

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

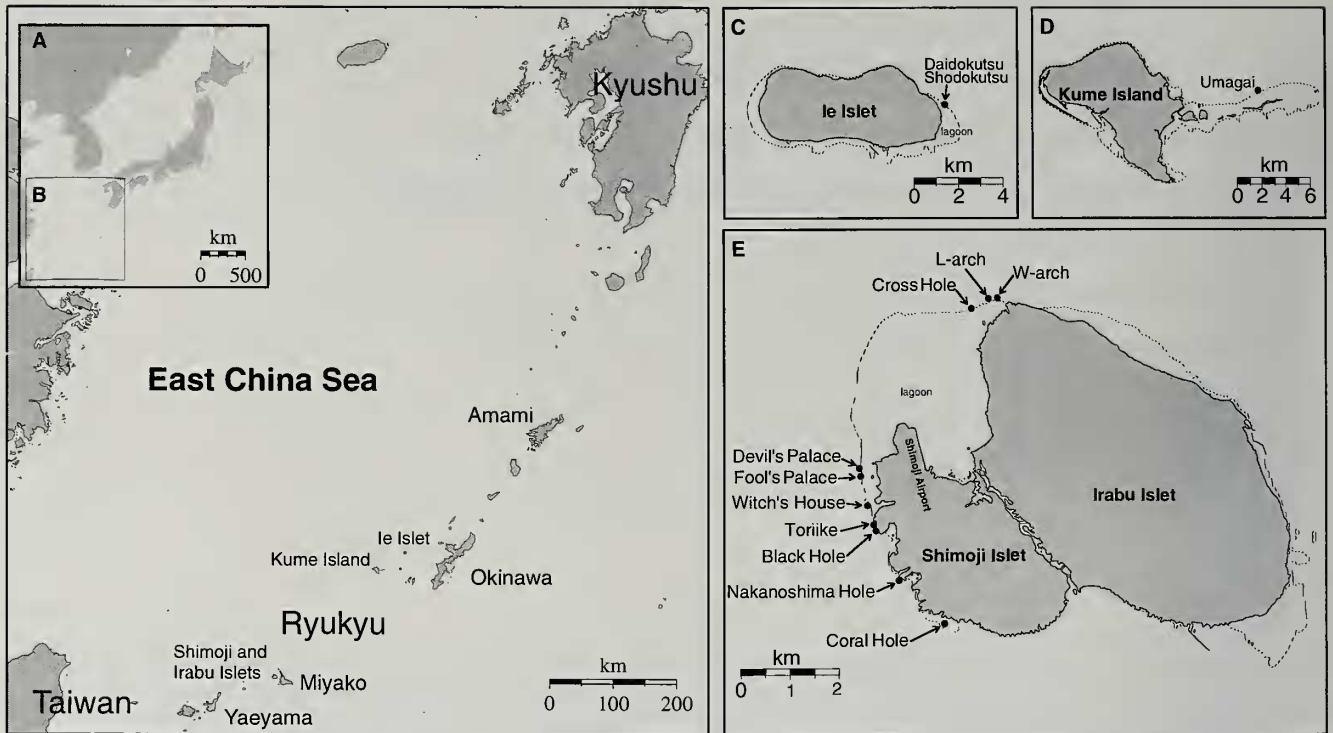


Figure 1. Locality maps (after Hayami and Kase, 1993). **A.** Index map. **B.** Detail of **A** showing Ie, Irabu and Shimoji Islands. **C.** Localities of submarine caves of Ie Islet. **D.** Localities of submarine cave of Kume Island. **E.** Submarine caves of Shimoji Islet and Irabu Islet in Miyako 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,

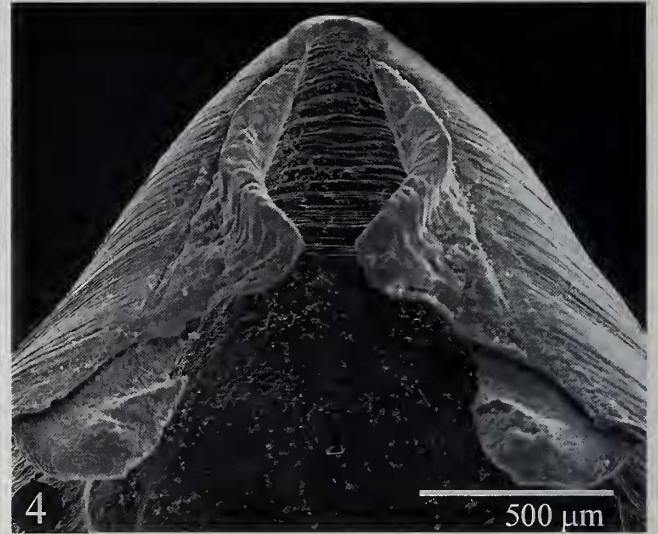
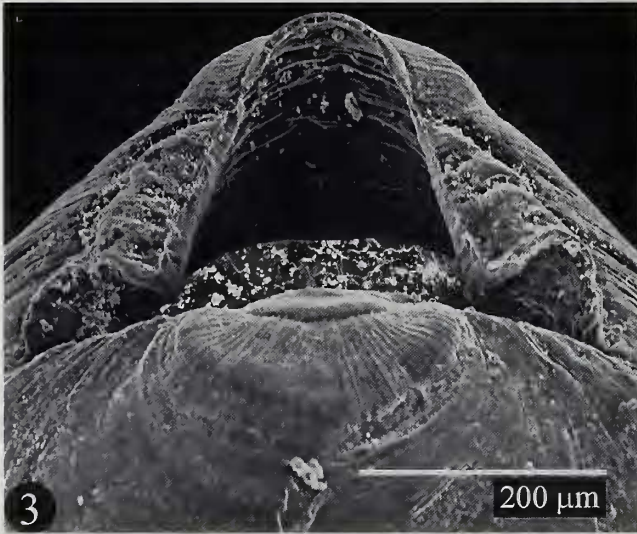
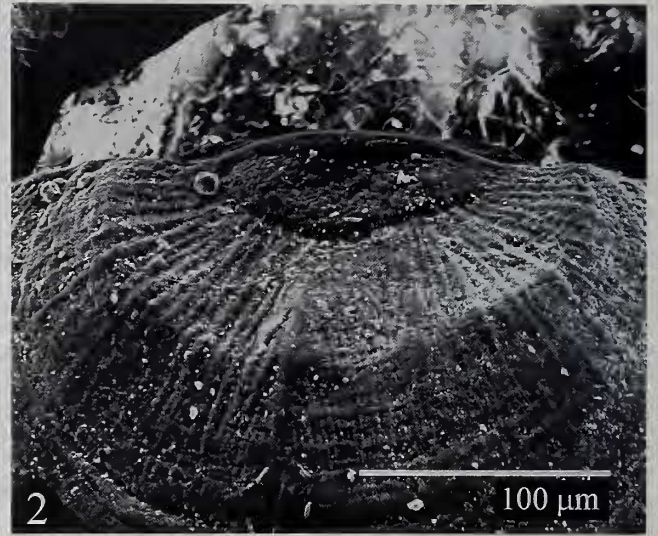
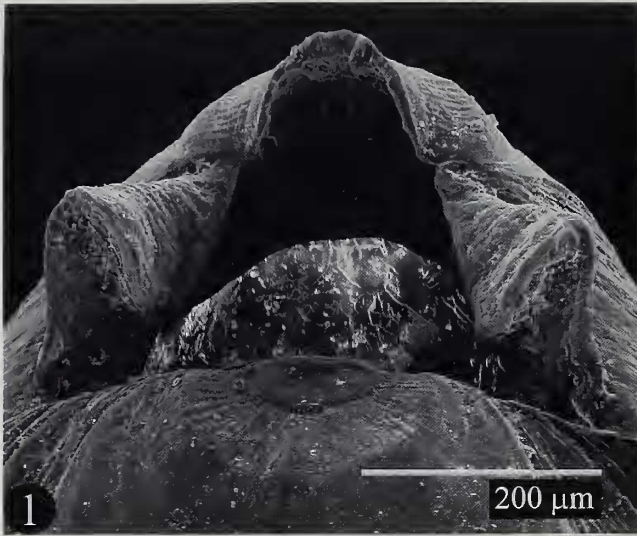
even though the hispanirhynchiid genera *Hispanirhynchia* Thomson and *Sphenarina* Cooper do not possess or have only a low median ridge in the dorsal valve and do not have a septalium by original diagnosis. However, according to our new observations (see below) on the type material of *Sphenarina*, 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, hypothyril 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 rhynchonellid 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 *Burmhirynchia 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

