
A


B

Frontispiece

Underwater photographs (by Mr. Mitsutoshi Taniguchi) of *in situ* individuals of a living fossil oyster, *Pycnodonte* (*Pycnodonte*) *taniguchii* Hayami and Kase, 1992, at the entrance of the submarine cave "Toriike" of Shimoji Islet of Ryukyu Islands. A: brownish individual, B: ivory individual (approximately natural size).

The University Museum
The University of Tokyo

Bulletin No. 35

SUBMARINE CAVE BIVALVIA FROM THE RYUKYU ISLANDS: SYSTEMATICS AND EVOLUTIONARY SIGNIFICANCE

Itaru HAYAMI and Tomoki KASE

1993 TOKYO

All communications pertaining to this Bulletin should be addressed to the Editorial Board, The University Museum, The University of Tokyo, 7–3–1 Hongo, Bunkyo-ku, Tokyo 113, Japan

Issued November 30, 1993
ISSN 0910–481X

Printed by University of Tokyo Press

This volume is also available in a clothbound
edition (price ¥17,000) from University of Tokyo Press,
7–3–1 Hongo, Bunkyo-ku, Tokyo 113, Japan

The University Museum, The University of Tokyo, Bulletin No. 35, 1993
133 pp., 3 maps, 379 figs., 6 tables

SUBMARINE CAVE BIVALVIA FROM THE RYUKYU ISLANDS: SYSTEMATICS AND EVOLUTIONARY SIGNIFICANCE

Itaru HAYAMI* and Tomoki KASE**

* *Geological Institute, University of Tokyo*

** *National Science Museum*

Contents

Abstract

A number of nearly or totally dark sublittoral limestone caves open to the fore-reef slopes of Ie, Shimoji and Irabu Islets of the Ryukyu Islands are inhabited by various interesting cryptic organisms. 48 cavernicolous bivalves, 31 of which were found alive, are systematically described here mainly with SEM photomicrography. Dominant species are mostly new and belong to *Huxleyia*, *Bentharca*, *Cosa*, *Cratis*, *Dacrydium*, *Urumella* (gen. nov.), *Parvamussium*, *Cyclopecten*, *Chlamydella*, *Divarilima*, *Ctenoides*, *Limatula*, *Cardita*, *Carditella*, *Salaputium* and *Halonympha*. The generic assemblage is considerably unique and extraneous for Indo-West Pacific sublittoral fauna, though several diminutive species of shallow-water genera (e.g. *Septifer*, *Streptopinna*, *Lima*, *Epicodakia*, *Rochefortina*, *Coralliophaga*, *Irus*) are often found alive in association. Except for a bradytelic species of *Pycnodonte* (s. s.), which is a member of the sclerosponge-brachiopod community, and for *Glossocardia obesa*, most cavernicolous bivalves are very small in adult size (generally less than 5 mm in length), often exhibiting remarkable stunting and paedomorphosis by progenesis.

The cavernicolous bivalves resemble deep-water ones not only in generic composition but also in developmental strategy: the predominance of non-planktotrophic (lecithotrophic and direct) development is strongly indicated by the large-sized prodissoconch I and in several species by parental incubation of embryos. These common characteristics may be related and are mainly caused by oligotrophic conditions in the caves, where suspension feeders have to depend on the limited phytoplanktons brought from exposed environments by weak currents. The archaic life mode of cavernicolous bivalves as well as the rarity of durophagous predators indicates that such submarine caves offer refuges for defenseless animals. Emphasis is laid upon the importance of the study of such cryptic faunas in evolutionary biology.

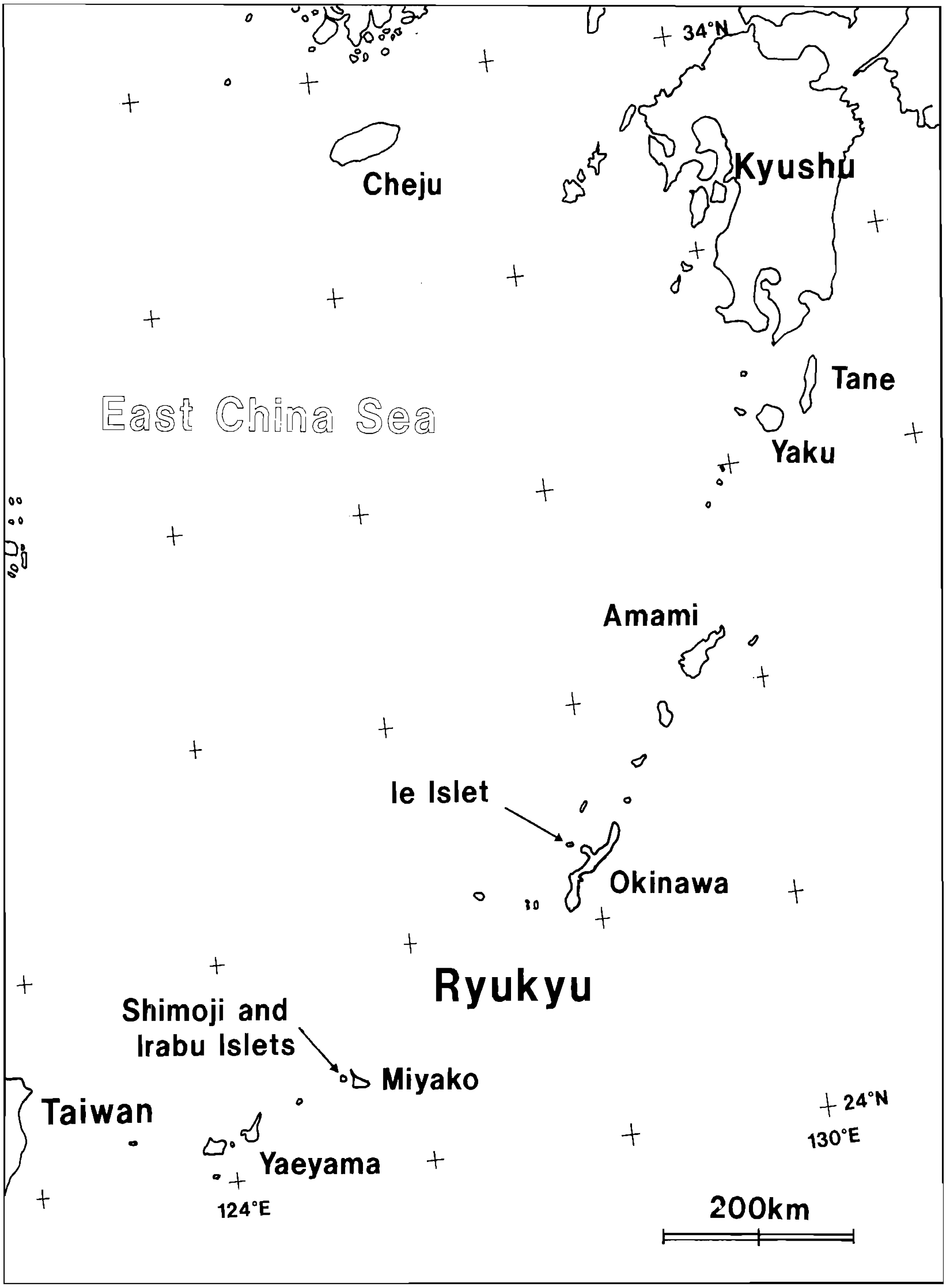
Introduction

Submarine sheltered environments in and around coral reefs are often inhabited by characteristic and interesting organisms. Since Hartman and Goreau (1970) discovered sclerosponges (coralline sponges) resembling Paleozoic-Mesozoic stromatoporoids in the sublittoral crevices of Caribbean coral reefs, similar sclerosponge-bearing cryptic communities have also been found in the Indo-West Pacific and Red Sea reefs, and their composition, origin and evolutionary significance have been discussed by several authors (Jackson, Goreau and Hartman, 1971; Jackson and Winston, 1982; MacIntyre et al., 1982; Kobluk, 1988). Little, however, had been known about the feature of molluscs of such sheltered environments until we found living individuals of *Neritopsis radula* and a relict species of *Pycnodonte* from the caves of the present area (Kase and Hayami, 1992; Hayami and Kase, 1992).

The interior of lightless submarine limestone caves is one of the most interesting places for the study of cryptic organisms, but they were not accessible until recent years, when the technical development and popularization of SCUBA diving enabled scientists to explore for the first time the biota of this unknown world. Recently, with the assistance of several skilled divers, many interesting benthic organisms have been found in a number of submarine caves at Ie Islet of Okinawa Islands and Shimoji and Irabu Islets of Miyako Islands, southern Japan (Maps 1–3). They contain numerous undescribed bivalves and gastropods in addition to some benthic foraminifers, soft sponges, sclerosponges, ahermatypic corals, bryozoans, articulate brachiopods, polychaetes, a chiton (*Lepidopleurus*), crustaceans (ostracods, amphipods and decapods) and echinoids, which are to be described hereafter by cooperative and other specialists.

While taxonomic investigation has to precede advanced studies, the study of cave biota will produce various kinds of contribution to evolutionary biology. Because sheltered places may offer refuge to archaic and anachronistic organisms, submarine cavernicolous biota has been emerging as an exciting subject of systematics and paleontology. In fact, the present cave molluscs contain several "living fossils" as well as a large number of unfamiliar species with archaic appearances. We may gain a glimpse of ancient biota in such a cryptic environment. Submarine caves are very local and semi-closed places, but intensive studies of the biota may provide some generalization about the causal relation between the peculiar environment and the adaptive strategy of marine organisms.

Several years ago, one of us (T. K.) learned that some lightless caves open to the sublittoral fore-reef slope of Ie Islet are inhabited by many individuals of *Neritopsis radula*, a famous bradytelic "living fossil" gastropod. At the same time it was found that the calcareous muddy sediments at the same site contain numerous molluscan shells of a unique assemblage. The preliminary reports (Hayami and Kase, 1991; Kase and Hayami, 1992) were based on the results of our field observation and laboratory



Map 1. Index map showing the location of Ie, Shimoji and Irabu Islets, Ryukyu Islands, southern Japan.

investigation during 1989–1991. In 1991–1993, our study of cavernicolous molluscs was extended to a number of similar submarine caves of Shimoji and Irabu Islets of Miyako Islands. Meanwhile, an enigmatic "living fossil" oyster, *Pycnodonte taniguchii,* was found alive in several caves of these islets, as described in a separate paper (Hayami and Kase, 1992).

The aim of this paper is to describe dominant bivalves from these caves and to discuss their evolutionary significance. Our systematic study, however, often encountered some difficulties. At present, anatomical study of these bivalves is not easy for us owing to their diminutive size. Nowadays, SEM observation and photomicrography of diminutive shells are rather easy, but close comparison with hitherto named species of similar size is often difficult unless the original materials have been examined through a similar procedure. In Japan and adjacent regions, greatly diversified marine bivalves have been known (Habe, 1977a; Higo and Goto, 1993), but our knowledge about the systematics of microscopic species and the ontogenetic development of larger species remains insufficient. The endemism of these species to cryptic environments often cannot be recognized on a firm basis. In some species we cannot necessarily deny the possibility that the cave material represents merely the juvenile stages of larger-sized non-cavernicolous species. The taxonomic identification and classification adopted in this paper, therefore, are often still provisional and will be improved by further studies.

On the other hand, there are many advantageous points in the cave mollusc materials. The sediments on the cave floors are almost wholly composed of calcareous mud and bioclasts, containing numerous molluscan shells and other organic remains. They are almost free of terrigenous clastic material, indicating the sedimentation must be relatively slow. Most bivalve species are represented by numerous specimens. In cavernicolous environments physical, chemical and biological destruction (or erosion) of molluscan shells seems to be generally slow, and various characteristics in the early developmental stages (especially the external features of larval shells) are directly observable on the umbonal area of living animals and empty shells. This condition is suitable for the inference of larval ecology and developmental strategy. As enumerated elsewhere (Kase and Hayami, 1992) and discussed in some detail in the present article, the cavernicolous bivalves reveal several common characteristic features, which seem to give a clue for testing some theories of evolutionary ecology and marine biogeography.

Submarine Caves in the Ryukyu Islands

A large number of submarine limestone caves have been found around relatively flat islets of the Ryukyu Islands. Most of them are winding, horizontal to stepwise tunnels, which are open to fore-reef slopes. Their entrances lie between sea level and about – 40 m, and their lengths range from several meters to more than 70 m. The inner part of these caves is almost or totally dark and accessible only to skilled divers.

All of these caves are in the Ryukyu Limestone (commonly 30–70 m thick), which was extensively deposited in this region during several interglacial stages of the Pleistocene (mainly after 500 Ka). They were probably formed by underground water during some lower sea-level stages and finally drowned during the post-glacial sea-level rise. Application of the accepted curves of the Holocene sea-level change in the Japanese Islands (Sugimura, 1977, etc.) indicates that all the marine organisms in these caves came from somewhere after 8,000 years B. P. Because the level of underground water is considered to lie near or slightly above sea-level, these submarine limestone caves are probably inactive at present. In fact, the salinity of the sea water in these caves is usually normal, as observed by divers. Owing to the low energy of sea water, the bottom sediments on the cave floor are generally very fine except for organic remains, and almost free of coarse terrigenous material.

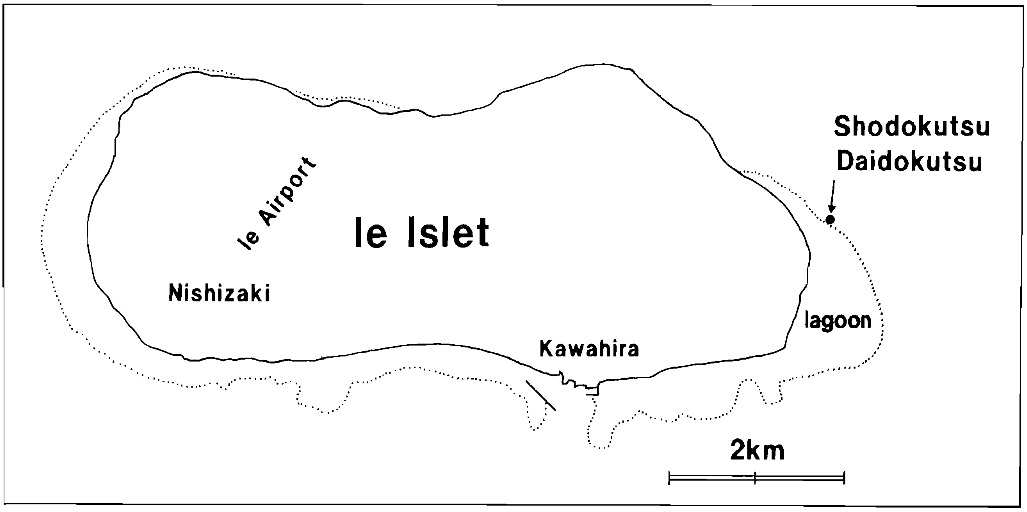
We examined cryptic organisms in two caves of Ie Islet of Okinawa (Map 2), seven caves of Shimoji Islet and four caves of Irabu Islet, Miyako Islands (Map 3). Their popular names (among divers), entrance locations, bottom depths (for the entrances and the innermost parts) and some other features are enumerated below.

