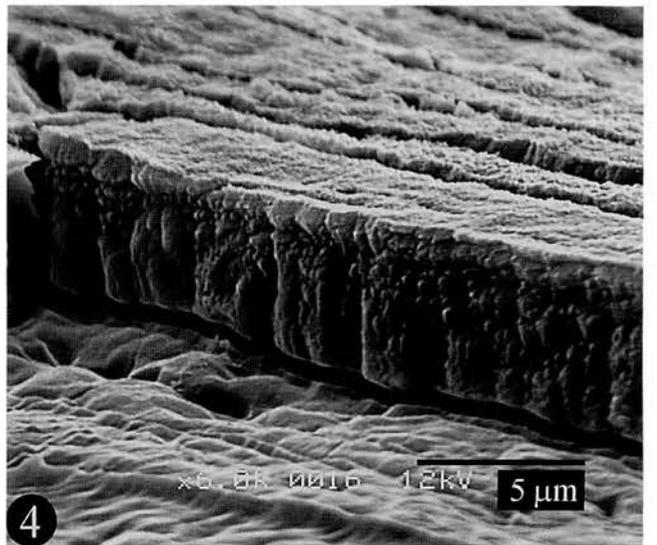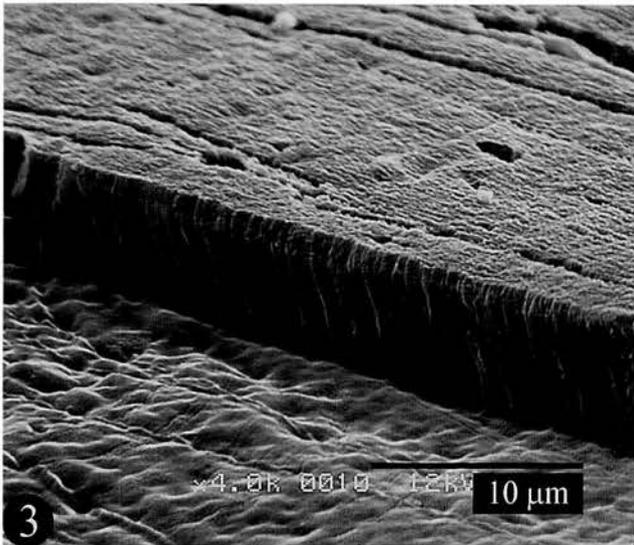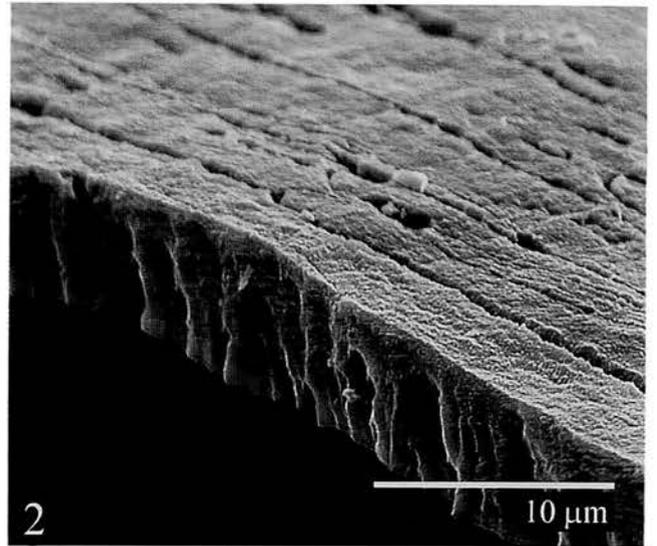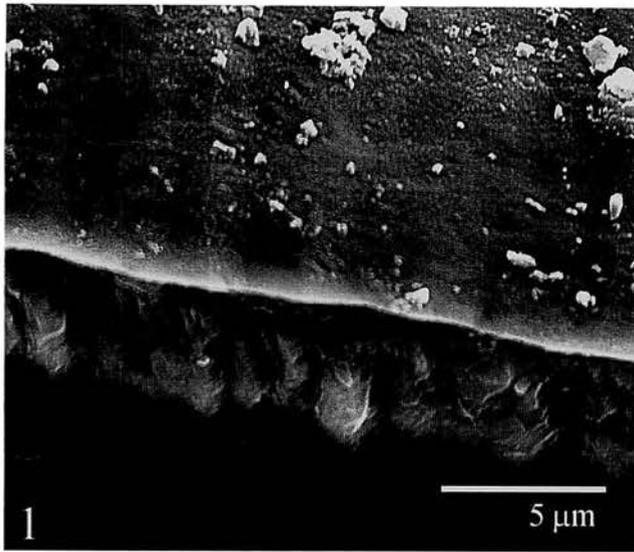
competition, sheltered microenvironment of the dark, oligotrophic submarine caves of Okinawa.