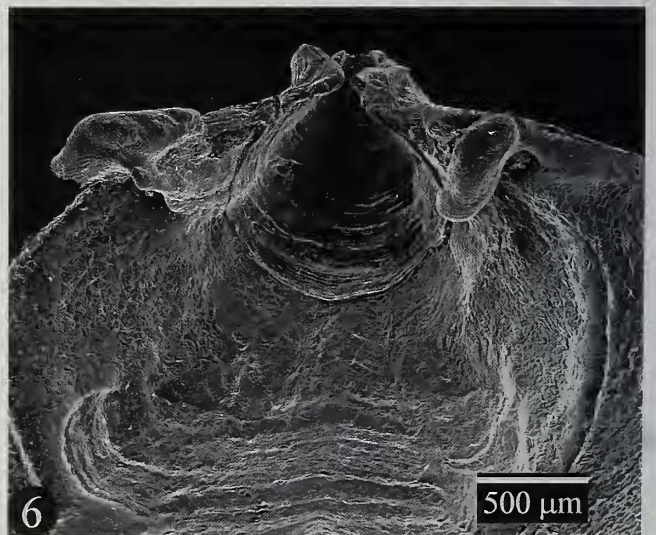
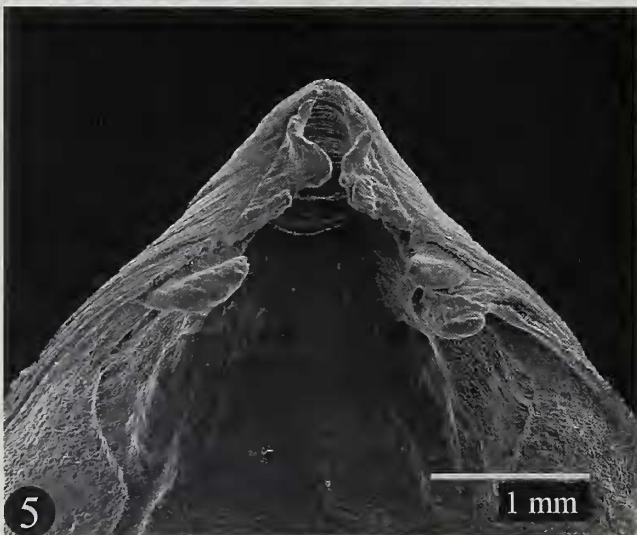
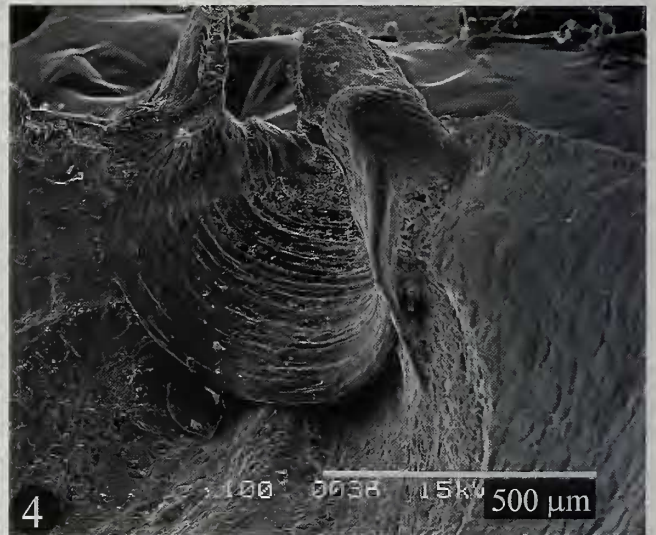
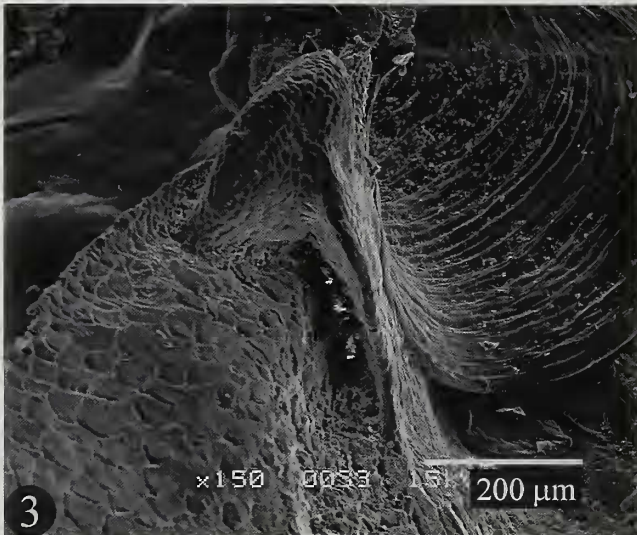
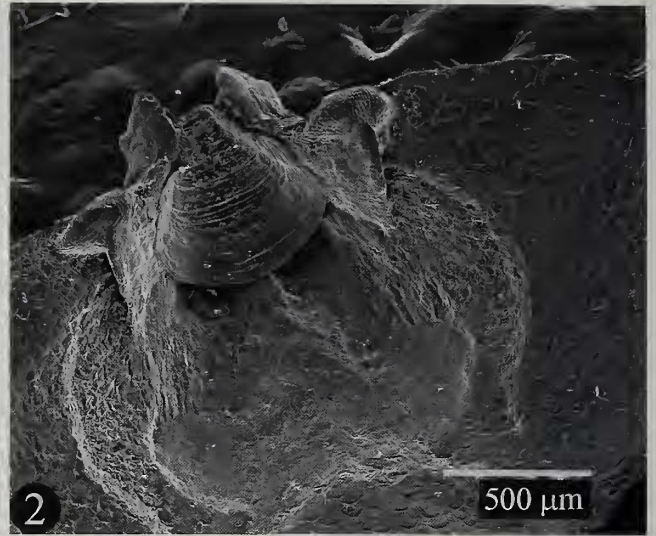
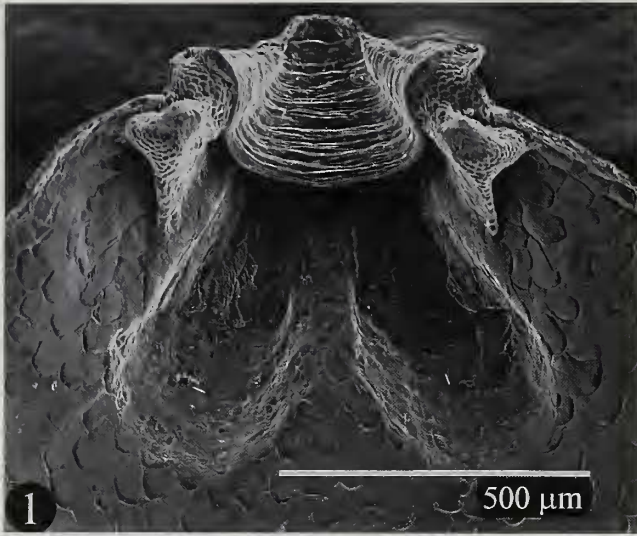
Sphenarina? sp., Saito *et al.*, 2000, p. 77; Saito *et al.*, 2001, p. 131, 132.