Ie Islet in Okinawa Islands (Map 2)

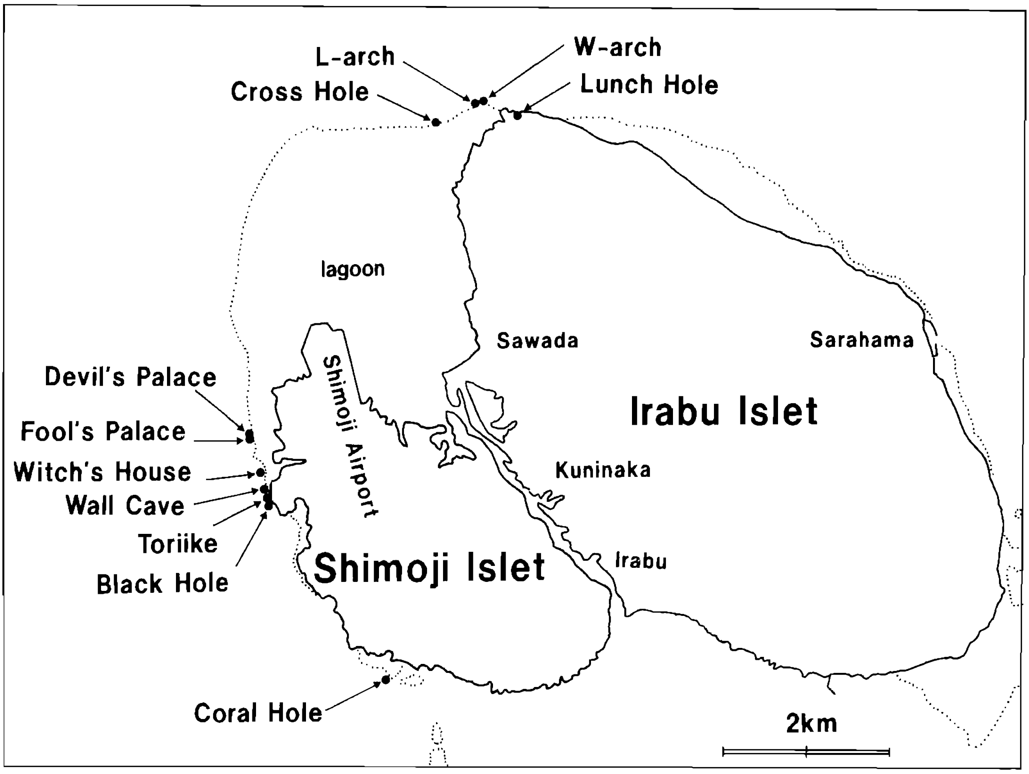
1. "Shodokutsu (= small cave)", 26°42.9′N, 127°50.1′E, more than 30 m long, totally dark, winding and branching tunnel (– 20 to – 7 m deep).
2. "Daidokutsu (= large cave)", 26°42.9′N, 127°50.1′E, about 10 m long, very dark, cathedral-like wide cave (– 20 m deep).

Shimoji Islet in Miyako Islands (Map 3)

3. "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.
4. "Fool's Palace", 24°49.6′N, 125°08.2′E, about 10 m long, almost totally dark tunnel (– 35 to –32 m deep).
5. "Witch's House", 24°49.3′N, 125°08.3′E, more than 10 m long, totally dark tunnel (– 37 to – 35 m deep).
6. "Wall Cave", 24°49.1′N, 125°08.3′E, about 5 m long, dark tunnel (– 35 m deep).
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 passing ponds (– 40 to – 12 m deep). Sampling was also made from a side cave.
8. "Black Hole", 24°49.1′N, 125°08.3′E, about 70 m long, totally dark stepwise tunnel with



Map 2. Location of surveyed submarine caves of Ie Islet, Okinawa Islands.



Map 3. Location of surveyed submarine caves of Shimoji and Irabu Islets, Miyako Islands.

an air pocket in the innermost part (– 35 to 0 m deep).
9. "Coral Hole", 24°48.0′N, 125°09.0′E, about 5 m long, dark hole and tunnel (– 35 m deep).

Irabu Islet in Miyako Islands (Map 3)

10. "Lunch Hole", 24°51.6′N, 125°10.0′E, totally dark hole with an entrance lying near the sea level (– 4 m deep). Unlike other caves the sediments contain considerable amount of terrestrial residual soil.
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).
12. "L-arch", 24°51.7′N, 125°09.7′E, very dark L-like hole and short cave (– 25 m deep).
13. "Cross Hole", 24°51.6′N, 125°09.5′E, dark complicated hole and 20 m long cave (– 25 to – 20 m deep).

From the inner part of each cave several samples were obtained by SCUBA diving, and living specimens and empty shells were sorted for taxonomic studies (Table 1). The microhabitat of living bivalves can be roughly classified into 1) soft bottom surface, 2) hard bottom surface (blocks of wall rocks), 3) surface of annelid tubes on the sediments, and 4) surface of walls and ceilings (Table 2 in p.108–109). Samples from the wall and ceiling were examined at several caves, especially "Shodokutsu", "Fool's Palace", "Witch's House", "Wall Cave", "Toriike", "Coral Hole", "W-arch" and "Cross Hole". Although sampling in other caves is still preliminary, we believe that most of the dominant bivalves in these caves are represented in our collection.

The sediment samples of the following caves outside the Ryukyu Islands were preliminarily examined for comparison. Only the occurrences of bivalves common with those in the Ryukyu Islands are listed in Table 2 and mentioned in the description of relevant species.

1. "Balicasag Cave", a diving point off Panglao Islet, southern coast of Bohol Island, the Philippines.
2. "Chandelier Cave", a popular diving point near Koror, Palau Islands (Republic of Belau).
3. Sheltered place around "Gyuchaku-iwa", at Kumoi near Matsuzaki, southwestern coast of Izu Peninsula, Shizuoka Pref., central Japan.

Table 1. Occurrence of cavernicolous bivalves from Ryukyu Islands

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Solemya (Petrasma) sp.			▲		▲								▲
2. Huxleyia cavernicola sp. nov. カクレキビガラガイ(新称)	○		■	▲	▲		●*	●	●	●	■	▲	■
3. Pronucula insignis sp. nov. ケシクルミガイ(新称)	△		△				△			▲*			○
4. Acar sp. aff. A. plicata (Dillwyn)	○		□	△	○		○						
5. Bentharca tenuis sp. nov. ウスクマサカヤドリ(新称)	□	△	□	○	□	▲	○	○	○	○	●	○	●*
6. Bentharca decorata sp. nov. カザリクマサカヤドリ(新称)	□*				△			△	△	△			
7. Bentharca irregularis sp. nov. ホソクマサカヤドリ(新称)	○*				○			○					
8. Bentharca excavata sp. nov. ベニクマサカヤドリ(新称)	●		□	○	○	▲		○	△	○	●	○	■*
9. Bathyarca sp. シラスナガイモドキ(新称)				△									
10. Cosa waikikia (Dall, Bartsch and Rehder)	■		■	■	●	●	■	■	●	●	■	●	■
11. Cosa kinjoi sp. nov. キンジョウシラスナガイモドキ(新称)	■	△			○		△	○	▲*		○	△	○
12. Cosa uchimae sp. nov. ウチマシラスナガイモドキ(新称)	○*												
13. Cosa sp.			△							△			
14. Cratis kanekoi sp. nov. カネコシラスナガイモドキ(新称)			△*										△
15. Cratis ohashii sp. nov. オオハシシラスナガイモドキ(新称)	○*			△		△							
16. Limopsoidea? gen. et sp. indet.	○				□		○				○		○
17. Brachidontes sp.	○			△					△			△	△
18. Septifer sp.			○	△		▲							▲
19. Crenella sp.	△		△	△		▲		△					
20. Dacrydium zebra sp. nov. ドウクツヒバリガイ(新称)	●		■*	●	●	▲	■	●	△	○	■	□	■
21. Urumella concava gen. et sp. nov. ウルマヒバリガイ(新称)			○	△	○	△	○	○		●	○	□*	○
22. Malleus (Malvufundus) sp.					▲	▲			●				▲
23. Parvamussium crypticum sp. nov. カクレツキヒガイ(新称)	■*	●											
24. Parvamussium decoratum sp. nov. ミジンツキヒガイ(新称)			△	○			△	△	▲				△
25. Cyclopecten ryukyuensis sp. nov. ケシハリナデシコ(新称)	○	△	△	○	○		△	△	△		△	△	●*
26. Chlamydella incubata sp. nov. コモチハリナデシコ(新称)	○		■	●	●	●	■	■	▲	●	■	■	■*

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
27. Chlamydella tenuissima sp. nov. ウスハリナデシコ(新称)	○		●	▲	○	▲	▲	●	▲	○	●	△	●*
28. Pycnodonte taniguchii Hayami and Kase オオベッコウガキ		▲	▲				●	▲	■		▲*	▲	▲
29. Lima sp.	△			△				△					▲
30. Divarilima elegans sp. nov. ヒメタキハネガイ(新称)	□*												
31. Ctenoides minimus sp. nov. ケシハネガイ(新称)	○		△	○			△	△	△		▲	○*	○
32. Isolimea limopsis (Nomura and Zinbo) シラスナユキミノガイ				△									
33. Limatula kinjoi sp. nov. キンジョウユキバネガイ(新称)	○		△	△	△		○	△	△		▲	△	●*
34. Limaria sp.	△			△				△				△	▲
35. Epicodakia pygmaea sp. nov. コビトウミアサガイ(新称)	△		▲	▲*				△		▲	△		▲
36. Cardita uruma sp. nov. イガトマヤガイ(新称)	▲		△	▲			●						
37. Cardita sp.	△												
38. Carditella iejimensis sp. nov. イエジマケシザルガイ(新称)	■*	●											
39. Carditella shimojiensis sp. nov. シモジケシザルガイ(新称)				■*			△	○					
40. Salaputium unicum sp. nov. チビモシオガイ(新称)	△		▲	●*									▲
41. Rochefortina sandwichensis (Smith) ハコベノハナガイ	○		○	▲	▲		△	○	△			●	■
42. Kelliella japonica sp. nov. マルケシハマグリ(新称)	△*			△					△				
43. Coralliophaga hyalina sp. nov. ガラスマツカゼガイ(新称)	○		●*	△	△				△	△	△		●
44. Glossocardia obesa (Reeve) ツキヨミガイ		△											△
45. Irus (Irus) sp.			△	△						▲			▲
46. Irus (Notirus) sp.	△		△										▲
47. Hiatella sp. aff. H. orientalis (Yokoyama)	○		△	△	△		△					△	
48. Halonympa asiatica sp. nov. ドウクツシャクシガイ(新称)	□*												

Locality. 1-2: Ie Islet [1: Shodokutsu, 2: Daidokutsu]. 3-9: Shimoji Islet [3: Devil's Palace, 4: Fool's Palace, 5: Witch's House, 6: Wall Cave, 7: Toriike, 8: Black Hole, 9: Coral Hole]. 10-13: Irabu Islet [10: Lunch Hole, 11: W-arch, 12: L-arch, 13: Cross Hole].
Occurrence. Living (■: abundant, ●: common, ▲: rare); Dead shell only (□: abundant, ○: common, △: rare), *: type locality.

Systematic Description

Repository. — All the specimens described in this article are preserved in the University Museum, University of Tokyo (UMUT). Each register number represents all the specimens of a species collected from one and the same cave, and type and illustrated specimens are specified with a suffix (a, b, c, . . .). Most living specimens, except illustrated ones (dried for SEM photography), are preserved in alcohol for further studies.

Abbreviations. — The following abbreviations are used in the description; RV: right valve, LV: left valve, CV: conjoined valves, Pd I: prodissoconch I, Pd II: prodissoconch II.

Illustrations. — All the figures except for the illustrations of a few large-sized species are SEM photomicrographs unless otherwise stated.

Measurements. — Measurements (Length × Height, accuracy: 1/20 mm) or magnifications of illustrated specimens are given in figure captions. Prodissoconch size was more accurately measured under SEM, and its range and mean are given in the description and Table 4.

Trivial names. — New Japanese trivial names are given in the figure captions.