Figure 13. Ultrastructure of two fragments of *Frieleia halli* Dall shell from the Smithsonian wet collection, USNM 421367, 550 m depth, 32° 40.7′ N, 117° 35.5′ W, San Diego Trough. **1.** Internal surface of the shell with orthodoxly stacked flat fibres, the apices of the terminal faces of which are wrinkled. **2.** External surface of the shell sporadically pitted. Nearly vertical planes-edges of aggregated of parallel rodlike calcite crystallites. **3.** Finely laminated primary layer, lamination parallel to bounding surfaces at higher magnification.

← **Figure 12.** *Parasphenarina cavernicola* gen. et sp. nov., 'Nakanoshima Hole', Shimoji Islet, Miyako Island. Different textures of the primary layer according to the way of treatment of the sample, the angle of observation and the magnification. **1.** Finely laminated (horizontal) texture. Stub #UMUT RB28220-ss1-dv, treated with 5% v/w bleach for 13h, not etched. **2-6.** Specimen UMUT RB28220-ss3-dv, fragment of a dorsal valve, treated with 5% v/w bleach for 13h and etched with 5% HCl for 5sec. **2.** Horizontal (parallel to the shell surface) lamination and vertical texture. **3.** Vertical texture. **4.** Vertical texture. **5.** Pseudo-porcelain appearance, probably an artifact due to overcoating with Pt-Pd alloy. **6.** Horizontal lamination.
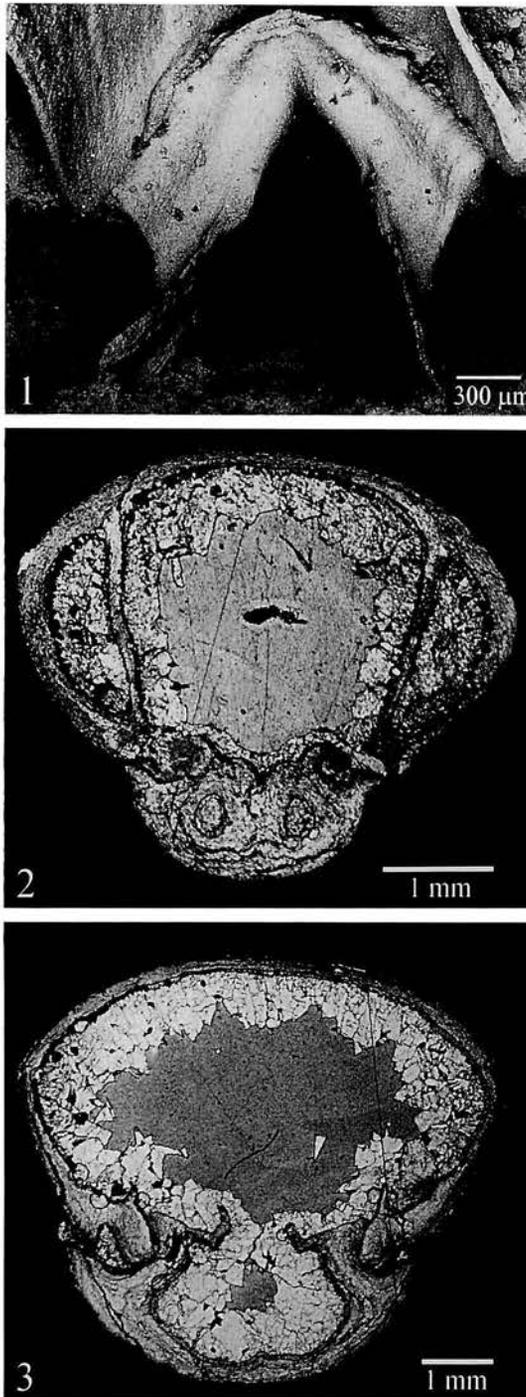
Figure 14. Sphenarina sicula Cooper.   Pliocene, Milazzo (labelled as Milasso), Messina, Sicily.   **1**. Cardinalia of specimen USNM 549381a, the same figured by Cooper (1959, p. 8-A, fig.7). Dimensions: L = 12.55 mm, W = 10.50 mm, T = 6.60 mm.   Note the incipient cardinal process.   **2, 3**. Two acetate peels showing selected serial sections of the interior of a larger specimen #549381b USNM. L = 15.60 mm, W = 15.10 mm, T = 8.40 mm.   **2**. Section 2.3 mm from the top of the ventral valve showing well developed divergent dental plates and incipient septalium.   **3**. Section 2.9 mm from the top of the ventral valve showing strong teeth, outer hinge plates, crural bases directed ventrally and low septum.