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-

◀ **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.

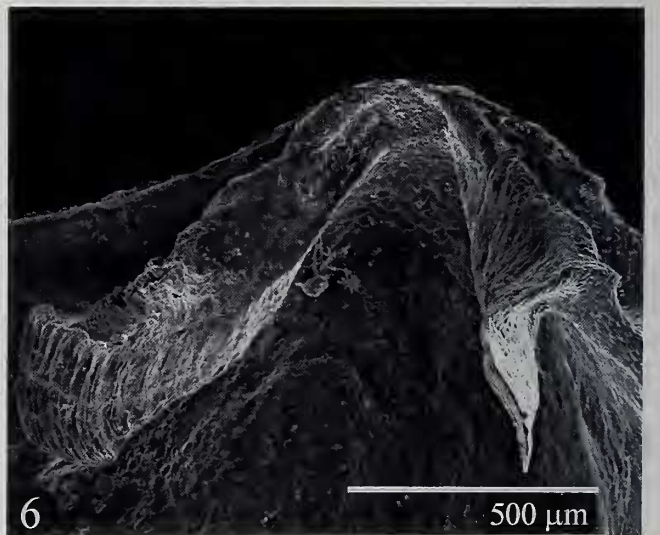
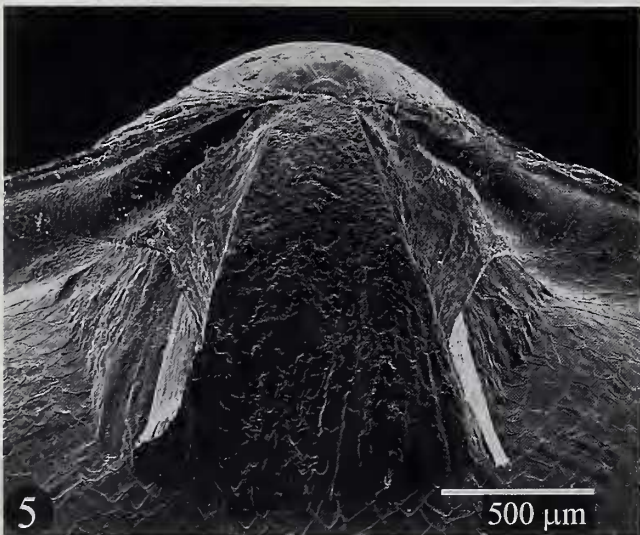
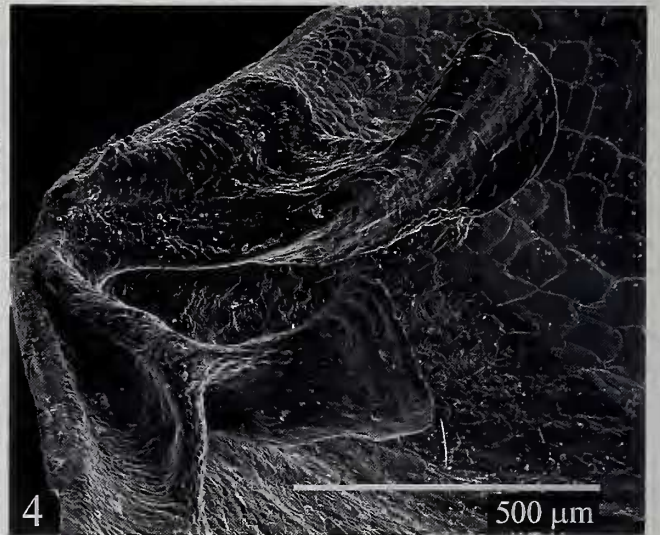
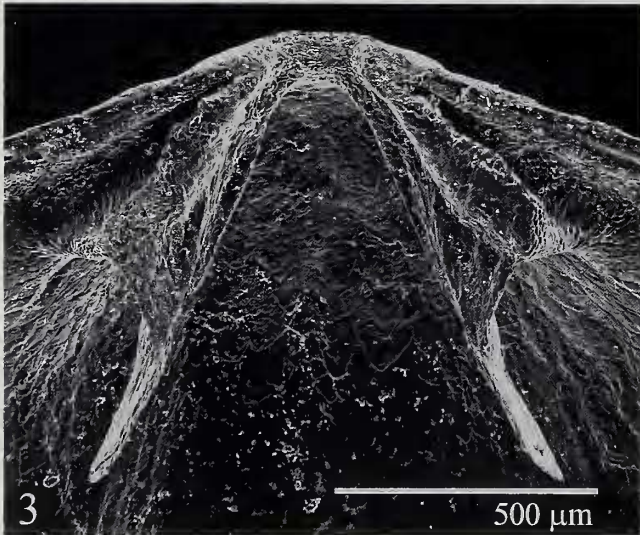
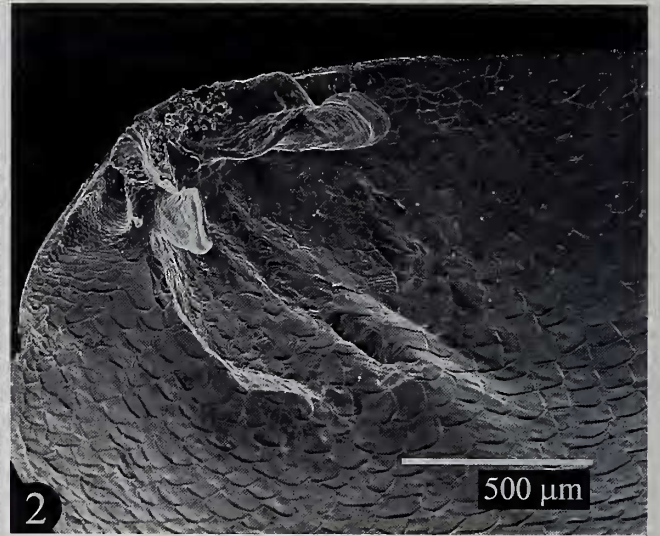
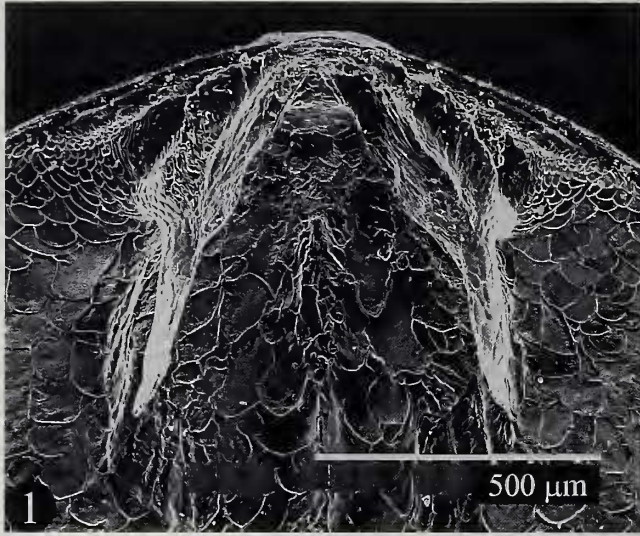
Ecology and associated brachiopods.—Live individuals of *Parasphenarina cavernicola* were mainly found attached to the undersides of hard substrates lying on the cave floor near the entrance, and were occasionally found on the cave wall at the middle of dark tunnels (such as 'Coral Hole') as

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 protogular node, finely capillate (Figure 3.1–3.3). Beak almost straight, foramen hypothrid, 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