Class **Bivalvia** Linnaeus, 1758
Subclass **Cryptodonta** Neumayr, 1884
Order **Solemyoida** Dall, 1889
Superfamily **Solemyoidea** Adams and Adams, 1857
Family **Solemyidae** Adams and Adams, 1857
Genus ***Solemya*** Lamarck, 1818
Subgenus ***Petrasma*** Dall, 1908

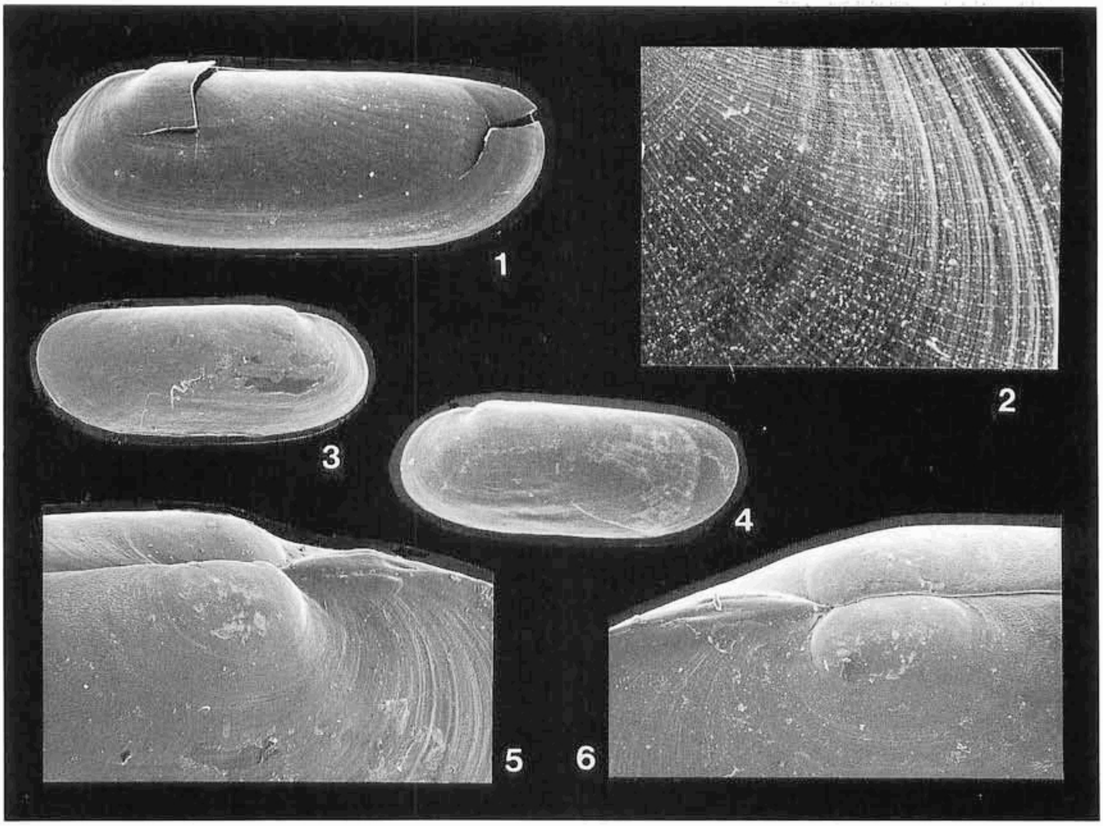
Solemya (***Petrasma***) sp. indet.

Figures 1–6

A few individuals of a small solemyid have been found alive on the bottom sediments of "Devil's Palace" (UMUT RM19345) and "Witch's House" (RM19573) of Shimoji Islet and "Cross Hole" (RM19346) of Irabu Islet, Miyako Islands.

The elongated oblong outline and opisthodetic subinternal ligament suggest subgenus *Petrasma* for this species. The subgeneric reference is, however, by no means convincing, because the detailed structure of the chondrophore is unknown. The surface is shiny, marked with several weak radial threads in addition to numerous divergent striae. There is a small post-umbonal flange supporting the subinternal ligament. Unlike many solemyids, the periostracum of this species is thin and scarcely extends beyond the ventral margin of calcareous shell.

The present species looks different from *Solemya* (*Petrasma*) *pusilla* Gould, 1861,



Solemya (*Petrasma*) sp. indet.
Figures 1–2: living specimen, RM19573a, 4.30 × 1.60 mm, from "Witch's House" [1: right view, 2: posterior surface of LV (× 100)]. Figures 3–6: living specimen, RM19345a, 2.85 × 1.10 mm, from "Devil's Palace" [3: left view, 4: right view, 5: left upper view (× 75), 6: right upper view (× 75)].

from the shallow-waters of north-central Japan, having a much smaller size (the maximum specimen in the present sample is only 4.8 mm long), undeveloped periostacum and a more elongated outline. If the difference in size is ignored, the shell shape is similar to that of *Solemya* (*Acharax*) *japonica* Dunker, 1882, from the lower sublittoral bottom of north-central Japan, but the ligament is subinternal, unlike that species. The present specimens probably belong to an undescribed species, but further examination is needed because of the possibility that they represent merely juvenile stages.

Superfamily **Nucinelloidea** Vokes, 1956
Family **Nucinellidae** Vokes, 1956

Genus ***Huxleyia*** Adams, 1860

The shell orientation of nucinellids was determined by Allen and Sanders (1969), who studied the soft part of *Nucinella serrei* Lamy in detail. They regarded the

Nucinellidae as belonging to the Solemyoida in terms of anatomy. The phylogenetic relation of this family was discussed again by Waller (1990). From a viewpoint of cladistics, he considered that the hinge teeth of *Nucinella* and *Huxleyia* are of palaeotaxodont type (instead of actinodont type) and that the origin of this family should be sought in a primitive Ordovician group also ancestral to the Solemyidae and Ctenodontidae.

Although Habe (1958, pl.11, fig.16, as cited by Keen and Newell *in* Cox et al., 1969, fig.C14) indicated the presence of posterior adductor muscle scar in *Huxleyia sulcata* Adams, 1860, the type-species of this genus, all the species of *Huxleyia* seem to be monomyarian, as pointed out by Allen and Sanders (1969) and Matsukuma, Okutani and Tsuchi (1982) on *Nucinella* species.

The bathymetric distribution of *Huxleyia* species in the Pacific has been regarded as restricted to lower sublittoral to upper bathyal soft bottoms (Habe, 1977a; Bernard, 1983; etc.). The abundant occurrence of living individuals of a species of this genus in sublittoral caves is remarkable.

Huxleyia cavernicola sp. nov.

Figures 7–15

1992. *Huxleyia* sp., Kase and Hayami, *Jour. Moll. Studies*, vol. 58, p.448, listed.

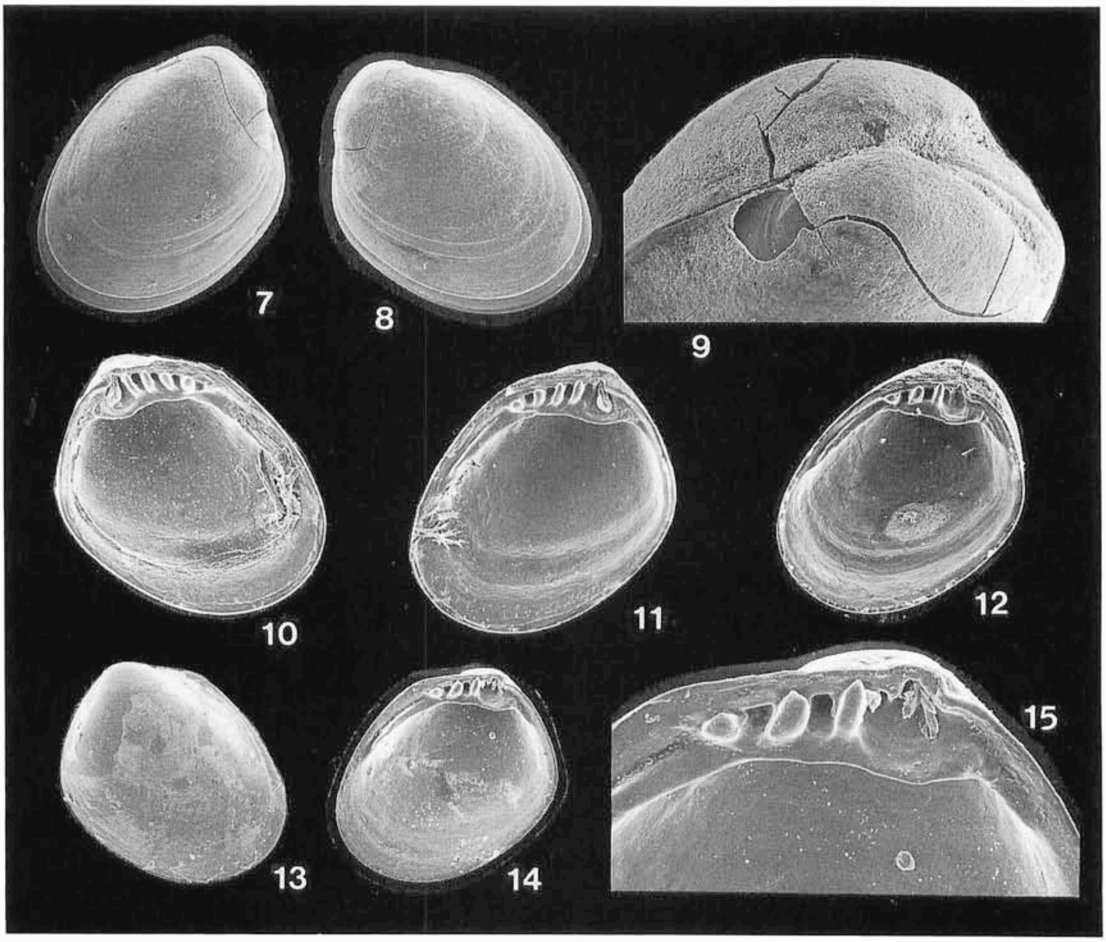
1993. *Huxleyia* sp., Hayami and Kase, *Univ. Mus. Univ. Tokyo, News*, no.27, p.3, fig.1.

Type and material. — Holotype: RM19350a, a living specimen from the bottom sediments of "Toriike" of Shimoji Islet. Miyako Islands. Paratypes: RM19347 (living) from "Devil's Palace", RM19348 (living) from "Fool's Palace", RM19349 (living) from "Witch's House", RM19350 (living) from the type locality, RM19351 (living) from "Black Hole", RM19575 (living) from "Coral Hole" of Shimoji Islet. RM19352 (living) from "Lunch Hole", RM19353 (living) from "W-arch", RM19574 (living) from "L-arch", RM19354 (living) from "Cross Hole" of Irabu Islet. RM19355 (dead) from "Shodokutsu" of Ie Islet.

Diagnosis. — Stunted species of *Huxleyia*, characterized by ovate outline, strong convexity, relatively short hinge line, large Pd I, thick, brownish (sometimes greenish) and shiny periostracum, and only four pre-umbonal teeth in each valve, of which the anteriormost tooth is commonly incipient.

Description. — Shell scarcely exceeds 1.2 mm in length and height, equivalve, opisthocline, considerably thick, obliquely elongated and ovate, slightly longer than high, strongly convex. Surface smooth except for growth-lines, covered with dark brownish (or greenish) thick periostracum. Hinge line relatively short, occupying about two-fifths of shell length. Antero-dorsal margin long, discriminated from dorsal margin by an obtuse angulation. Hinge plate broad, with large resilium pit below umbo and three or four opisthoclinal pre-umbonal teeth in each valve; two or three teeth near umbo obliquely elongated and stout, while the anteriormost tooth is commonly tubercular and incipient. RV has an elongated lateral tooth along the antero-dorsal margin, and LV has a groove for its reception. Anterior adductor scar not strongly impressed but large and suboval, whereas posterior adductor is absent even in young individuals. Pd I very large, nearly smooth, ranging 247–276 μm in maximum diameter, hidden by periostracum; Pd II not discriminated.

Remarks. — A large number of individuals were found alive on the bottom sedi-



Huxleyia cavernicola sp. nov.　カクレキビガラガイ (新称)
Figures 7–9: Holotype, living specimen, RM19350a, 1.05 × 1.00 mm, from "Toriike" [7: left view, 8: right view, 9: oblique view of umbonal area with cracked periostracum (× 75)]. Figures 10–11: living specimen (separated valves), RM19350b, 1.10 × 1.10 mm, from "Toriike" [10: interior of LV, 11: interior of RV]. Figure 12: interior of RV, RM19575a, 1.00 × 1.05 mm, from "Coral Hole". Figures 13–15: immature RV, RM19350c, 0.90 × 0.85 mm, from "Toriike" [13: exterior, 14: interior, 15: hinge area (× 100)].

ments in many caves of Shimoji and Irabu Islets. The present species is undoubtedly referable to *Huxleyia* by the completely internal ligament and characteristic hinge teeth. It resembles *Cyrilla dalli* Hedley, 1902, from eastern Australia in the small shell-size and the number of pre-umbonal teeth, but the shell is more obliquely elongated, and the antero-dorsal area is more clearly angulated. *Cyrilla minuta* Dall, 1898, from the Eastern Pacific and *Nucinella* (*Huxleyia*) *ochiaiensis* Chinzei, 1959, from the Pliocene of north Japan have less elongated outlines, larger shell size and commonly five or more pre-umbonal teeth in the adult stage.

In the outline it may be closer to *Huxleyia sulcata* Adams, 1860, from Japanese waters, but the adult shell size is smaller by half and the surface is not marked with strong commarginal lamellae. The pre-umbonal teeth are decidedly fewer; they number four in the adult stage (Figures 10, 11), while five to six teeth are commonly present in *H. sulcata*. There is a possibility that the present species is a paedomorphic form of some larger-sized species, but these features seem to deserve a distinction at the species level.

Distribution. — Common in sublittoral caves of Shimoji, Irabu and Ie Islets of the Ryukyu Islands. The present species also occurs in "Balicasag Cave" off Panglao Islet of Bohol Island, the Philippines.

Subclass **Palaeotaxodonta** Korobkov, 1954

Order **Nuculoida** Dall, 1889

Superfamily **Nuculoidea** Gray, 1824

Family **Nuculidae** Gray, 1824

Genus ***Pronucula*** Hedley, 1902

Pronucula is a small sized nuculid genus which seems to be characterized by small shell-size, arcuate (instead of angular) hinge-line, fine marginal crenulations and relatively small number of palaeotaxodont teeth. The resilifer is subvertical, flanked by a pair of tooth-like projections and different from the oblique chondrophore of *Nucula* and *Acila*, while this is probably a paedomorphic feature. *Pronucula*, together with *Austronucula*, had been known predominantly from the lower neritic to abyssal substrates of the southern hemisphere (Hedley, 1902; Dell, 1956; Powell, 1958; Knudsen, 1970). Living and dead specimens of a representative species of this genus, though rather rare, occur in some caves of Ryukyu Islands, as described below.