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First finding of an articulated actinopterygian skeleton from the Upper Devonian of Siberia and a reappraisal of the family Moythomasiidae Kazantseva, 1971 (Osteichthyes)

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Abstract. *Krasnoyarichthys jesseni* gen. et sp. nov. is described from the Upper Devonian (Famennian) of Western Siberia. It is the first finding of a Devonian actinopterygian in Siberia. This new genus is closely related to *Moythomasia*, *Mimia* and *Kentuckia*, but differs from those genera in the relative position of the fins, longer pelvic fin base and other dermal roof bones and scales characters in combination. The family Moythomasiidae with the above-mentioned genera and possibly *Orvikuina* is re-diagnosed and compared.

Key words: Actinopterygii, Moythomasiidae, systematics, Upper Devonian, Western Siberia.

Introduction

Actinopterygian remains from the Devonian are known usually by isolated scales and disarticulated bones, or by highly incomplete fragments of skeletons; more or less completely articulated specimens are rare. Such remains are known from Western Europe and the Baltic region of Central Europe, Spitzbergen, Afghanistan, North and South America and Australia (Agassiz, 1833–1844; Woodward and White, 1926; Gross, 1942, 1950, 1953; Lehman, 1947; Casier, 1952, 1954; Gardiner, 1963; Berg *et al*, 1964; Jessen, 1968; Schultze, 1968; Gardiner and Bartram, 1977; Pearson and Westoll, 1979; Blieck *et al.*, 1982; Janvier and De Melo, 1987; Long, 1988; Gagnier *et al.*, 1989; Taverne, 1997). Only isolated scales identified as cf. *Moythomasia* sp. were found in Afghanistan (Blieck *et al.*, 1982) and no more or less completely articulated specimens of Devonian actinopterygians were described from Asia. However, a collection of the Paleontological Institute (PIN) in Moscow includes a single nearly complete skeleton from the Upper Devonian deposits of the Krasnoyarski Krai in Western Siberia. This specimen shares many similarities with the genus *Moythomasia* Gross but differs from the latter in several other respects (see below). In the present paper it is described as a new genus and species, *Krasnoyarichthys jesseni*. The family Moythomasiidae Kazantseva, 1971 is reappraised as a consequence of the description of the new

taxon.

Notes on geography and stratigraphy

The fossil site is situated 150 km westward from Krasnoyarsk close to Nazarovo City in the southwestern part of the Krasnoyarski Krai (Figure 1). In an abandoned quarry near the Atshinsk-Abakan railroad, brown sandstones are exposed interrupted by calcareous alveolites with rare concretions. These layers belong to the Famennian Stage (Sidorenko, 1964). The specimen was found in a concretion.

Systematic paleontology

Order Cheirolepiformes
(sensu Kazantseva-Selezneva, 1977)
Family Moythomasiidae Kazantseva, 1971

Emended diagnosis. — Relatively small fishes with fusiform body. Frontal bones as long as or 1.7 times longer than parietals. Both intertemporal and supratemporal present [intertemporal is not documented in *Kentuckia*, however, it might be present according to its reconstruction (Rayner, 1951, p. 56)]. Supratemporal not contacting frontal. Antorbital and single supraorbito-infraorbital present. Postorbital portion of maxillary well
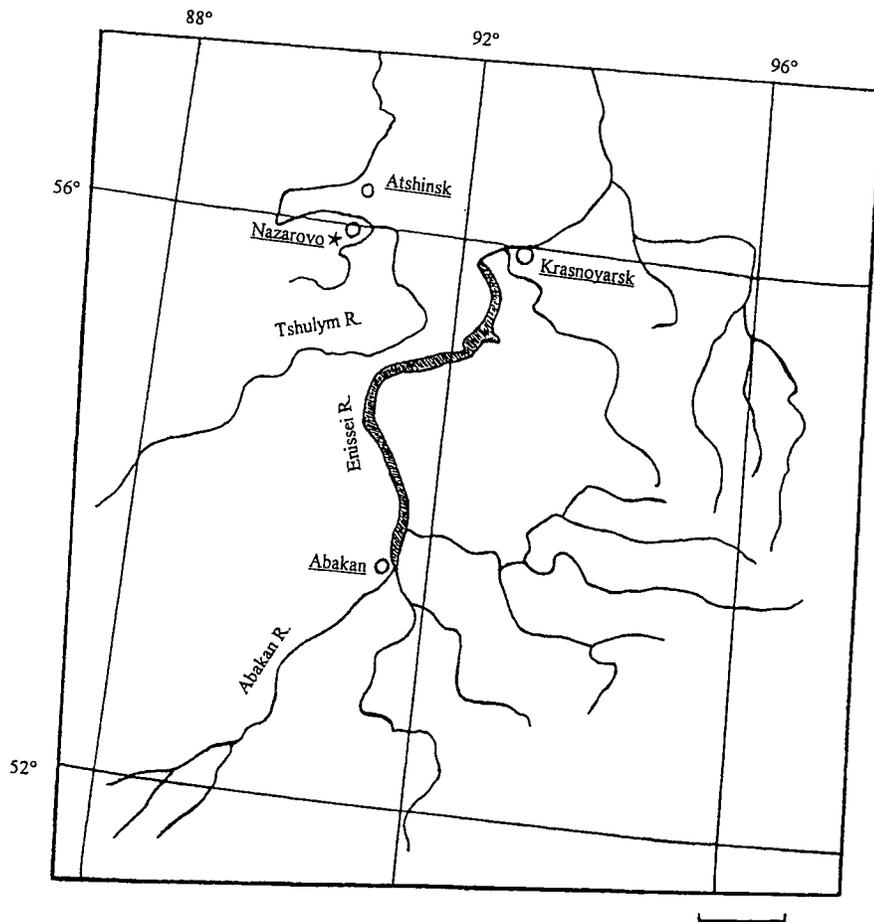
Figure. 1. Map of a section of Western Siberia illustrating the location of the fossil site (★). Scale bar 75 km.