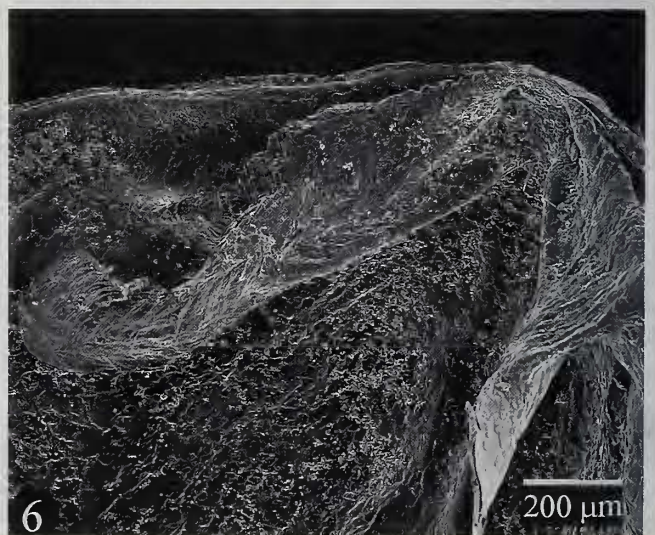
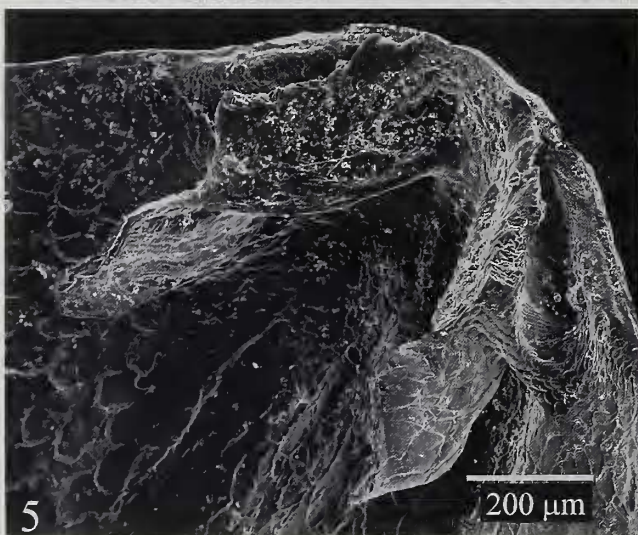
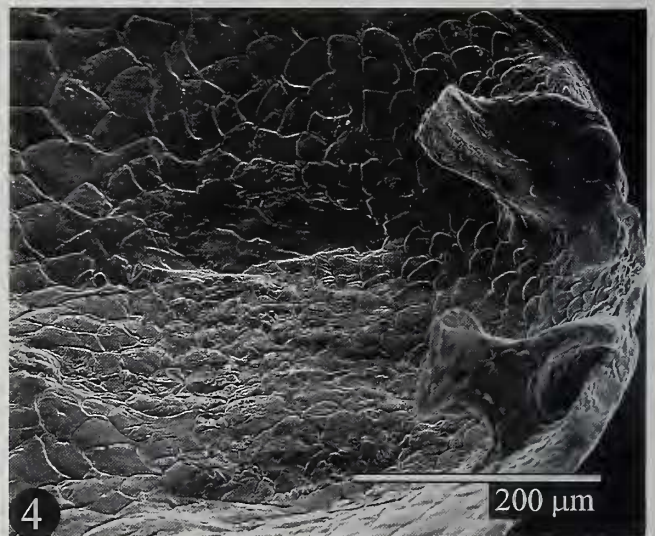
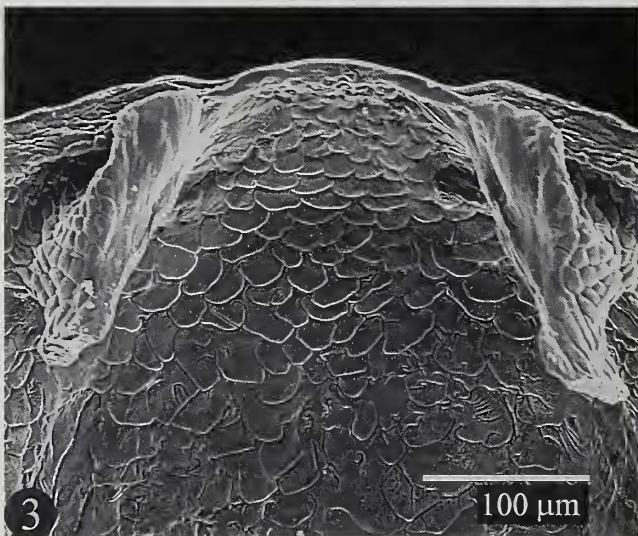
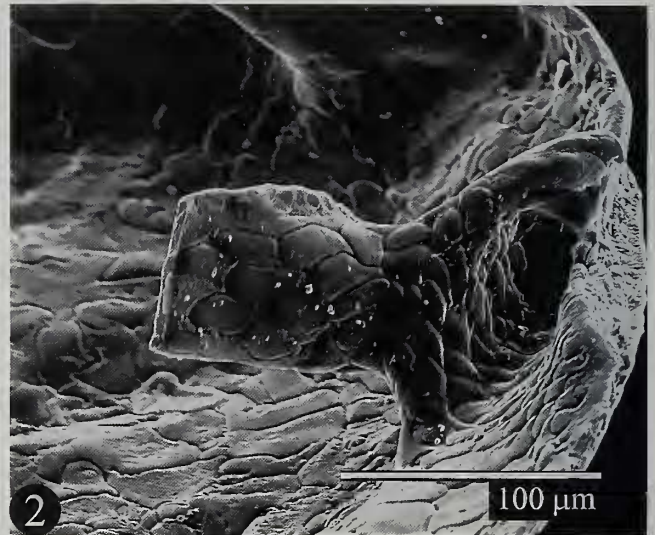
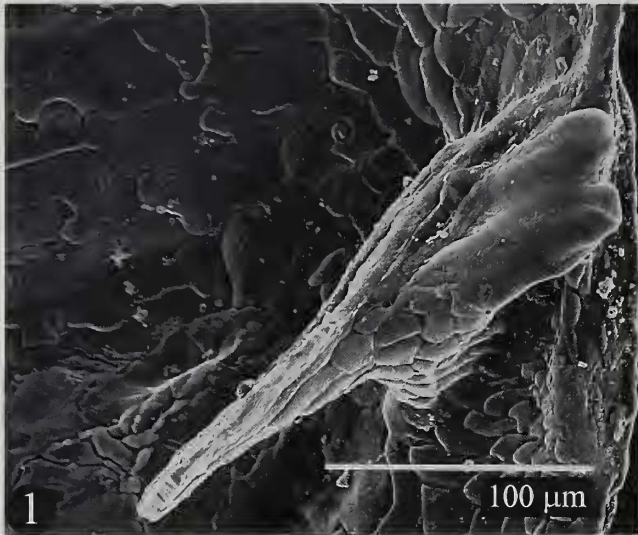
(Figure 8.2).

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 protogular 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

← **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.