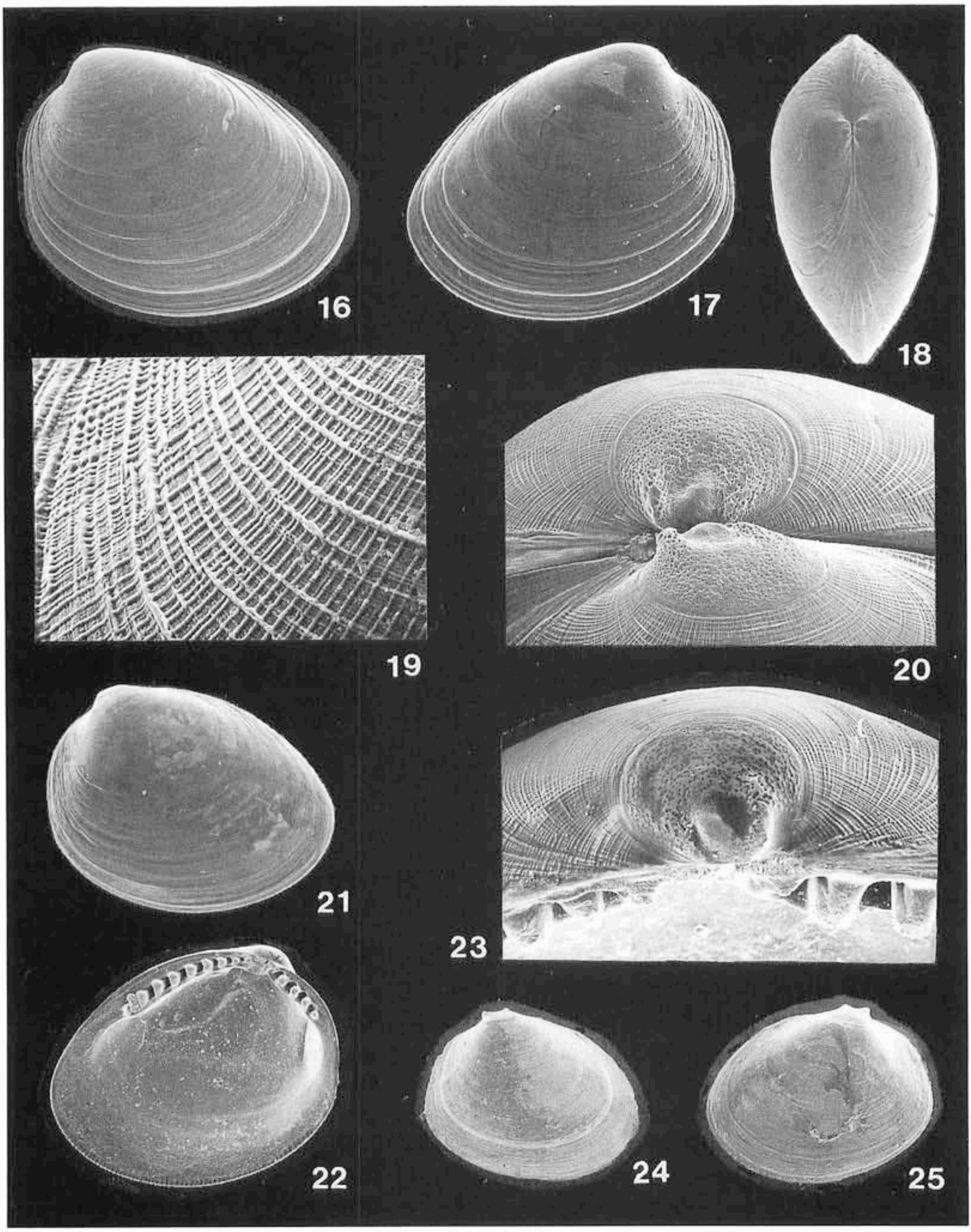
Pronucula insignis sp. nov.

Figures 16–25

Type and material. — Holotype: RM19358a, a living specimen from the bottom sediments of "Lunch Hole" of Irabu Islet, Miyako Islands. Paratypes: RM19358 (living) from the type locality, RM19356 (dead) from "Devil's Palace", RM19357 (dead) from "Toriike", RM19359 (dead) from "Cross Hole" of Shimoji-Irabu Islet. RM19360 (dead) from "Shodokutsu" of Ie Islet.

Diagnosis. — Small subtriangular species of *Pronucula*, characterized by truncated posterior margin, subquadrate resilifer, relatively few paleotaxodont teeth, numerous divergent threads on external surface, finely crenulate inner margin, and large saucer-shaped Pd I with an irregularly depressed summit.

Description. — Shell rarely exceeds 2.2 mm in length, nacreous, translucent, subtriangular, about 1.3 times longer than high. Periostracum pale brownish, very thin. Antero-dorsal and postero-dorsal margins continuously arcuate below umbo, but forming obtuse angles with anterior and posterior margins; the former much longer than the latter. Umbo orthogyrous, located about a third of a shell length from the front. Surface nearly smooth except for numerous faint divergent threads, which almost perpendicularly cross irregular growth lamellae. Inner margin of valve very finely crenulate in accordance with subinternal radial threads only in adult stage.



Pronucula insignis sp. nov.　ケシクルミガイ (新称)
Figures 16–20: Holotype, living specimen, RM19358a, 2.10 × 1.80 mm, from "Lunch Hole" [16: right view, 17: left view, 18: dorsal view, 19: middle surface of LV (× 300), 20: umbonal area (× 100)]. Figures 21–23: RV, RM19358b, 1.95 × 1.65 mm, from "Lunch Hole" [21: exterior, 22: interior, 23: umbonal area (× 100)]. Figure 24: immature RV, RM19359a, 1.00 × 0.80 mm, from "Cross Hole". Figure 25: immature LV, RM19359b, 1.00 × 0.80 mm, from "Cross Hole".

Resilifer deep and large, subquadrate, situated just below umbo, flanked by a pair of symmetrical tooth-like projections, not forming an oblique chondrophore. Teeth tubercular, about eight on anterior and three or four on posterior hinge plate in the largest specimens. Pd I very large, 240–285 μm in maximum diameter, saucer-shaped, with irregularly depressed summit and pockmarked surface; Pd II absent.

Remarks. — This is a solitary paleotaxodont species from these submarine caves. Several individuals from the type locality ("Lunch Hole") are considered to be adult. All the dead specimens (e. g. Figures 24, 25) from other caves of Shimoji, Irabu and Ie Islets, however, are much smaller (rarely exceeding 1.2mm) and have fewer paleotaxodont teeth than those from the type locality, though the prodissoconch and surface features are the same. It is unknown whether these smaller specimens indicate a stunting as an adaptation to the cavernicolous environment or represent only the juvenile stage.

The huge saucer-shaped Pd I (Figures 20, 23) seems to characterize the present species because such a feature has scarcely been described in nuculids. The posteriorly truncated outline and subinternal radial threads may remind one of those of *Nucula paulula* Adams, 1856, a common Japanese nuculid, but, so far as we observed the specimens of that species from several localities, the shell grows much larger, and the Pd I is much smaller and not saucer-shaped.

In view of the undeveloped chondrophore, continuously arcuate dorsal margin and relatively few palaeotaxodont teeth, this species is referable to *Pronucula* rather than *Nucula* (s. s.). It resembles *Pronucula decorosa* Hedley, 1902, the type species of this genus, from the lower sublittoral bottom of New South Wales, but the outline is more trigonal and the posterior part is more reduced. In the truncated posterior margin it resembles *Nucula minuta* Tenison-Woods, 1878, from the same region, which was also referred to *Pronucula* by Hedley (1902), but its radial (or divergent) threads may be weaker. *Pronucula maoria* Powell, 1937, if his illustrated specimen is adult, has fewer anterior teeth. *Nucula certisina* Finlay, 1927, the holotype of which was refigured by Dell (1956), reveals similar hinge structure to the present cave species, but the shell is taller and probably the external surface is covered with more prominent growth lamellae. According to Powell (1958) and others, some species of *Austronucula* from Australia and New Zealand reveal somewhat similar outlines to the present species, but the genus is generally characterized by entire inner margin.

LaBarbera (1974) examined the larval and post-larval shell development of an incubated species, *Nucula proxima*, from the Miocene of Florida. In that species prereleased juveniles (smaller than 600 μm in length) show quite different morphology from the adults, e.g. subquadrate resilifer flanked by a pair of symmetrical tooth-like projections, a few tubercular palaeotaxodont teeth and numerous fine diverging threads, all of which are shared with the present new species. It is, therefore, likely that the present and other species of *Pronucula* were derived from *Nucula* species through paedomorphic evolution.

Distribution. — This species has been found in a few sublittoral caves of Shimoji, Irabu and Ie Islets, Ryukyu Islands.

Subclass **Pteriomorphia** Beurlen, 1944
Order **Arcoida** Stoliczka, 1871
Superfamily **Arcoidea** Lamarck, 1809

Family **Arcidae** Lamarck, 1809

Cryptic arcids from the submarine caves of the Ryukyu Islands have great species diversity; at least six diminutive species can be distinguished in the present samples. Only two of them, however, have been found alive, and most specimens are disarticulated valves.

Many of these cave arcids seem to be related and are regarded as epibyssate species in view of the subtrapezoidal shell and nearly straight (or slightly concave) ventral margin. They share a more or less reduced anterior part, a small number of prionodont teeth, sharply truncated posterior margins and well-developed commarginal lamellae on the external surface. These characters are indicative of a deep-water genus *Bentharca*. Yet their generic assignment is not very conclusive, because the posterior carina and radial ornaments are generally stronger than those of typical deep-water species of this genus, and because some of them are also similar to shallow-water species of *Acar*. Knudsen (1967, 1970) synonymized *Bentharca* with *Acar*, while Oliver and Allen (1980) and many others regarded them as distinct genera. As noted by Habe (1977a) and Oliver and Allen (1980), *Bentharca* has been represented by several Atlantic and northern Pacific species, the occurrences of which have been restricted to bathyal-abyssal depths, at least in low-middle latitudinal regions. Interestingly, these cavernicolous arcids, except one species, are regarded as non-planktotrophic, because of the very large Pd I and the absence of Pd II. This is unusual for shallow-water arcids in low latitudinal regions. Although the cardinal area commonly attains a certain breadth with growth, alivincular ligament sometimes persists until the adult stage, suggesting a paedomorphic feature. The alivincular ligament is situated just below the primary ligament of prodissoconch.

Genus ***Acar*** Gray, 1857

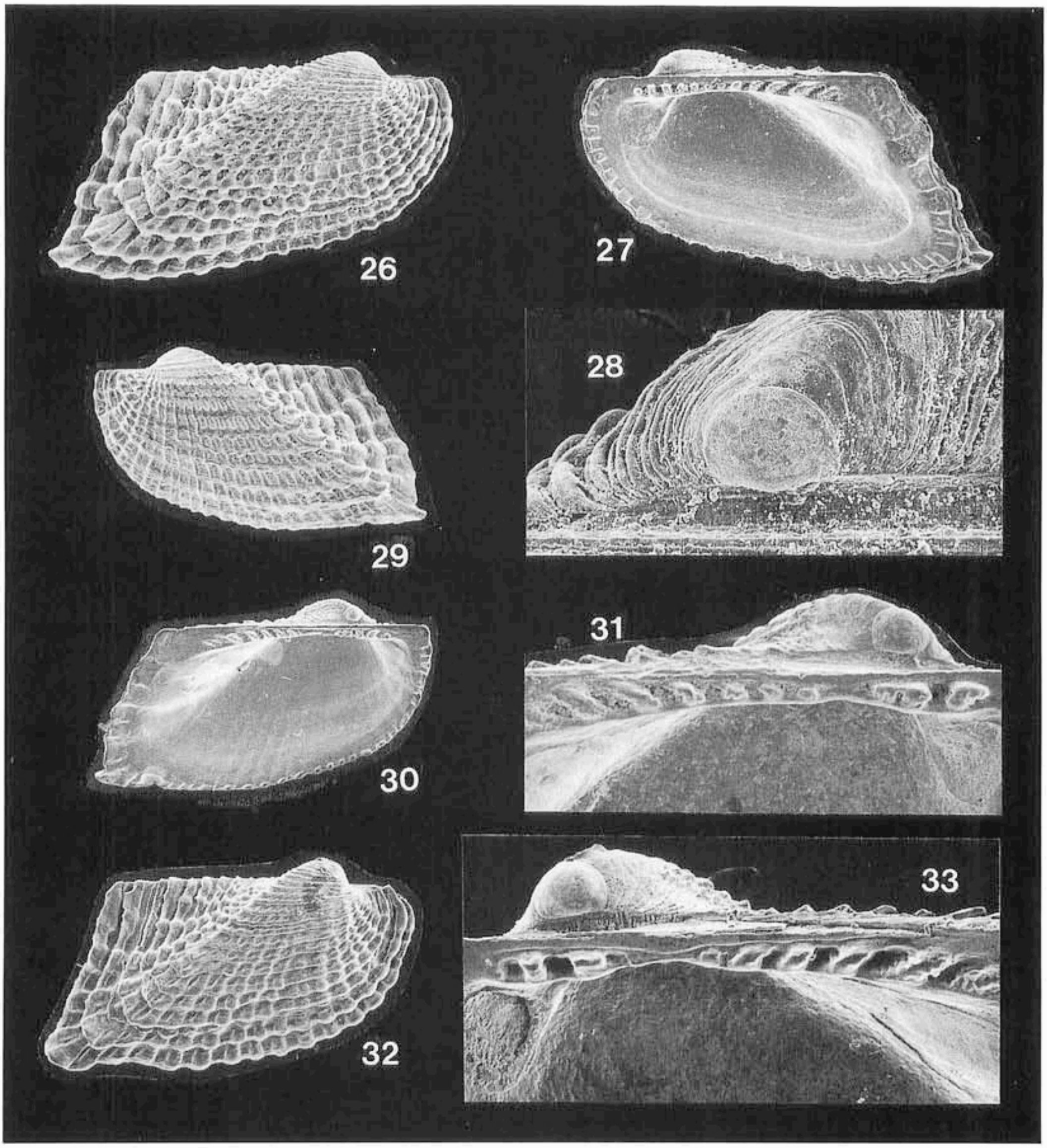
Acar sp. aff. ***A. plicata*** (Dillwyn)

Figures 26–33

1992. *Bentharca*? sp. A, Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Material. — RM19361 (dead) from "Devil's Palace", RM19362 (dead) from "Fool's Palace", RM19363 (dead) from "Witch's House", RM19576 (dead) from "Toriike", RM19364 (dead) from "Black Hole" of Shimoji Islet. RM19365 (dead) from "Shodokutsu" of Ie Islet. Living specimens have not been found.