developed. Mandibular suspension oblique. Both dermohyal and epipreopercle present, completely separating opercle and preopercle. Preopercle with two branches. Opercle larger than subopercle. Skull roofing bones ornamented with longitudinal ridges of ganoine. All fins with minute fringing fulcra and with rays articulated and distally bifurcating. Dorsal and anal fins completely or partially opposite to one another; anal fin originating on the same level as the dorsal fin origin or behind it. Pelvic fin base shorter than anal fin base. Caudal fin heterocercal. Dorsal and ventral ridge scutes present. Scales ornamented with diagonal ridges which end on the posterior scale margins as a series of serrations; all body scales with peg-and-socket articulations.

Included genera.—*Moythomasia* Gross, 1950 (Middle-Upper Devonian, Western and Central Europe, ?Afghanistan, Western Australia); *Kentuckia* Rayner 1951 (Lower Carboniferous, USA); *Mimia* Gardiner and Bartram 1977 (Upper Devonian, Western Australia); *Krasnoyarichthys*, gen. nov. (Upper Devonian, Western Siberia); possibly also *Orvikuina* Gross, 1953 (Middle Devonian, Central Europe), which is known only by isolated scales.

Krasnoyarichthys gen. nov.

Type species. — *Krasnoyarichthys jesseni*, sp. nov.; monotypic genus.

Etymology.—From the Krasnoyarsky Krai, and-*ichthys* (Greek), fish; masculine.

Diagnosis.—Same as that of the type species.

Krasnoyarichthys jesseni sp. nov.

Holotype.—PIN, nr. 4890-1, nearly complete skeleton lacking snout, anterior parts of the skull roof and of the cheek, and caudal fin, with poorly preserved cephalic sensory canals and limits of scales on the caudal peduncle; single plate (Figure 2a); Western Siberia, Krasnoyarski Krai, vicinity of Nazarovo City, Preobrazhensky Village, quarry near railroad; Upper Devonian (Famennian). Species is known only by the holotype.

Ethymology.—Species named in honour of Hans Jessen for his great contribution to palaeoichthyology.