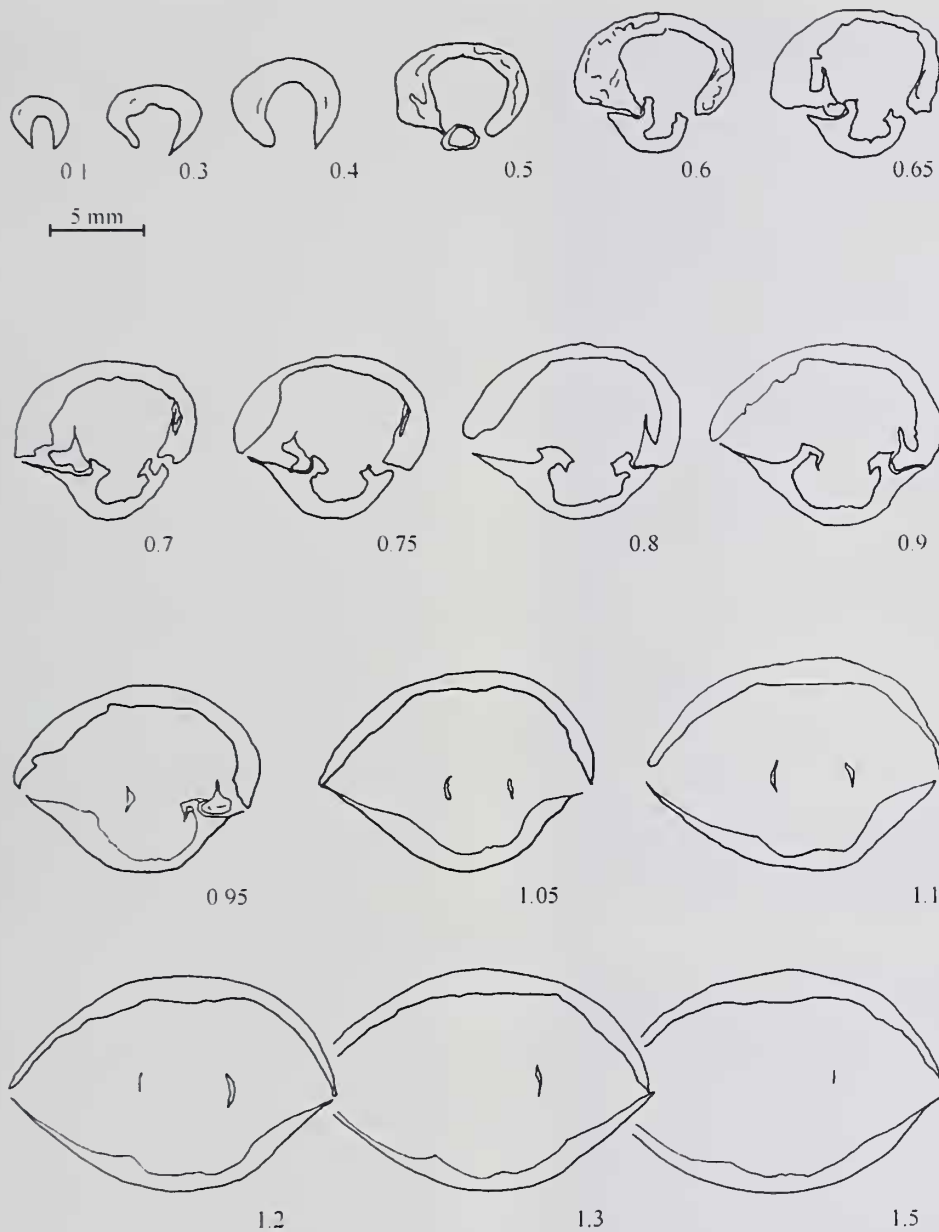


Figure 7. Sixteen quasitransverse serial sections through the umbo of *Parasphenarina cavernicola* gen. et sp. nov. Specimen UMUT RB28220-MN01-c, 'Nakanoshima hole' Shimoji Islet, Miyako Island. L = 4.5 mm, W = 4.1 mm; T = 2.3 mm. Distance from ventral umbo given in mm. The asymmetry of the sections 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.

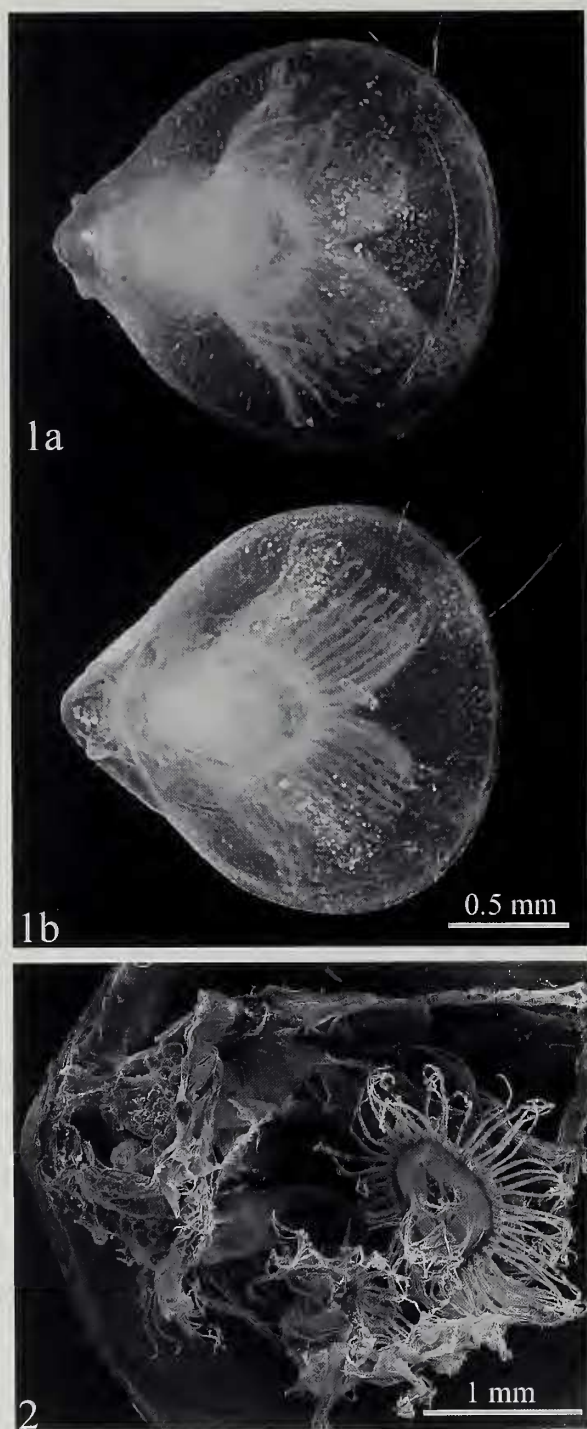


Figure 8. *Parasphenarina cavernicola* gen. et sp. nov. 1. Setae and schizolophous lophophore in juvenile specimen seen through the transparent shell. 1a, ventral side. 1b, dorsal side. Specimen UMUT RB28214-MD03-a, 'Devil's Palace', Shimoji Islet, Miyako Island. 2. Distorted spirolophous lophophore 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 Dagens (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