Description. — Shell small, variable in outline but commonly subtrapezoidal, white and opaque, elongate transversely, about 1.7 times longer than high, comparatively thick, strongly carinated. Dorsal margin truncated obtusely by nearly straight posterior margin. Anterior part reduced. Ventral margin nearly straight, with indistinct byssal indentation. Umbo prosogyrous, incurved, situated about one-fifth of dorsal margin from the anterior end. Flank except for umbonal area reveals strongly cancellate sculpture, which consists of about 17 radial ribs and commarginal lamellae of subequal prominence, producing nodes at intersections and spinose projections on



Acar sp. aff. *A. plicata* (Dillwyn)
Figures 26–28: RV, RM19361a, 3.20 × 1.80 mm, from "Devil's Palace" [26: exterior, 27: interior, 28: dorsal view of umbonal area (× 100)]. Figures 29–30: LV, RM19361b, 4.15 × 2.40 mm, from "Devil's Palace" [29: exterior, 30: interior]. Figure 31: hinge area of RV, RM19365a, 2.20 × 1.30 mm, from "Shodokutsu" (× 40). Figures 32–33. RV, RM19365b, from "Shodokutsu" [32: exterior, 33: hinge area (× 50)].

posterior carina. Posterior area triangular and depressed, with four or five strong upward-curving ribs angularly abutting against posterior carina. Ventral and posterior margins strongly crenulated internally in accordance with external ribs, although crenulations are weakened in the antero-median part of ventral margin. Cardinal area moderate in breadth, with vertical striations and a vestige of alivincular ligament.

Dentition consists of 2–3 small prosoclinal anterior teeth and 6–7 short opisthoclinal posterior teeth. Two or three posteriormost teeth strongly crenulated. Hinge plate leaves wide edentulous areas near anterior and posterior ends. Pd I large, D-shaped, nearly smooth, ranging 170–196 μm in maximum diameter; Pd II not discriminated.

Remarks. — This species differs from other cave arcids in the thicker shell, well-developed cancellate sculpture, strong marginal crenulations. The outline and sharp posterior carina of these specimens more strongly resemble those of *Acar congenita* (Smith, 1885) than *Acar plicata* (Dillwyn, 1817). *A. congenita* has been recorded from deeper waters than *A. plicata*, but some authors regarded them as conspecific. Because *A. plicata* commonly occurs outside the caves of this region, the possibility of ecophenotypic effect is not necessarily ruled out for the cave specimens. Some specimens from "Shodokutsu" (e.g. Figure 32) reveal a narrower umbonal area in comparison with the specimens from the Shomoji caves, but the difference may be attributable to intraspecific variation.

The adult size of this species is still obscure, because somewhat larger specimens occur in the cave sediments of Bohol and Palau. We assume that the present specimens represent stunting populations of *Acar plicata* adapted to cavernicolous environments.

Distribution. — Common in several sublittoral caves of Ie and Shimoji Islets of Ryukyu Islands. According to our preliminary survey, this species also occurs in "Balicasag cave" off Panglao Islet of Bohol Island, the Philippines, and "Chandelier Cave" near Koror of Palau Islands.

Genus **Bentharca** Verrill and Bush, 1898

Bentharca tenuis sp. nov.

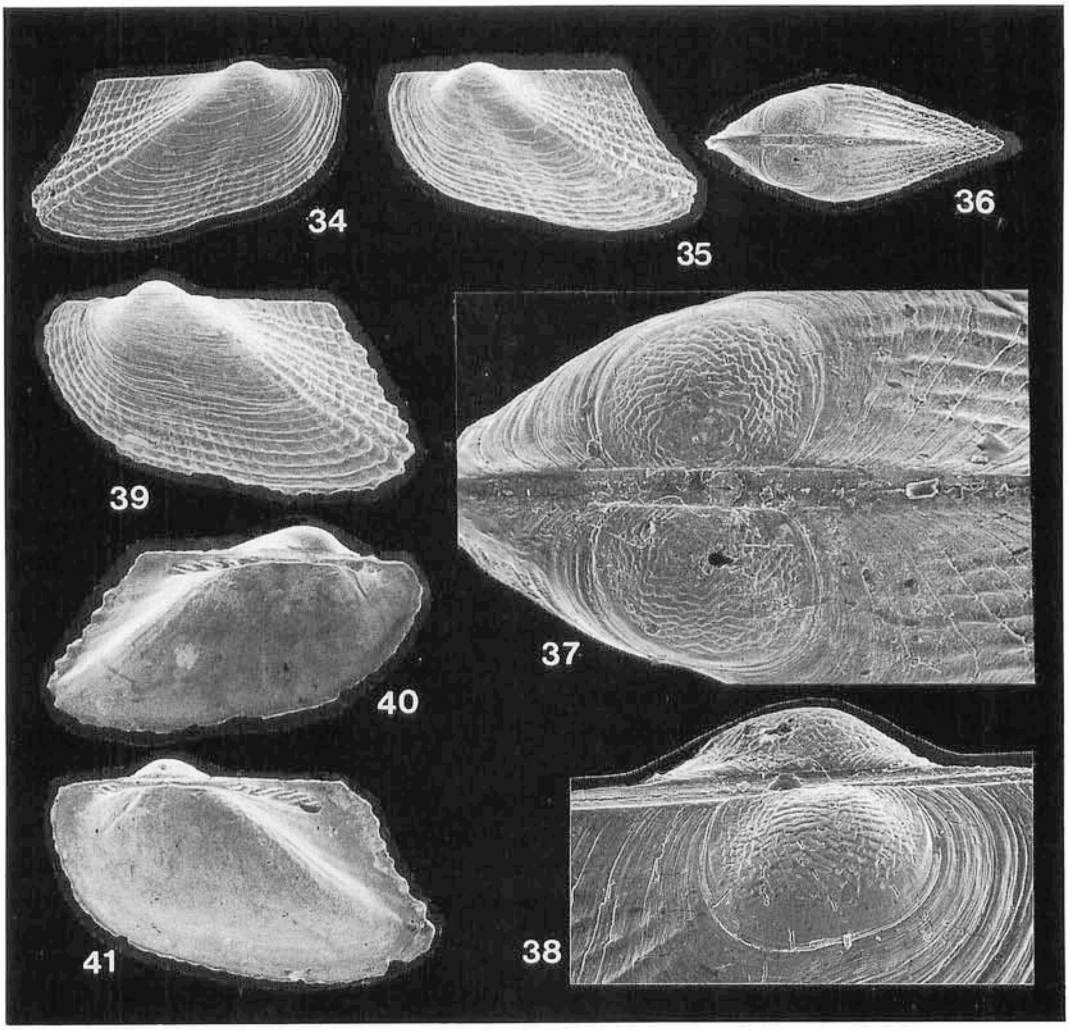
Figures 34–41

1992. *Bentharca* sp. B, Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Type and material. — Holotype: RM19374a, a living specimen from the bottom sediments of "Cross Hole" of Irabu Islet, Miyako Islands. Paratypes: RM19366 (dead) from "Devil's Palace", RM19367 (dead) from "Fool's Palace", RM19368 (dead) from "Witch's House", RM19578 (living) from "Wall Cave", RM19369 (dead) from "Toriike", RM19370 (dead) from "Black Hole", RM19577 (dead) from "Coral Hole" of Shimoji Islet. RM19371 (dead) from "Lunch Hole", RM19372 (living) from "W-arch", RM19373 (dead) from "L-arch", RM19374 (living) from "Cross Hole" of Irabu Islet. RM19375 (dead) from "Shodokutsu" and RM19567 (dead) from "Daidokutsu" of Ie Islet.

Diagnosis. — Very small, thin-shelled species of *Bentharca*, characterized by subtrapezoidal and roundly carinate outline, numerous radial ribs of variable prominence, shallow byssal indentation especially in early stage, relatively small number of hinge teeth, and large D-shaped Pd I with strong zig-zag ornament.

Description. — Shell scarcely exceeds 2.0 mm in length, thin, colorless and translucent, subtrapezoidal with not much reduced anterior part, about 1.7 times longer than high. Posterior margin slightly concave, forming an obtuse angle with dorsal. Ventral margin slightly concave in the middle part (especially distinct in early growth stage).



Bentharca tenuis sp. nov. ウスクマサカヤドリ (新称)
Figures 34–38: Holotype, living specimen, RM19374a, 1.45 × 0.85 mm, from "Cross Hole" [34: right view, 35: left view, 36: dorsal view, 37: dorsal view of umbonal area (× 100), 38: oblique view of umbonal area (× 100)]. Figures 39–40: LV, RM19375a, 1.85 × 1.05 mm, from "Shodokutsu" [39: exterior, 40: interior]. Figure 41: interior of RV, RM19375b, 1.90 × 1.10 mm, from "Shodokutsu".

Umbo nearly orthogyrous, incurved, situated about one-third of dorsal margin from anterior end. Flank broadly concave in the middle, with densely spaced commarginal lamellae and about 30 radial ribs of variable prominence, though early dissoconch is almost free of these sculptures. Posterior area depressed, with about seven prominent radial ribs. No marginal crenulations except for posterior periphery. Internal surface radially striated. Alivincular ligament persistent throughout growth. Cardinal area relatively narrow. Hinge plate only with about two prosoclinal anterior and three opisthoclinal posterior teeth. Pd I very large, D-shaped, with characteristic zigzag ornament, ranging 275–340 µm in maximum diameter; Pd II absent.

Remarks. — The present species attaches by byssus to the surface sediments, annelid tubes and cave walls. It differs from other cave arcids in the thinner shell, variably developed (generally weaker) radial ribs on the flank, and the huge and strongly ornamented Pd I. It resembles *Bentharca xenophoricola* Kuroda, 1930, from Japanese waters, especially the fossil specimens from the Shinzato Formation of Okinawa (Noda, 1980). However, the shell size is much smaller and the posterior carina is more prominent.

Distribution. — Common in many sublittoral caves of Ie and Shimoji-Irabu Islets of Ryukyu Islands. This species also occurs in "Balicasag cave" off Panglao Islet of Bohol Island, the Philippines.

Bentharca decorata sp. nov.

Figures 42–49

1992. *Bentharca* sp. C, Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.447, figs.1A, B, p.448, listed.

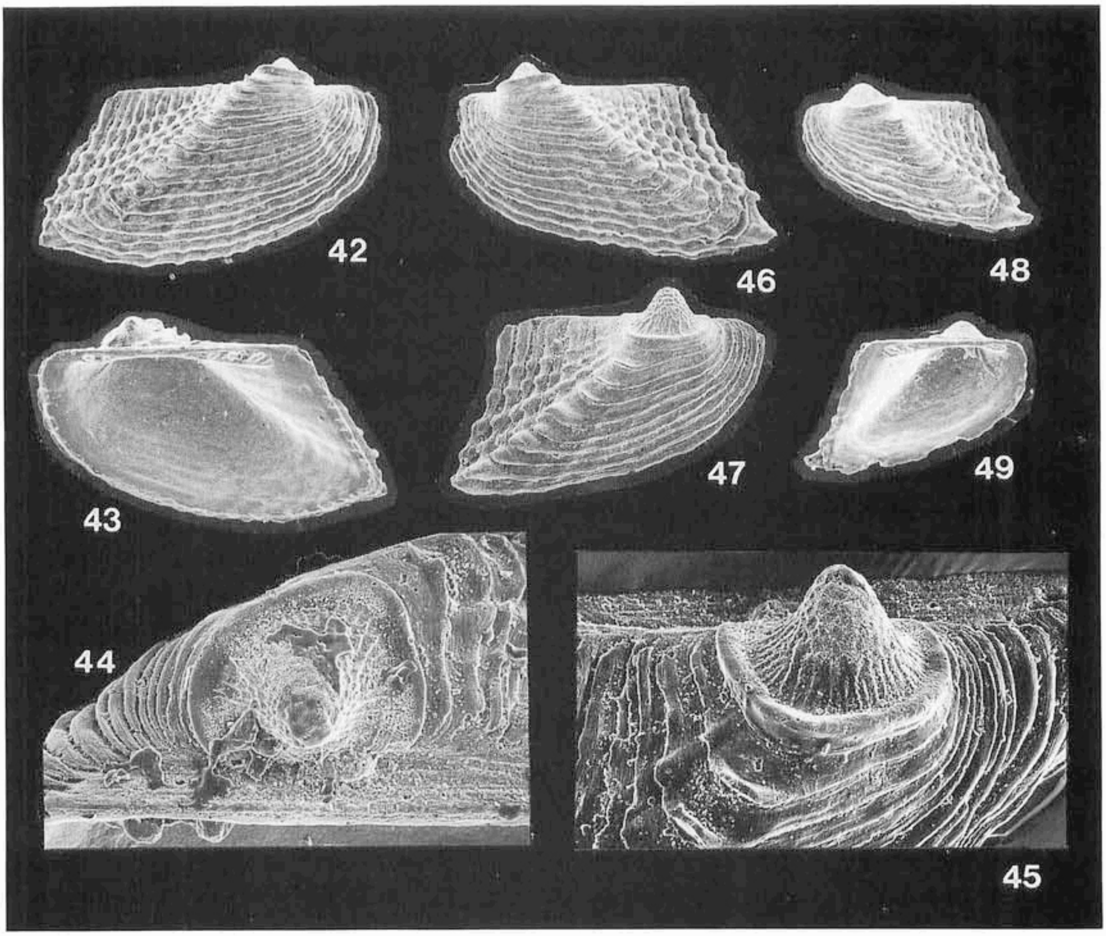
1993. *Bentharca* sp., Hayami and Kase, *Univ. Mus. Univ. Tokyo, News*, no.27, p.3, fig.2.

Type and material. — Holotype: RM19379a, a right valve from the bottom sediments of "Shodokutsu" of Ie Islet, Okinawa. Paratypes: RM19376 (dead) from "Witch's House", RM19377 (dead) from "Black Hole", RM19579 (dead) from "Coral Hole" of Shimoji Islet. RM19378 (dead) from "Lunch Hole" of Irabu Islet. RM19379 (dead) from the type locality. Living specimens have not been found.

Diagnosis. — Very small, thick, subtrapezoidal and sharply carinated species of *Bentharca*, characterized by very strong and regularly spaced commarginal lamellae, obscure radial ribs on flank, depressed posterior area, indistinct marginal crenulation and very large hat-shaped Pd I.

Description. — Shell never exceeds 1.8 mm in length, white and opaque, thick, subtrapezoidal, about 1.6 times longer than high, sharply carinated. Posterior margin a little concave, obliquely truncates dorsal margin and forms an acute angle with venter. Ventral margin broadly convex; byssal indentation indistinct. Umbo slightly prosogyrous, incurved, located about one-fourth of dorsal margin from anterior end. Flank not sulcated, covered with very conspicuous and subequally spaced commarginal lamellae and about 15 obscure radial ribs. Commarginal lamellae on flank more prominent than radial ribs, forming conspicuous scaly projections on the posterior carina. Posterior area depressed, marked with cancellate sculpture consisting of strong commarginal lamellae and about six radial ribs. Marginal crenulations indistinct except for several along posterior margin. Ligament area moderately wide. Dentition consists of two or three granular anterior teeth and three or four short opisthoclinal posterior teeth. Pd I extremely large, hat-shaped with a highly salient central boss and a broad and flattened brim, radially or diagonally sculptured, ranging 279–301 μm in maximum diameter; Pd II absent.