Diagnosis. — Relatively small fishes reaching a total length of about 10 cm. Maximum body depth contained
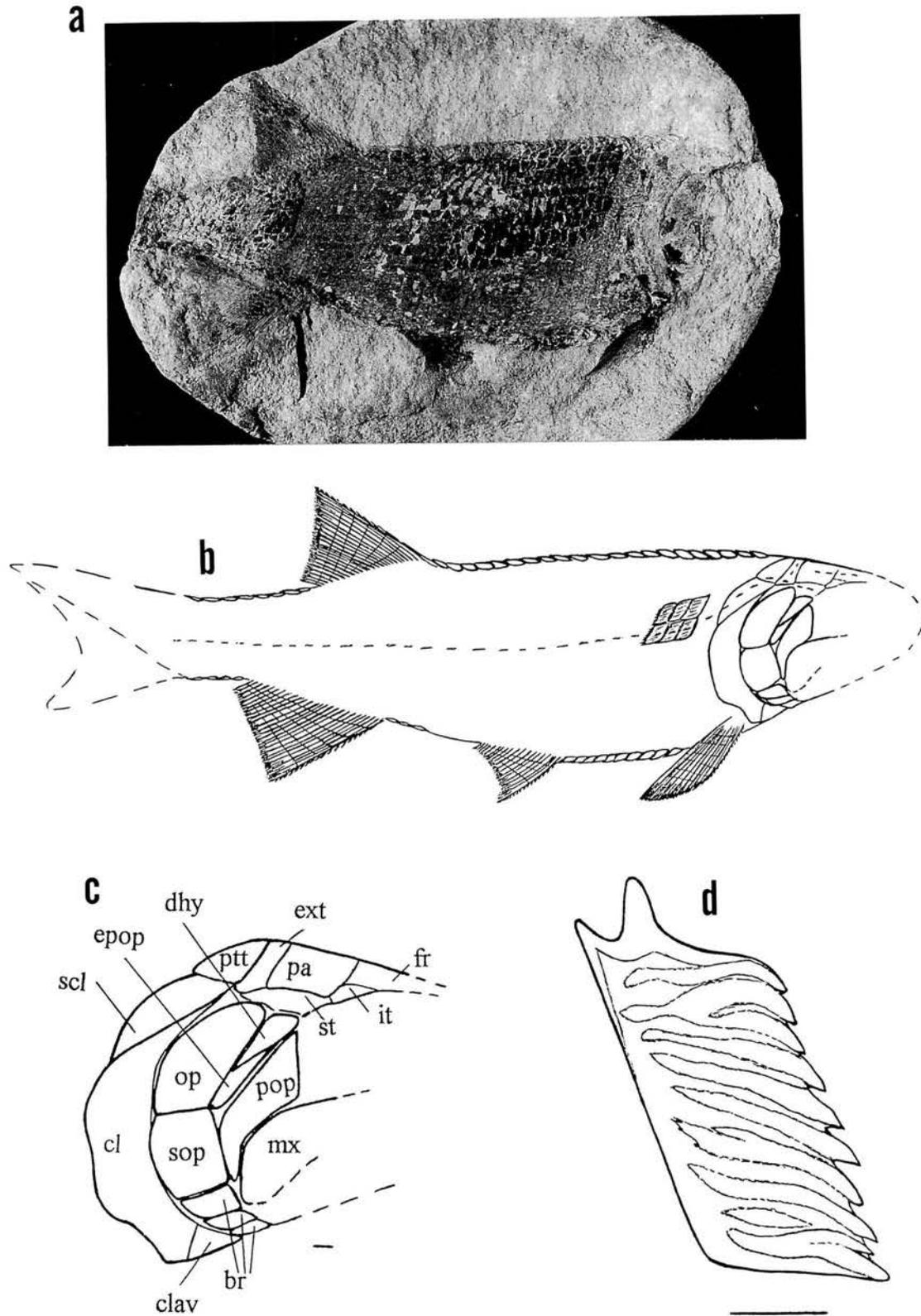
Figure. 2. *Krasnoyarichthys jesseni* gen.´ et sp. nov., Upper Devonian (Famennian) of Krasnoyarski Krai (Siberia). **a**. Holotype, PIN, nr. 4890-1 (natural size). **b**. Reconstruction of the lateral view. **c**. Reconstruction of the postorbital part of the skull and of the pectoral girdle (as the cephalic sensory canals are poorly preserved they are omitted in figure). **d**. Isolated scale from left side of body. Scale bars 1 mm. Abbreviations: br, branchiostegal rays; cl, cleithrum; clav, clavicle; dhy, dermohyal; epop, epipreopercle; ext, extrascapular; fr, frontal; it, intertemporal; mx, maxillary; op, opercle; pa, parietal; pop, preopercle; ptt, posttemporal; scl, supracleithrum; sop, subopercle; st, supratemporal.

approximately 3.5 times in the total length. Extrascapular single on each side of skull, two times larger than long. Postorbital portion of maxillary deep. Opercle 1.5 times deeper than long. Subopercle 1.5 times smaller than opercle. Pelvic fin originating equidistantly from the pectoral and anal fin origins; pelvic base only 1.5 times shorter than anal fin base. Dorsal fin origin in front of that of anal fin; posterior edge of anal fin noticeably behind that of dorsal fin. Approximate numbers of fin-rays: dorsal 40, anal 40, pelvic 30, pectoral 30. Roofing bone ornament consisting of coarse longitudinal and diagonal ridges of ganoine. Scales rhomboidal, ornamented by up to 10 diagonal ridges which end on posterior scale margins as series of serrations. Middle trunk scales approximately twice, or less, deeper than long. Dorsal and ventral ridge scutes weakly developed.