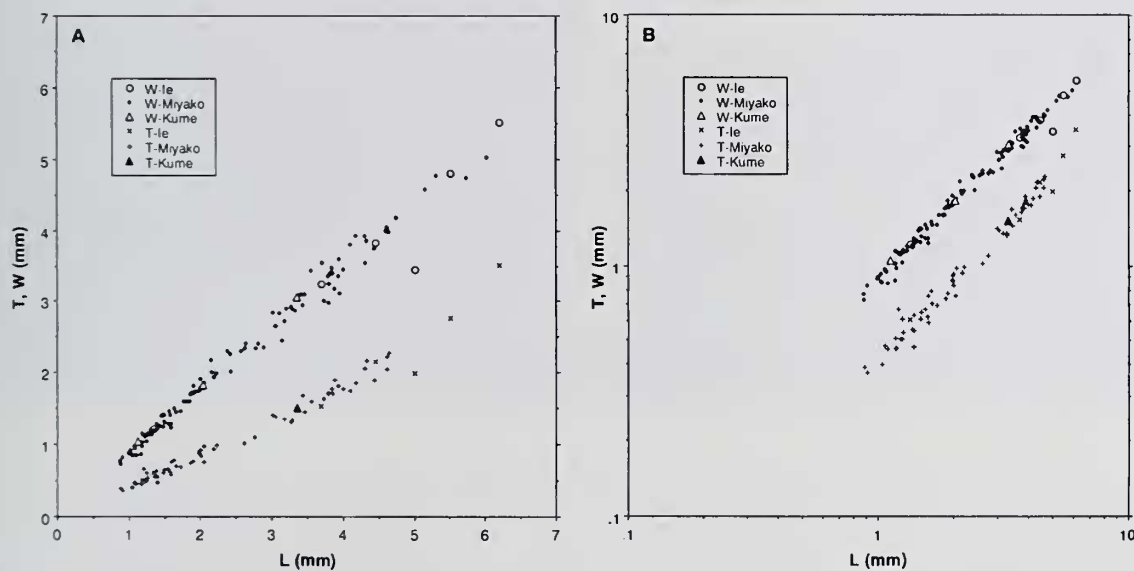


Figure 9. Shell measurements of *Parasphenarina cavernicola* gen. et sp. nov. Scatter plots (A) and double logarithmic scatter plots (B) of shell length (L) versus maximum shell width (W) and thickness (T). Specimens from Ie, Miyako (Irabu and Shimoji islands), and Kume Islands are indicated separately.

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

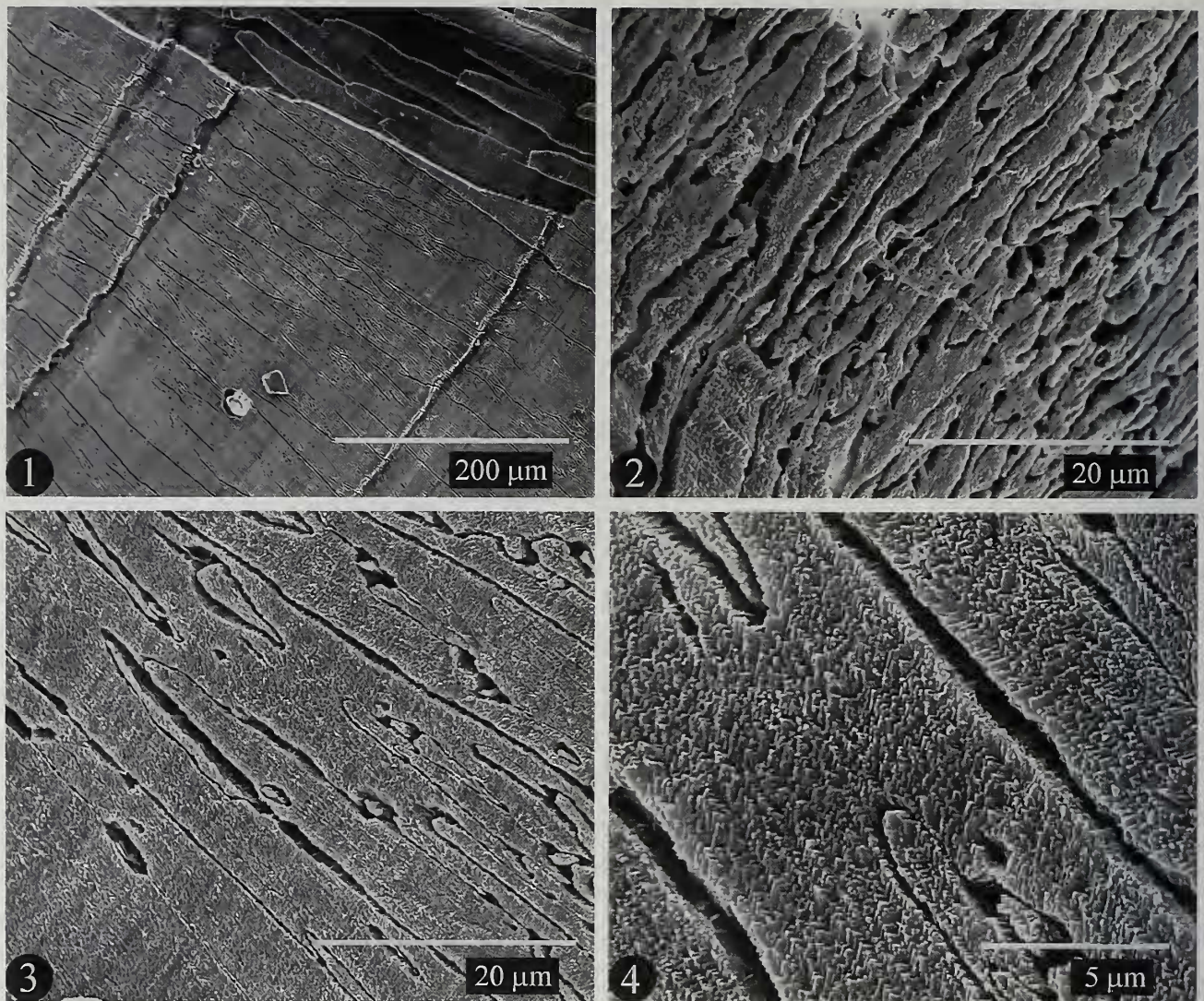


Figure 10. Views of the external surface of the primary layer of *Parasphenarina cavemicola* gen. et sp. nov., 'Nakanoshima Hole', Shimoji Islet, Miyako Island. **1, 3, and 4** specimen UMUT RB28220-ss3-vv, fragment of a dorsal valve, treated with 5% v/w bleach for 13h and etched with 5% HCl for 5sec. **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 Frieleidae 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