Remarks. — The present species is represented by numerous disarticulated valves from the bottom sediments of "Shodokutsu". It is easily distinguishable from other cave arcids by the presence of widely spaced strong commarginal lamellae and huge hat-shaped Pd I (Figures 44, 45). The prodissoconch feature suggests non-planktotrophic development and probably parental incubation of juveniles, but we have not yet succeeded in collecting living specimens.



Bentharca decorata sp. nov. カザリクマサカヤドリ (新称)
Figures 42–45: Holotype, RV, RM19379a, 1.60 × 1.00 mm, from "Shodokutsu" [42: exterior, 43: interior, 44: dorsal view of umbonal area (× 100), 45: oblique view of umbonal area (× 100)]. Figure 46: LV, RM19379b, 1.60 × 0.95 mm, from "Shodokutsu". Figure 47: immature RV, RM19379c, 1.00 × 0.60 mm, from "Shodokutsu". Figures 48–49: immature LV, RM19379d, 1.00 × 0.60 mm, from "Shodokutsu" [48: exterior, 49: interior].

Such an abnormal shape of Pd I was described and illustrated by Barnard (1964, p.372) in a specimen of "*Arca* (*Acar*) *plicata*" from the lower neritic bottom of Natal. *Arca* (*Acar*) *aghulhasensis* Thiele *in* Thiele and Jaeckel (1931) from Torres Strait, which was regarded by Barnard (1964) as synonymous with *A.* (*A.*) *plicata*, may also have abnormal Pd I, judging from the original line-drawing figure. *Arca* (*Acar*) *plicata* (Dillwyn, 1817) has been regarded as widely distributed in the Indo-West Pacific, but, so far as we are aware, no Japanese specimen of this species reveals such an abnormal prodissoconch. Furthermore, *A.* (*A.*) *plicata* differs from the present species in the much larger shell size, less reduced anterior part and more strikingly cancellate ornament on the flank.

Distribution. — Common in a sublittoral cave of Ie Islet, and rare in a few sublittoral caves of Shimoji Islet, Ryukyu Islands.

Bentharca irregularis sp. nov.

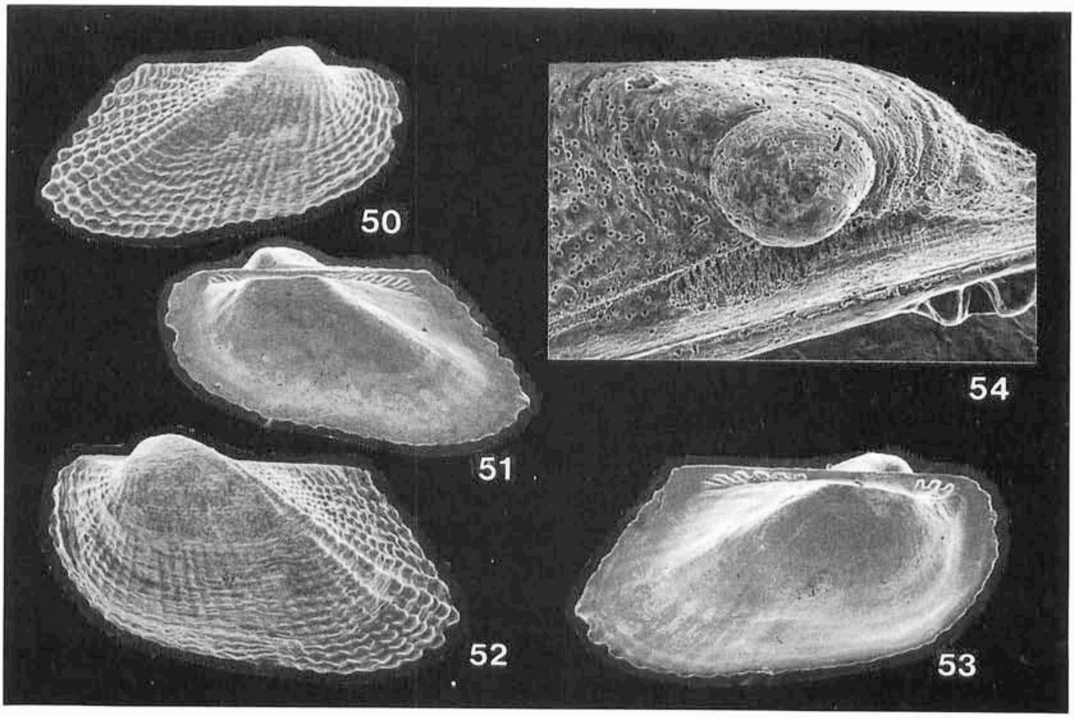
Figures 50–54

1992. *Bentharca* sp. D, Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Type and material. — Holotype: RM19382a, a right valve, from the bottom sediments of "Shodokutsu" of Ie Islet, Okinawa. Paratypes: RM19380 (dead) from "Witch's House", RM19381 (dead) from "Lunch Hole" of Shimoji-Irabu Islet. RM19382 (dead) from the type locality. Living specimens have not been found.

Diagnosis. — Small-sized, transversely elongated, weakly carinated species of *Bentharca*, characterized by not much reduced anterior part, weakly sulcated central part of flank, relatively weak commarginal lamellae, often bifurcated radial ribs, weak marginal crenulation, relatively small D-shaped Pd I, and distinct Pd II.

Description. — Shell rarely exceeds 3.0 mm in length, transversely elongated, roundly subtrapezoidal but somewhat irregular in outline, moderate in shell thickness, about 2.0 times longer than high. Posterior carina relatively weak and rounded; posterior area not much depressed. Posterior margin nearly straight, passing gradually into venter. Ventral margin commonly indented in the middle but sometimes nearly



Bentharca irregularis sp. nov.　ホソクマサカヤドリ (新称)
Figures 50–51: Holotype, RV, RM19382a, 2.10 × 1.20 mm, from "Shodokutsu" [50: exterior, 51: interior]. Figures 52–54: LV, RM19382b, 2.55 × 1.40 mm, from "Shodokutsu" [52: exterior, 53: interior, 54: dorsal of umbonal area (× 100)].

straight. Umbo large, orthogyrous, situated at one-fourth of dorsal margin from anterior end. Flank and posterior area with numerous, often bifurcated radial ribs and relatively weak commarginal lamellae, tuberculated at their intersections. Radial ribs commonly weakened in the middle part of the flank. Marginal crenulation indistinct. Ligament area moderate in breadth, vertically striated. Dentition consists of two or three small anterior and five or more short opisthoclinal posterior teeth. Pd I D-shaped, ranging 101–151 μm in maximum diameter; Pd II clearly demarcated, veliconch (Pd I + Pd II) ranging 174–269 μm in maximum diameter.

Remarks. — The present species is probably closely related to *Bentharca tenuis* sp. nov. in view of the outline, surface sculpture and hinge structure, but the umbo is larger, the radial ribs are more strongly tuberculated and the Pd I is much smaller. It is easily distinguishable from other cave arcids by the weaker posterior carina, the not much reduced anterior part, weaker commarginal lamellae and clearly demarcated Pd II (Figure 54). In the outline the present species is also somewhat similar to *Bentharca xenophoricola* (Kuroda), but differs from that species in its much smaller size, strongly tuberculated radial ribs and not much reduced anterior part. Because of the presence of well-developed Pd II suggesting planktotrophic development and the ignorance of ultimate shell size, it is not convincing that the present species is really indigenous to cavernicolous environment.

Distribution. — Common in a sublittoral cave of Ie Islet, and rare in a few sublittoral caves of Shimoji and Irabu Islets, Ryukyu Islands.

Bentharca excavata sp. nov.

Figures 55–64

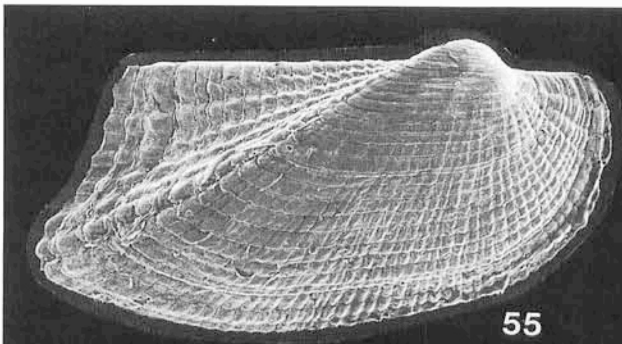
1992. *Bentharca* sp. E, Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Type and material. — Holotype: RM19390a, a living specimen, from the bottom sediments of "Cross Hole" of Irabu Islet, Miyako Islands. Paratypes: RM19383 (dead) from "Devil's Palace", RM19384 (dead) from "Fool's Palace", RM19385 (dead) from "Witch's House", RM19582 (living) from "Wall Cave", RM19580 (living) from "Toriike", RM19386 (dead) from "Black Hole", RM19581 (dead) from "Coral Hole" of Shimoji Islet. RM19387 (dead) from "Lunch Hole", RM19388 (living) from "W-arch", RM19389 (dead) from "L-arch", RM19390 (living) from "Cross Hole" of Irabu Islet. RM19391 (living) from "Shodokutsu" of Ie Islet.

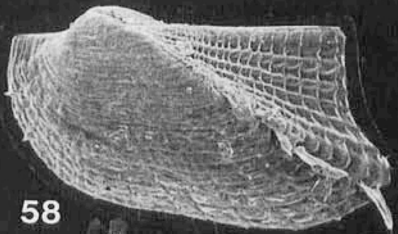
Diagnosis. — Small species of *Bentharca*, characterized by reddish shell, rounded carina, excavated posterior area with frequently auriculate postero-dorsal end and deeply concave posterior margin, finely cancellate sculpture on flank, and weakly rimmed Pd I.

Bentharca excavata sp. nov. ベニクマサカヤドリ（新称）

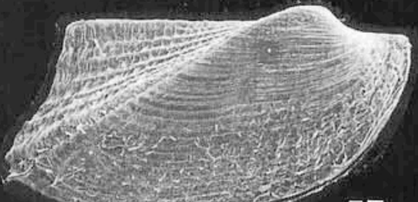
Figures 55–56: RV, RM19383a, 3.40 × 1.90 mm, from "Devil's Palace" [55: exterior, 56: interior]. Figure 57: living specimen, RM19390b, 2.30 × 1.35 mm, from "Cross Hole". Figures 58–61: Holotype, living specimen, RM19390a, 2.20 × 1.25 mm, from "Cross Hole" [58: left view, 59: dorsal view, 60: oblique view of umbonal area, showing alivincular ligament (× 100), 61: dorsal view showing incipient duplivincular ligament (× 100)]. Figures 62–64: LV, RM19383b, 2.60 × 1.35 mm, from "Devil's Palace" [62: exterior, 63: interior, 64: oblique view of umbonal area (× 100)].



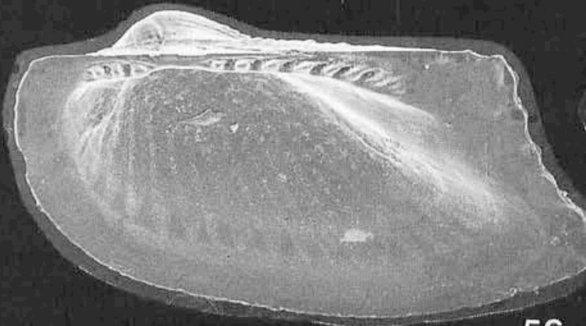
55



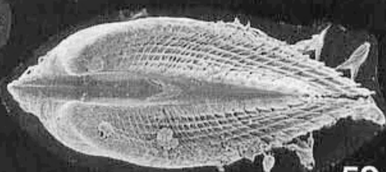
58



57

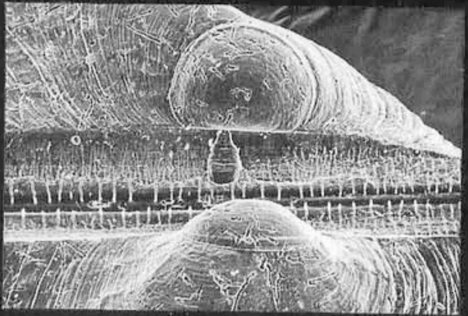


56



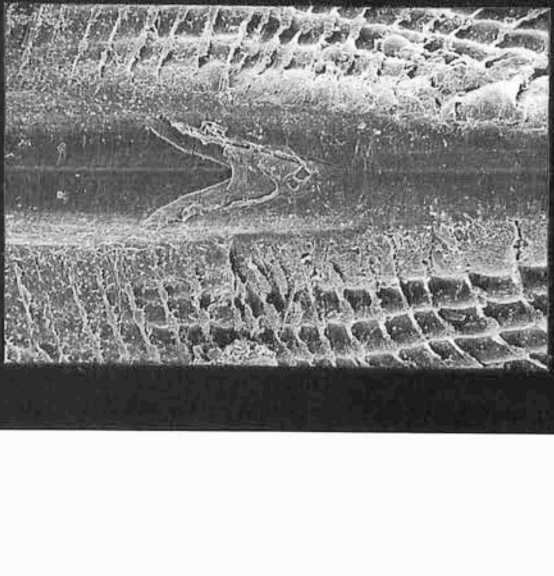
59

64

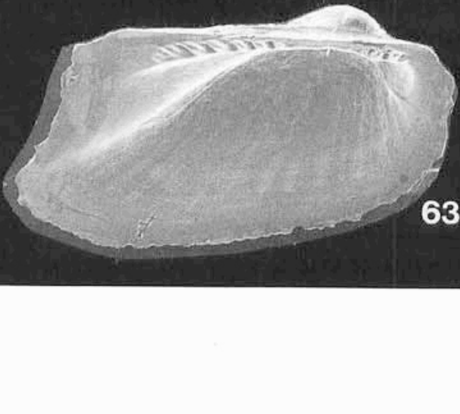


60

61



62



63

Description. — Shell scarcely exceeds 4.0 mm in length, scarlet or reddish brown in color, subtrapezoidal, about 1.8 times longer than high, moderately inflated. Posterior area delimited by rounded carina, remarkably excavated and often auriculated. Posterior margin deeply concave, almost rectangularly meeting dorsal margin. Ventral margin slightly concave in the middle or nearly straight. Umbo prosogyrous, incurved, located about one-fifth of dorsal margin from anterior end. Flank and posterior area similarly marked with cancellate sculpture consisting of fine commarginal lamellae and numerous radial ribs. No distinct marginal crenulations except in posterior area. Internal surface striated radially. Cardinal area moderate in breadth, vertically striated; alivincular ligament persistent throughout growth, while duplivincular ligament is only incipiently developed. Anterior teeth granular, about three in number; posterior teeth about seven, relatively strong and transversely crenulated. A wide edentulous area present in posterior portion of hinge plate. Pd I normal in shape, nearly smooth but with slightly elevated rim, ranging 173–183 μm in maximum diameter; Pd II not discriminated.