Description (Figure 2).—Besides the characters given in the diagnosis there are several additional features. The estimated standard length of the holotype is approximately 100 mm. Measurements in mm: length from the posterior border of the cleithrum to the caudal base 76, length from the posterior border of the cleithrum to the dorsal fin origin 41, the same length to the anal fin origin 46, the same length to the pelvic fin origin 24, distance between the pectoral and pelvic fin origins 26, distance between the pelvic and anal fin origins 26, maximum body depth 32, caudal peduncle depth 8, dorsal fin base length 16, anal fin base length 16, pelvic base length 11, dorsal fin height 20, anal fin height 18, pelvic fin height 9, pectoral fin height 11. The transverse rows of scales on the body are approximately 50 in number. There are 16 longitudinal rows of scales on the body. The dorsal ridge scutes are continuous from the occiput to the dorsal fin origin, and between the dorsal and caudal fins. The ventral ridge scutes are between pectoral and pelvic fins, and between anal and caudal fins; at least three slightly enlarged ventral scales are present before anal fin origin.

Discussion

Based on its similar body form, position of the fins, cranial roofing bones and structure of the scales *Krasnoyarichthys* undoubtedly belongs to the family Moythomasiidae. However, the new genus differs from both *Moythomasia* and *Mimia* in the relative position of the dorsal and anal fins (dorsal fin origin and ending in front of those of anal fin vs. dorsal and anal fins opposite one another in the compared genera) and in the slightly longer pelvic fins (1.5 times in the length of the anal fin base vs. twice in the compared genera). It further differs from *Moythomasia* in the presence of a single extrascapular on each side of the skull (vs. two in *Moythomasia*), which is noticeably larger than long (the extrascapulars are approxi-

mately as large as long in *Moythomasia*). *Krasnoyarichthys* is distinguished from *Mimia* in the middle trunk scales being no more than twice times deeper than long (vs. 3-4 times deeper than long in *Mimia*) and in the much less prominent ridge scutes. The new genus differs from *Kentuckia*, which is known only by the skull, in the opercle 1.5 times (vs. 2.5 times) deeper than long and 1.5 times (vs. twice) larger than the subopercle, and in the deep postorbital portion of the maxillary. The new genus is distinct from *Orvikuina*, which is known only by isolated scales, in having scales deeper than long (vs. much longer than deep), bearing up to 10 serrations (vs. 2-3 in *Orvikuina*).

The family Moythomasiidae is neglected in the literature. The genus *Moythomasia* together with *Kentuckia* Rayner and *Stegotrachelus* Woodward and White were placed by Gardiner (1963) in the family Stegotrachelidae. Later, Gardiner and Bartram (1977) added the genus *Mimia* to this family. However, the subsequent reconstruction of *Moythomasia* published by Jessen (1968) shows numerous distinctions between the latter and *Stegotrachelus*. Kazantseva (1971) indicated the principal differences between *Stegotrachelus* and *Moythomasia* were in the structure of the bones of the cheek region (both dermohyal and epipreopercle are absent in *Stegotrachelus*) and transferred *Moythomasia* and *Kentuckia* to another family, the Moythomasiidae. Unfortunately, this decision was never discussed by other authors (Gardiner, 1984; Gardiner and Schaeffer, 1989; Taverne, 1997).

In their phylogenetic analysis of the basal actinopterygians, Gardiner and Schaeffer (1989) placed *Mimia* and *Tegeolepis* into a «*Mimia* group», and *Moythomasia*, *Howqualepis* and *Stegotrachelus* into a «*Moythomasia* group»; the «*Mimia* group» was considered as a sister taxon for the «*Moythomasia* group» plus other actinopterygians excluding *Cheirolepis* and the polypterids. Unfortunately, this analysis is based on many characters not preserved in numerous paleoniscoid groups known to date (i.e. characters of the neurocranium, pectoral and pelvic girdles, axial skeleton, etc.), and their phylogenetic significance therefore needs further elucidation. In our opinion, the structure of the dermal skull bones provides the most important data for elucidation of paleoniscoid relationships, because they are always preserved in fossils and indicate the different evolutionary trends (Kazantseva-Selezneva, 1981). The only dermal bone character mentioned by Gardiner and Schaeffer (1989) as common to *Stegotrachelus* and *Moythomasia* is the absence of a true dermopterotic. The *Cheirolepis*, *Mimia* and *Moythomasia* groups of Gardiner and Schaeffer (1989) have no dermopterotic but two bones (intertemporal and supratemporal) in this region of the skull. However, in Gardiner's (1963: 296, fig. 12) reconstruction of the