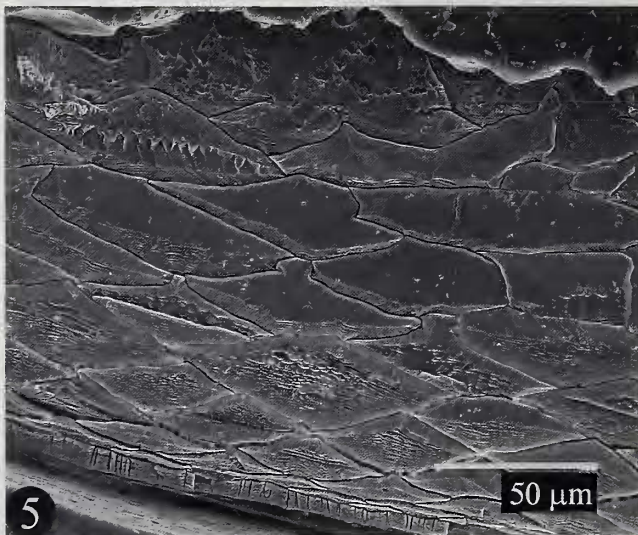
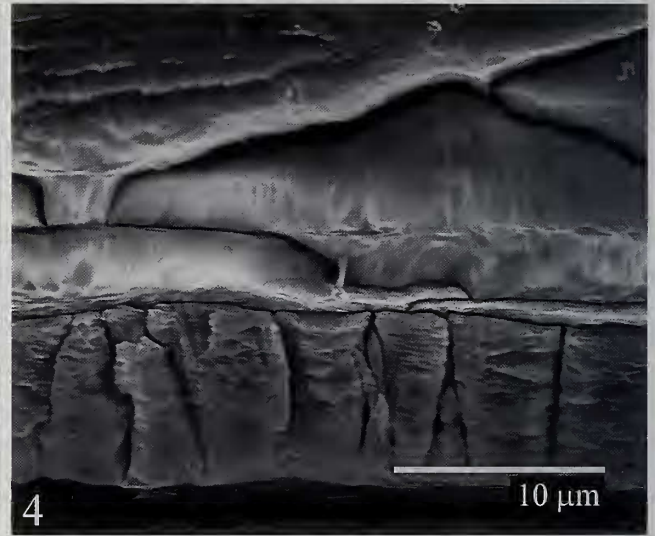
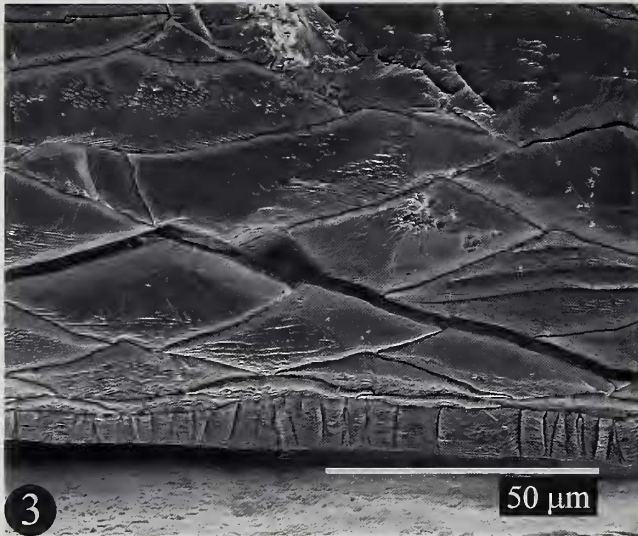
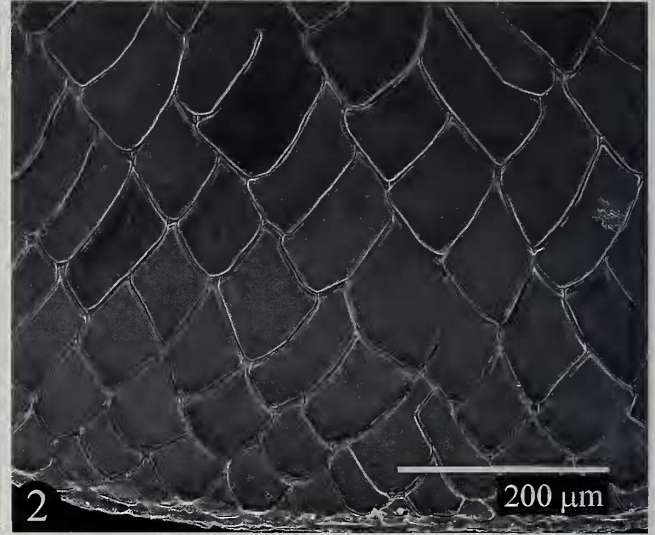
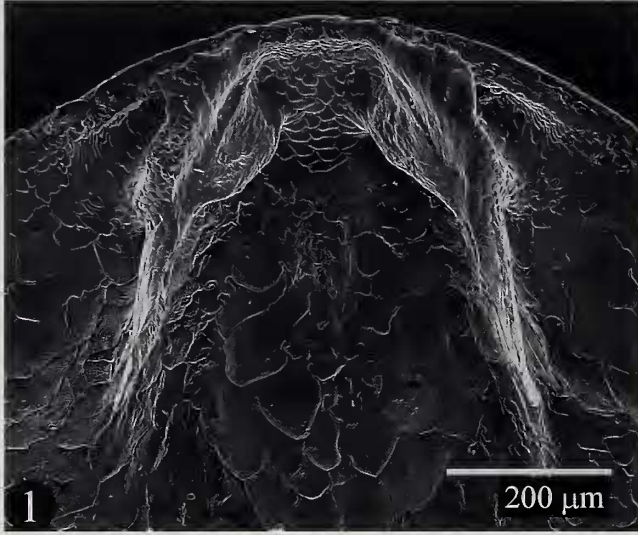
number AB053201 (Saito *et al.*, 2001).

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 rhynchonellid 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 protogular 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 Frieleidae, 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.

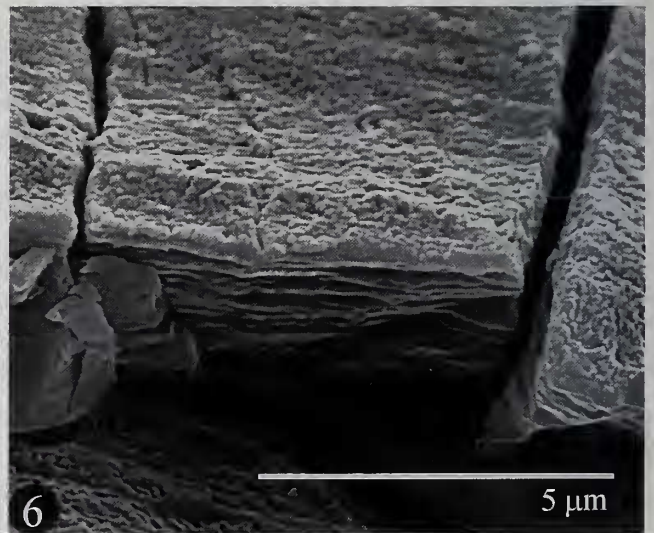
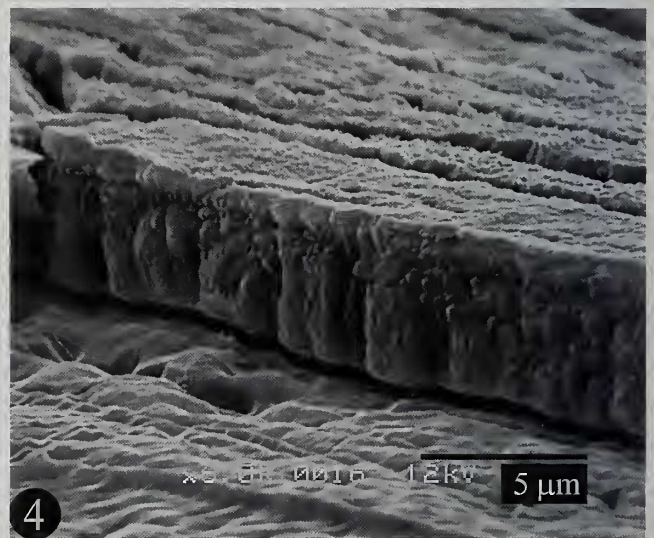
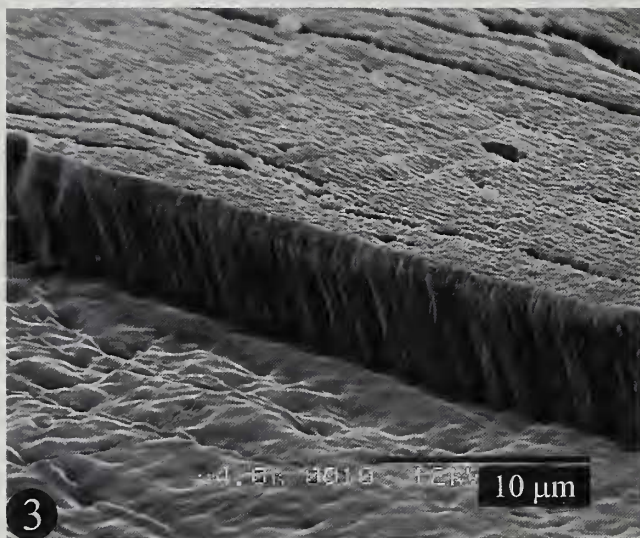
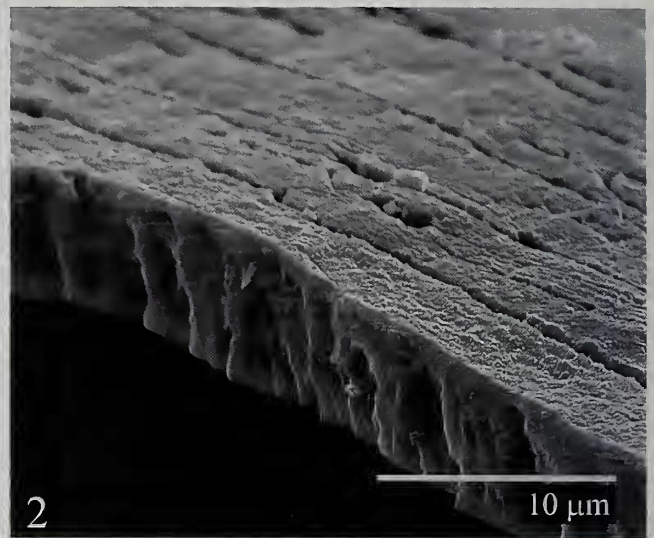
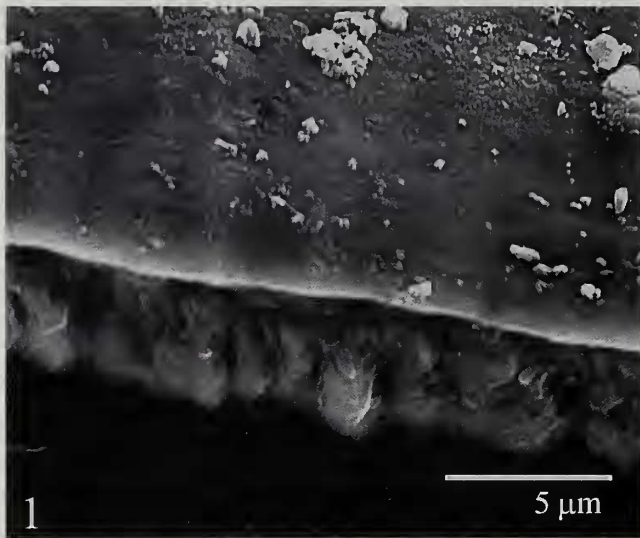
Several authors in the past have drawn attention to the need to include in taxonomic descriptions detailed accounts of growth stages (Surlyk, 1972; Lee and Wilson, 1979). A detailed account of the growth stages in *Notosaria nigricans* was given by Lee and Wilson (1979). Manceñido and Walley (1979) point 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