Remarks. — The present species was found alive on both the sediment surface and cave walls. It is characterized and readily distinguishable from other cave arcids by the deeply excavated and often auriculated posterior area, reddish coloration and finely cancellated surface. The persistent primary fibrous ligament and incipient duplivincular ligament are well observed in the holotype specimen (Figures 59–61). Not only the external but also the internal surface of living specimens is scarlet or reddish brown. The coloration seems to remain long in dead specimens.

Bentharca rubrotincta Kuroda and Habe, 1958, in Habe (1958: 252) reveals similarly cancellate sculpture and reddish coloration of shell, but its posterior part is not so deeply excavated. Although the illustration of that species first appeared in Habe (1961b, pl.49, fig.6), the lectotype has not been designated. The shell of *B. rubrotincta* commonly exceeds 8mm in length and is much larger than that of the present species (or any other species of *Bentharca* described here).

Distribution. — Common in many sublittoral caves of Ie, Shimoji and Irabu Islets of the Ryukyu Islands.

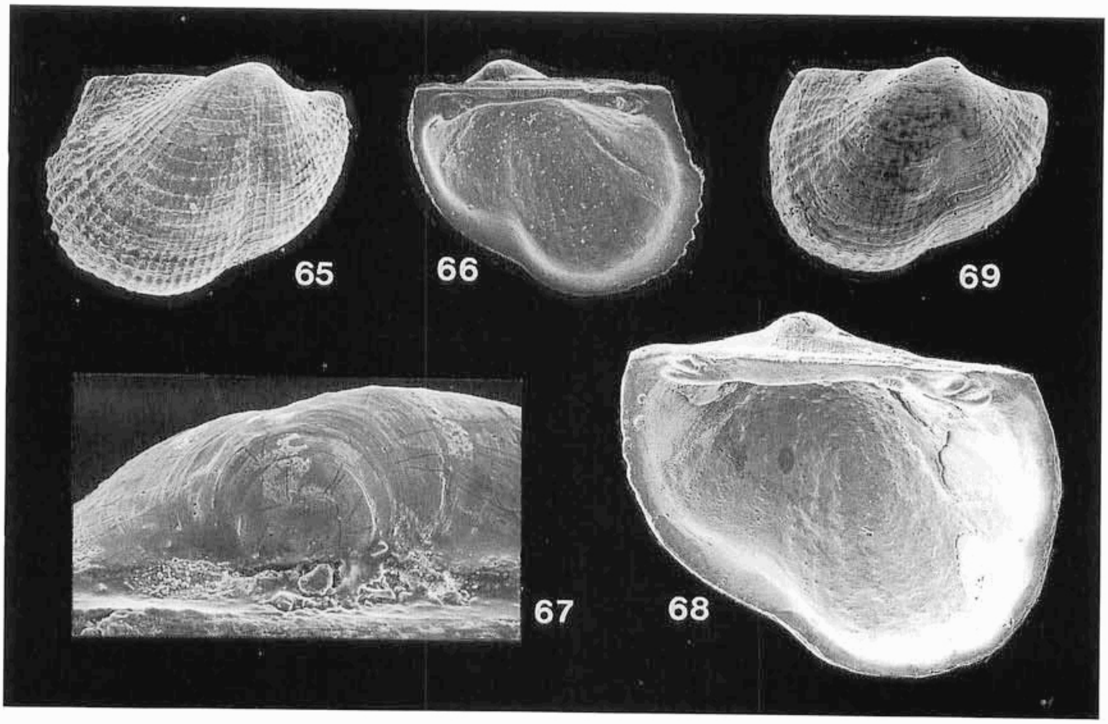
Genus ***Bathyarca*** Kobelt, 1891

Bathyarca sp. indet.

Figures 65–69

The present species is represented only by a few dead specimens (RM19392) from the bottom sediments of "Fool's Palace" of Shimoji Islet, Miyako Islands. It clearly differs from the above described species of *Bentharca* and may belong to *Bathyarca*, which has been known as another deep-water arcid genus.

The shell is smaller than 2 mm in length, not carinate, relatively short, and characterized by much reduced anterior part, distinct byssal indentation, undeveloped marginal crenulations, only two or three short anterior and posterior teeth, numerous vertical striations on the middle part of hinge plate, and radially sculptured surface without developed commarginal lamellae. Pd I is D-shaped and about 135μm in maximum diameter; prodissoconch II is not clearly marked.



Bathyarca sp. indet.
Figures 65–67: RV, RM19392a, 1.75 × 1.40 mm, from "Fool's Palace" [65: exterior, 66: interior, 67: dorsal view of umbonal area (× 150)]. Figures 68–69. RV, RM19392b, 1.70 × 1.35 mm, from "Fool's Palace" [68: interior, 69: exterior].

The outline and hinge teeth of the present species somewhat resemble those of *Bathyarca pectunculoides* (Scacchi, 1834), the type species of this genus, from wide areas of the Atlantic (Oliver and Allen, 1980), but the shell is much smaller, the anterior part more reduced, and the byssal notch more deeply indented. *Bathyarca kyurokusimana* Nomura and Hatai, 1940, from the lower sublittoral and bathyal bottom of central-south Japan (Habe, 1958), differs from the present species in its more semicircular outline and shorter dorsal margin.

The present species is probably closely related to *Bathyarca perversidens* Hedley, 1902, from the lower sublittoral bottom of New South Wales. Though the present specimens show smaller shell size, less elongated anterior and posterior teeth and less developed marginal crenulations than Hedley's illustrated specimens, further comparison with immature stages of the Australian species seems to be necessary.

Superfamily **Limopsoidea** Dall, 1895

Family **Philobryidae** Bernard, 1897

Philobryids consist of small-sized paedomorphic prionodonts which have been known from waters of various depth mainly in the southern hemisphere (Cotton and

Godfrey, 1938; Powell, 1958; Nicol, 1966; Cox et al., 1969; Tevesz, 1977; Dell, 1990; etc.). In the northwest Pacific (except Hawaii) there is no formally described species of this family, but Kaneko (1984, 1991) preliminarily illustrated a few unnamed species from beach and dredged sands at several localities in south Japan, which he regarded as belonging to *Cosa* and *Cratis*.

Philobryids are often dominant in the cave bivalve fauna, exhibiting great species diversity. Thanks to Kaneko's personal communications (August 12 and 30, 1991) replying to our inquiry, the relation between his species and the present cave species became clearer. Dell (personal communication, March 25, 1993) also gave us very useful comments about the relation between these cave species and southern Pacific and Hawaiian philobryids.

This family in general is an interesting group from the viewpoint of evolutionary biology. Many species are of diminutive size and retain numerous denticles of provinculum until the latest growth stage, indicating significant paedomorphosis. In a comprehensive systematic study of the Philobryidae, Tevesz (1977) regarded philobryids as derived from the limopsids and as constituting a neotenous group. Morton (1978) also regarded the ligament of *Philobrya* as having evolved neotenously from some ancestors of the Limopsidae. Considering the significant reduction of adult size, however, the evolutionary change, if real, may be better called paedomorphosis by progenesis (instead of neoteny) in accordance with Gould's (1977) and McKinney and McNamara's (1991) definitions.

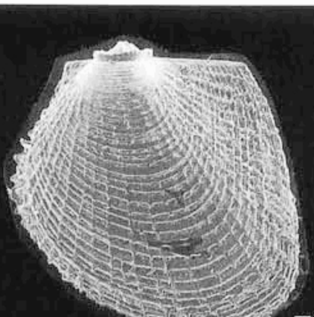
Prezant (1990) studied the ontogeny of an Antarctic brooding philobryid, *Lissarca notorcadensis* Melvill and Standen, 1907, in detail. He described that species as having very small Pd I and large Pd II, which were regarded as atypical features for a brooding bivalve. However, the Pd I is generally very large in this family (commonly exceeding 200 μm in diameter), indicating large size and relatively small numbers of eggs. Moreover, many species of this family are characterized by hat-shaped Pd I, which, we presume, indicates parental incubation of juveniles. In an individual of *Cosa waikikia* from the cave "Devil's Palace", several hat-shaped juveniles have been found *in situ* within the valves (Figures 79, 80). Although many philobryids have been known in exposed environments, this family may have been able to adapt easily to such an oligotrophic cavernicolous environment owing to its intrinsically stunted and progenetic properties.

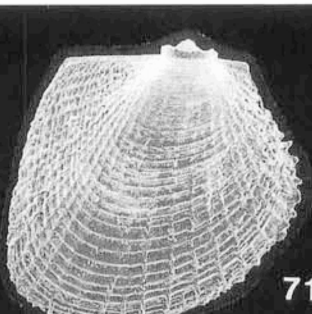
Genus **Cosa** Finlay, 1927

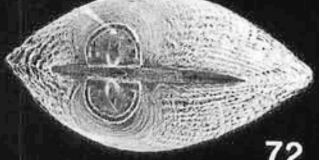
Four philobryids from submarine caves are regarded as belonging to *Cosa* in view of the persistent denticles of provinculum, undeveloped prionodont teeth and small tri-

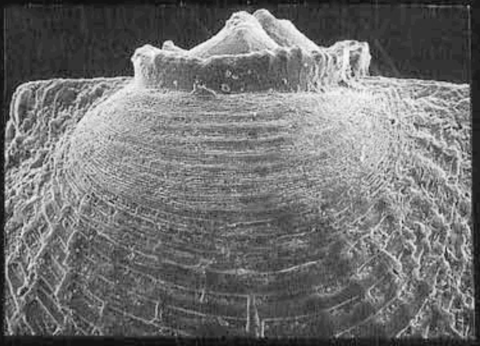
---

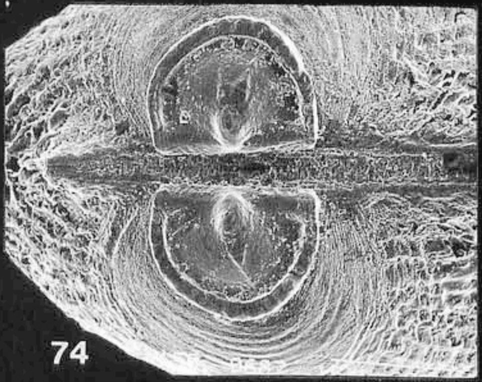
Cosa waikikia (Dall, Bartsch and Rehder) シラスナガイモドキ (新称)
Figures 70–74: living specimen, RM19393a, 1.40 × 1.45 mm, from "Devil's Palace" [70: left view, 71: right view, 72: dorsal view, 73: umbonal area (× 100), 74: dorsal view of umbonal area (× 80)]. Figures 75–76: RV, RM19393b, 1.65 × 1.70 mm, from "Devil's Palace" [75: interior, 76: hinge area (× 50)]. Figures 77–78: LV, RM19393c, 1.60 × 1.55 mm, from "Devil's Palace" [77: interior, 78: hinge area (× 50)].

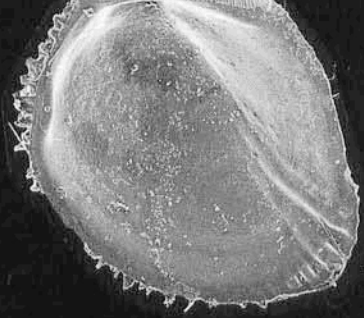

70

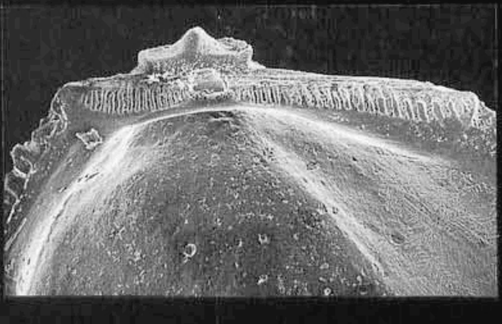

71


72

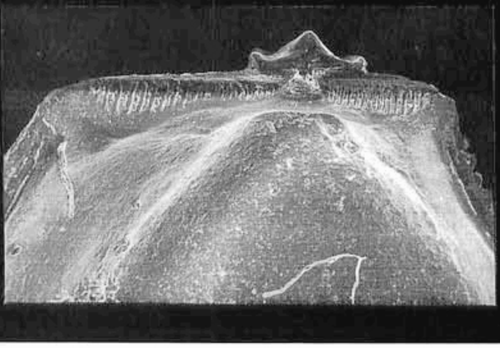

73


74


75


76


77


78

angular (not much elongated) ligament pit interrupting the denticles of provinculum. The outline, surface sculpture, position of umbo and shape of Pd I, however, are different between the species. In shell outline and surface features some species resemble *Philobrya* species, but the ligament pit is acline or only a little prosocline, and never obliquely elongated.

Several species of *Cosa* were described from New Zealand and Australia, as listed by Powell (1955, 1958) and Laseron (1953). Because of the diminutive shell size, diagnostic characters of some early proposed species are often difficult to recognize from their original descriptions and accompanying line-drawings. Though more exhaustive study on this genus is needed, we here regard these cavenicolous species except for *Cosa waikikia* as distinct from those Oceanic species.

Cosa waikikia (Dall, Bartsch and Rehder)

Figures 70–83

1938. *Limopsis waikikia* Dall, Bartsch and Rehder, *Bernice P. Bishop Mus., Bull.*, 153, p.42, text-fig.13, pl.7, fig.1.

1979. *Limposis waikikia*: Kay, *Hawaiian Marine Shells*, sec.4, p.505, figs.160A, B.