Stegotrachelus skull the intertemporal is not figured. The other dermal skull characters of *Stegotrachelus* [absence of accessory opercular bones, long supratemporal (or dermopterotic) contacting frontal, small parietals, very narrow extrascapulars, numerous suborbitals] clearly distinguish the latter from the other members of the above-mentioned groups. According to Kazantseva-Selezneva (1981), the family Moythomasiidae seems to be closely related to the Cheirolepididae and Cosmoptychiidae rather than to the Stegotrachelidae. On the other hand, Taverne (1997) considered all the Devonian genera, *Cheirolepis* and *Dialipina* excluded, as the sister group of «polypteriforms». This opinion is doubtful judging from the close relationships between the Polypteridae and the peculiar Triassic Scanilepiformes (Sytchevskaya, 1999), and Lund's (2000) cladistic analysis of the polypteriforms which has specified sister relationships between the polypterids plus guildayichthyiforms and the platysomiforms.

According to Kazantseva (1971, 1974a, 1974b, 1977, 1981), the presence or absence of the dermohyal and epipreopercle is highly significant for the higher classification of the paleoniscoid fishes and indicates different types of breathing. Kazantseva-Selezneva (1977, 1981) divided the order Palaeonisciformes into three separate orders (Cheirolepiformes, Elonichthyiformes and Palaeonisciformes s. str.), of which both the dermohyal and epipreopercle are present only in the Cheirolepiformes. Among the Cheirolepiformes, the structure of the cranial roofing bones of the Moythomasiidae is similar to that in the Cheirolepididae. Both families have a single supraorbito-infraorbital, large parietals, the supratemporal lacking contact with the frontal bone, and the preopercle and opercle completely separated by the dermohyal and epipreopercle. However, the Cheirolepididae sharply differ from the Moythomasiidae in the structure of their scales, which are minute, square, not overlapping, with an internal boss, and quite similar to those of the acanthodians in the Cheirolepididae (contrary to the typical palaeoniscoid scales of the Moythomasiidae). The other distinctions include the presence of a separate antorbital in the Moythomasiidae [vs. completely fused with the premaxillary into the rostro-premaxillo-antorbital bone (Gardiner, 1963; Pearson and Westoll, 1979)], the anal fin origin opposite the dorsal fin origin or just behind it in the Moythomasiidae (vs. in advance of the dorsal fin origin in the Cheirolepididae), the pelvic base shorter than the anal base, and the ridge scutes present in the Moythomasiidae (in contrast to the reverse conditions in the Cheirolepididae) and the body form less elongate in the Moythomasiidae.

In our opinion, the family Moythomasiidae is valid and closely related to the Cheirolepididae. Such cranial characters as long parietals, presence of intertemporals, supratemporals lacking contact with frontal bones, single infraorbito-suborbital, and dermohyal and epipreopercle completely separating the preopercle from the opercle characterising both these families seem to be primitive, according to the undoubted position of *Cheirolepis* as the most primitive actinopterygian (Berg *et al.*, 1964; Pearson and Westoll, 1979; Patterson, 1982; Lauder and Liem, 1983; Gardiner and Schaeffer, 1989; etc.). The orbit relatively larger with regard to the overall body size, the shorter body, the short-based pelvic fins, the presence of peg-and-socket scale articulations on the body scales and ridge scutes on the body contours indicate the advanced status of the Moythomasiidae. The peculiar Australian genus *Howqualepis* has small orbits, a long body, and long-based pelvic fins, and it lacks dorsal and ventral ridge scutes, which establishes its similarity to *Cheirolepis*; however, the supratemporal has contact with the frontal and the parietals are two times shorter than the frontals in *Howqualepis* (Long, 1988). All these characters undoubtedly exclude *Howqualepis* from the Moythomasiidae. The other Devonian genera (*Dialipina* and *Ligulalepis*, which are known only by isolated scales; *Osorioichthys* and *Tegeolepis*) sharply differ from the Moythomasiidae in the cranial and scale characters and the two latter belong to other families (Osorioichthyidae and Tegeolepididae, respectively) (Schultze, 1968; Gardiner, 1963, 1967; Kazantseva-Selezneva, 1977, 1981).

Conclusion

Krasnoyarichthys jesseni gen. et sp. nov. from the Upper Devonian (Famennian) of Western Siberia belongs to the family Moythomasiidae, and differs from the other members of this family in the following combination of characters: single extrascapular on each side of the skull, which is noticeably larger than long; deep postorbital portion of maxillary; opercle 1.5 times deeper than long and 1.5 times larger than the subopercle; dorsal fin origin in front of that of anal fin; posterior edge of anal fin noticeably behind that of the dorsal fin; pelvic fin base 1.5 times in the anal fin base length, and middle trunk scales no more than twice deeper than long. The family Moythomasiidae presently is recognized as distinct and closely related to the Cheirolepididae, on the basis of their similar cranial roofing bone characters. However, the moythomasiids seem to be more advanced than the cheirolepidids judging from their relatively larger orbit with regard to the overall body size, shorter body, short-based pelvic fins, the presence of peg-and-socket scale articulations on the body scales and ridge scutes on the body contours.