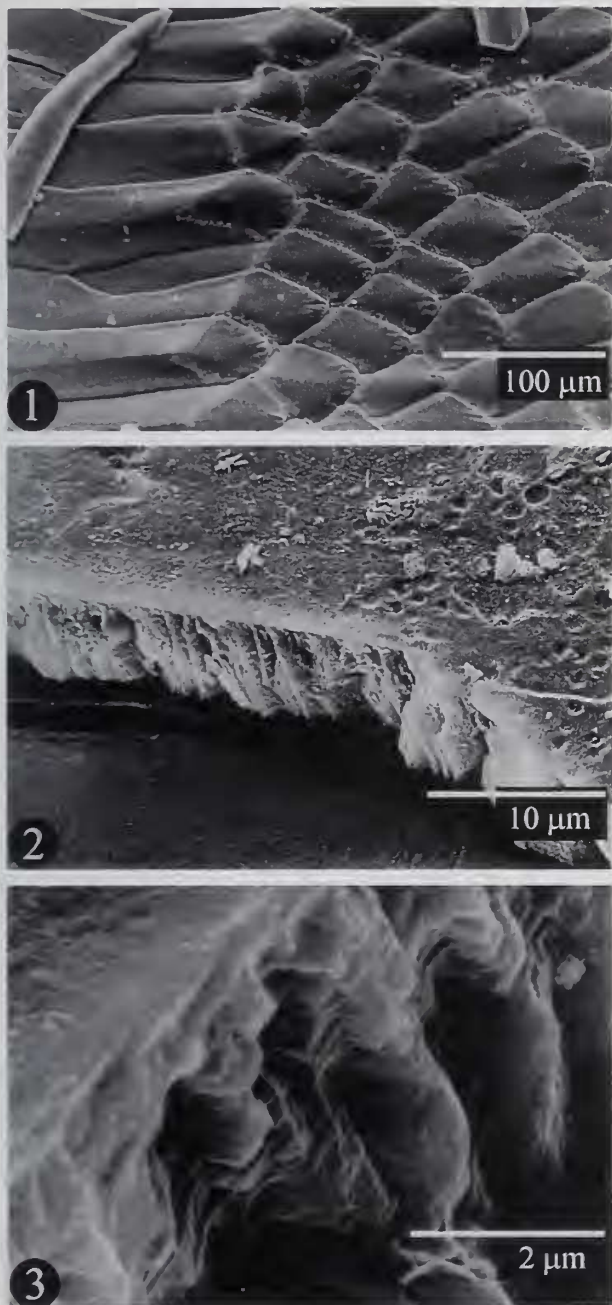
absence of septalium (for instance *Sphenarina*) should be carefully revised.

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. Frieleids 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 (Manceñido 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 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.

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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.

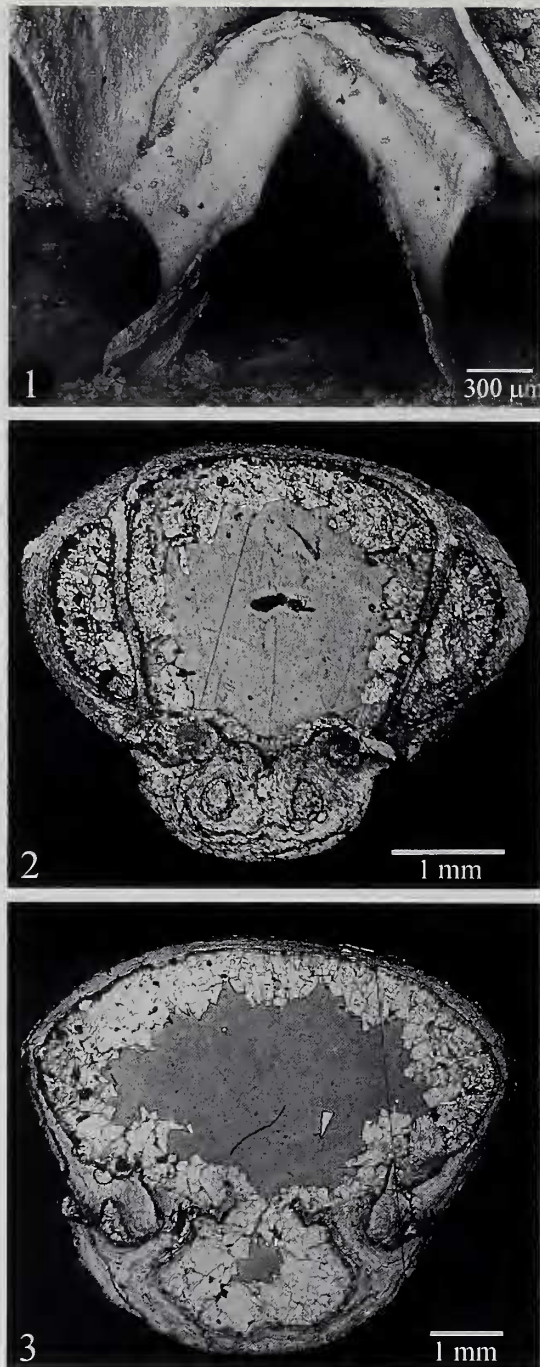


Figure 14. *Sphenarina sicula* Cooper. Pliocene, Milazzo (labelled as Milasso), Messina, Sicily. 1. Cardinalia of specimen USNM 549381a, the same figured by Cooper (1959, p. 8–A, fig.7). Dimensions: L = 12.55 mm, W = 10.50 mm, T = 6.60 mm. Note the incipient cardinal process. 2, 3. Two acetate peels 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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