The moythomasiids and other Devonian actinopterygians are recorded in marine sediments only (Jessen, 1968; Schultze, 1968; Gardiner, 1984; Janvier and De Melo,

1987; etc.), and Sidorenko (1964) noted a marine origin for the deposits, in which the holotype of *Krasnoyarichthys* subsequently was found. This taxon is the first finding of the Moythomasiidae in Siberia. Further investigations of the Preobrazhensky fossil site are needed since they have special interest for the morphology, taxonomy and paleobiogeography of Devonian actinopterygians.

Acknowledgements

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Errata

In the article by Takashi Matsubara (*Paleontological Research*, Vol. 6, No. 2, pp. 127–145), the following corrections should be made:

page	table/column	line	read	for
130	Table 1	9	*Acila (Truncacila)* cf. *nagaoi*	*Acila (Truncacila)* cf. nagaoi
130	Table 1	11	*Glycymeris (Glycymeris)* sp.	*Glycymeris (glycymeris)* sp.
130	Table 1	15	*Chlamys (Leochlamys) namigataensis*	*Chlamys (leochlamys) namigataensis*
130	Table 1	16	*Crassostrea* sp.	*Crassastrea* sp.
130	Table 1	17	Lucinidae gen. et sp. indet.	Luchinidae gen. et sp. indet.
130	Table 1	18	*Cyclocardia* sp.	*Cyclocardin* sp.
130	Table 1	20	*Megangulus maximus* (Nagao)	*Megangulus maximus* (Nagano)
141	Left	44	[delete]	Fo
141	Left	45	Formation	rmation
142	Left	4	Activities, Hyogo/Himeji Institute	Activities, Hyogo Himeji Institute
143	Right	7	*Editio duodecima*	*Editio decima*
144	Right	21	*siciliale*	*Siciliale*
144	Right	23	*Tome 2*	Tom 2
144	Right	30	*Pars secunda*, viii+199 p.	*Pars Secunda*, viii-199p.

A GUIDE FOR PREPARING MANUSCRIPTS

PALEONTOLOGICAL RESEARCH is dedicated to serving the international community through the dissemination of knowledge in all areas of paleontological research. The journal publishes original and unpublished articles, normally not exceeding 24 pages, and short notes, normally less than 4 pages, without abstract. Manuscripts submitted are subject to review and editing by reviewers and a language editor. Manuscripts accepted for publication will generally be published in order of submission. Authors submit three copies of their manuscript to: Dr. Kazushige Tanabe, Editor of Paleontological Research, Department of Earth and Planetary Science, University of Tokyo, Hongo 7-3-1, Tokyo 113-0033, Japan. After review, two copies of the revised manuscript are to be returned for copy editing.

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Text should be typed always in double space on one side of white paper of not less than either 210 × 280 mm (A4 size) or 8 1/2 × 11 inches in the following order.

Cover sheet. Cover sheet should contain (1) full name, address, phone and fax numbers, and e-mail address of the author taking responsibility for the galley proofs, (2) running title composed of less than 40 characters, and (3) the numbers of tables and figures.

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The typical format for arrangement of systematic paleontology can be learned from current issues of the Journal. All descriptions of new taxa must include a diagnosis, and, as appropriate, stratigraphic and geographic indications, designation of a type or types, depository information, and specification of illustrations. In synonymies use an abbreviated form of the reference, consisting only of authors of reference, date of publication, and number of pages, plates, figures and text-figures referring to the organism or organisms in question.

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Illustrations. All illustrations, including maps, geologic sections, and halftone illustrations (including "plates") are to be called figures and must be numbered in the same sequence as they are first cited in the text. Citations of illustrations in the text are to be spelled out in full (e. g., Figure 2 or Figure 2.1). Figure captions are to be typed separately. Plan the illustrations so that they take up either the entire width of the printed page (170 mm) or the width of one column (80 mm). Originals should not be smaller than the final intended size for printing. No foldouts will be accepted. Mark all originals clearly with authors' names and figure number. Photographs of all specimens except sections must be illuminated from the upper left side, as is conventional.

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

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―――― 行 事 予 定 ――――

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

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

個人講演・シンポジウム案の申し込み方法

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

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