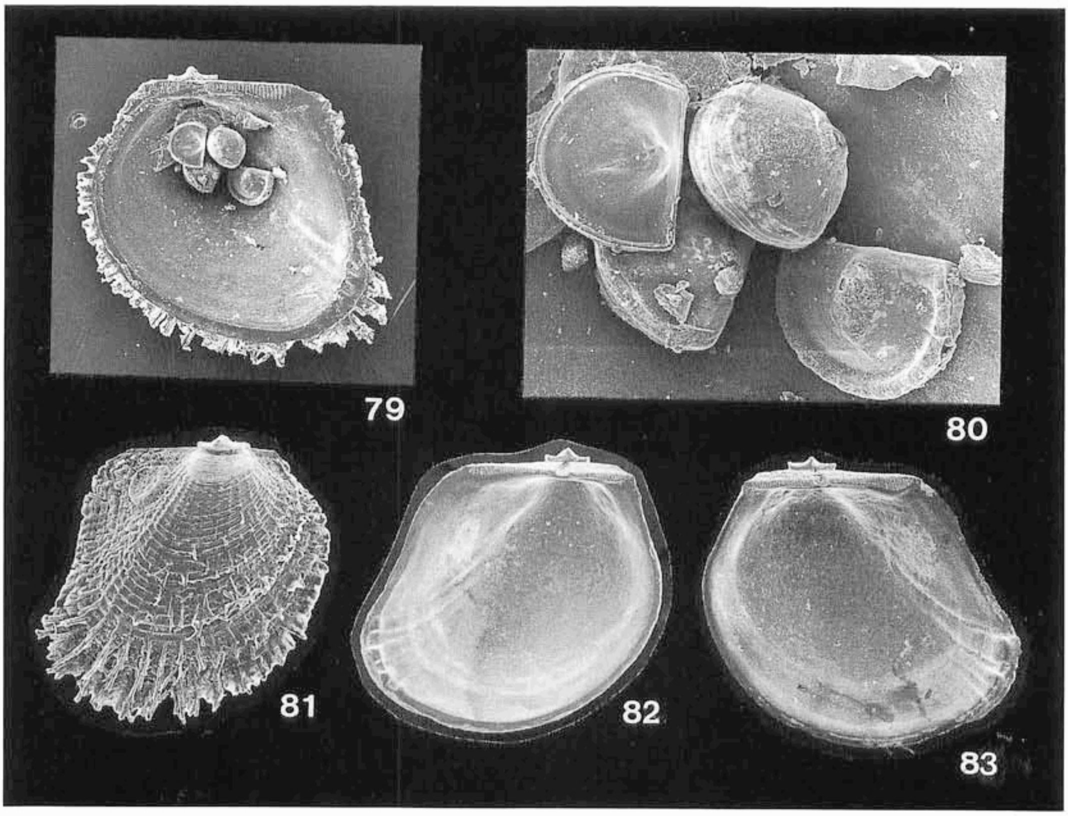
1992. *Cosa* sp. A, Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.447, figs.1C, D, p.448, listed.

1993. *Cosa* sp., Hayami and Kase, *Univ. Mus. Univ. Tokyo, News*, no.27, p.3, fig.3.

Material. — RM19393 (living) from "Devil's Palace", RM19394 (living) from "Fool's Palace", RM19395 (living) from "Witch's House", RM19584 (living) from "Wall Cave", RM19396 (living) from "Toriike", RM19397 (living) from "Black Hole", RM19583 (living) from "Coral Hole" of Shimoji Islet. RM19398 (living) from "Lunch Hole", RM19399 (living) from "W-arch", RM19400 (living) from "L-arch", RM19401 (living) from "Cross Hole" of Irabu Islet. RM19402 (living) from "Shodokutsu" of Ie Islet. The holotype of this species (USNM no.484219) was dredged off Waikiki, Oahu at 25-50 fathoms.

Description. — Shell small, rarely exceeding 2.0 mm in length and height, light tannish (rarely reddish) in color, roundly trapezoidal, not much elongated, weakly carinate, strongly inflated. Dorsal margin considerably long; anterior margin nearly straight or a little concave, indicating a byssal indentation; posterior margin passes gradually into venter. Umbo orthogyrous, located about one-third of dorsal margin from anterior end. Surface has cancellate ornaments consisting of wide-spaced commarginal lamellae and about 35 weak radial ribs. Periostracum brownish, hairy, well developed on radial ribs. Marginal crenulations absent except for a few near the distal end of posterior carina. Ligament pit triangular, only slightly prosoclinal. Provinculum persistent until the latest growth stage, consisting of about 16 anterior and about 25 posterior subvertical denticles. Adult teeth undeveloped. Pd I large, ranging 243–308 μm in maximum diameter, hat-shaped with pointed central boss and highly elevated and subvertically truncated brim margin. Pd II absent, though the early part of dissoconch is free from radial ribs and marked with densely spaced commarginal lamellae.

Remarks. — The present species is the most ubiquitous and dominant philobryid in the examined caves; numerous individuals were found alive on the sediment surface, polychaete tubes and surfaces of rock fragments, walls and ceilings. It is easily distin-



Cosa waikikia (Dall, Bartsch and Rehder)　シラスナガイモドキ (新称)
Figures 79–80: living specimen, RM19393d, 1.45 × 1.50 mm, from "Devil's Palace" [79: interior of RV with incubated juveniles, 80: incubated juveniles (× 100)]. Figure 81: right view of living specimen, RM19394a, 1.70 × 1.70 mm, from "Fool's Palace". Figure 82: interior of LV, RM19394b, 1.85 × 1.85 mm, from "Fool's Palace". Figure 83: interior of RV, RM19394c, 2.00 × 1.85 mm, from "Fool's Palace".

guishable from other cave species of *Cosa* by the cancellate ornaments, more posteriorly located umbo and finely frilled and steep brim margin of Pd I.

In every shell character including the size, surface sculpture, periostracum, hinge and prodissoconch, the present specimens are taxonomically indistinguishable from the holotype of *Limopsis waikikia* Dall, Bartsch and Rehder, 1938, from off Waikiki of Oahu Island, which is surely referable to *Cosa*. According to Dell (personal communication, March 25, 1993), the original material of *Hochstetteria pacifica* Thiele *in* Thiele and Jaeckel (1931) from Samoa, unlike the original line drawing, is, if not identical with, very similar to the Hawaiian species. At present, we regard *Cosa waikikia* as widely distributed in the tropical-subtropical seas of the western Pacific.

It also resembles an unnamed species, "*Cosa* sp. II", recorded by Kaneko (1991, p.158, fig. II) from Okinawa in the trapezoidal shell form, non-terminal umbo, cancellate ornaments and many other characters, but the margin of Pd I is less rounded in the present species.

This is evidently a brooding species. Several pre-released embryos, which are identical in shape and size to the Pd I, were actually found in the valves of living specimens (Figures 79, 80). The present materials exhibit a wide range of morphologic variation. A few specimens are tinged with reddish color. The samples from "Fool's Palace" and "Wall Cave" often bear many individuals having thicker periostracum and remarkably concave posterior margin (Figures 81–83). Their taxonomic distinction, however, seems to be difficult because the morphologic difference is gradational.

Distribution. — This species has been known from Hawaii, Samoa (?), south Japan. In the Ryukyu Islands, it occurs abundantly in many sublittoral caves of Shimoji, Irabu and Ie Islets. Two left valves which were collected by Mr. Hideharu Tomari from the beach sands at Fukuma, Fukuoka Prefecture, north Kyushu, and now preserved in the National Science Museum (Tokyo), are also indistinguishable from the present species.

Cosa kinjoi sp. nov.

Figures 84–92

1992. *Cosa* sp. B, Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

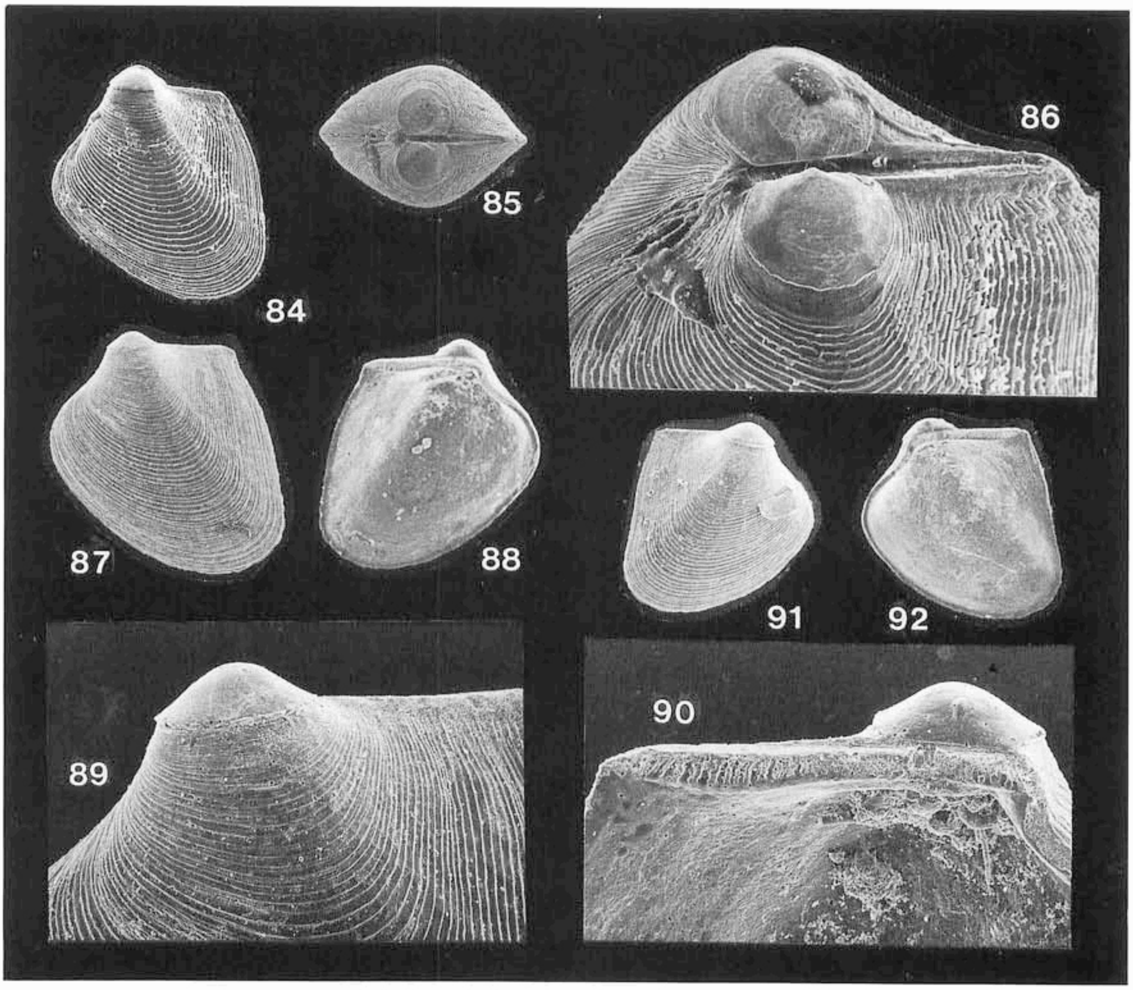
Type and material. — Holotype: RM19586a, living specimen, from the cave wall of "Coral Hole" of Shimoji Islet, Miyako Islands. Paratypes: RM19404 (dead) from "Witch's House", RM19585 (dead) from "Toriike", RM19405 (dead) from "Black Hole", RM19586 (living) from "Coral Hole" of Shimoji Islet. RM19406 (dead) from "W-arch", RM19407 (dead) from "L-arch", RM19408 (dead) from "Cross Hole" of Irabu Islet. RM19409 (living) from "Shodokutsu", RM19568 (dead) from "Daidokutsu" of Ie Islet.

Diagnosis. — Very small-sized, wedge-like trapezoidal species of *Cosa*, characterized by thin periostracum, projected anterior part of shell, fine but sharp commarginal lamellae, generally undeveloped radial ribs, entire inner margin, and anteriorly located, large and D-shaped Pd I.

Description. — Shell very small, scarcely exceeding 1.2 mm in length and height, wedge-like trapezoidal in outline, expanded anteriorly and postero-ventrally, roundly carinate. Periostracum thin, not hairy. Dorsal margin moderate in length; anterior margin short, deeply concave; posterior margin nearly straight. Umbo slightly prosogyrous, located anteriorly. Surface commonly marked only with dense but sharp commarginal lamellae, although sometimes (especially in samples from Shimoji Islet) several obscure radial ribs are developed. No marginal crenulations. Ligament pit small, subquadrate, slightly prosocline, located about one-fourth of dorsal margin from anterior end. Provinculum persistent until the latest growth stage, consisting of about 8 anterior and about 23 posterior subvertical denticles. Adult teeth absent. Pd I large, smooth, ranging 235–263 μm, D-shaped with no marginal brim, but having a small tubercular boss near dorsal margin. Pd II absent.

Remarks. — In many caves the present species is represented by empty shells, but in "Coral Hole" of Shimoji Islet and "Shodokutsu" of Ie Islet some individuals have been found alive mainly on the cave walls. Unlike *Cosa waikikia*, the periostracum is rather thin and not hairy.

Such normally shaped (not hat-shaped) Pd I may be unfamiliar in the genus *Cosa*,



Cosa kinjoi sp. nov. キンジョウシラスナガイモドキ (新称)
Figures 84–86: Holotype, living specimen, RM19586a, 0.85 × 0.95 mm, from "Coral Hole" [84: left view, 85: upper view, 86: oblique view of umbonal area (× 100)]. Figures 87–90: LV, RM19404a, 1.00 × 1.00 mm, from "Witch's House" [87: exterior, 88: interior, 89: hinge area (× 100), 90: umbonal area (× 100)]. Figures 91–92. RV, RM19404b, 0.75 × 0.80 mm, from "Witch's House" [91: exterior, 91: interior].

though there is a small central boss near the dorsal margin (Figures 86, 88). We think that the size and shape of prodissoconch is generally stable in a population but considerably plastic in one and the same genus. Fine and sharp commarginal striae and an obliquely expanded wedge-shaped outline also characterize the present species. Most specimens from the type locality are free from radial ribs, whereas the samples from the caves of Shimoji Islet exhibit a wide range of variation in the development of radial sculpture.

The species name is dedicated to Mr. S. Kinjo, the chief of Ie SCUBA Diving Service, who kindly provided us various facilities during our field work.

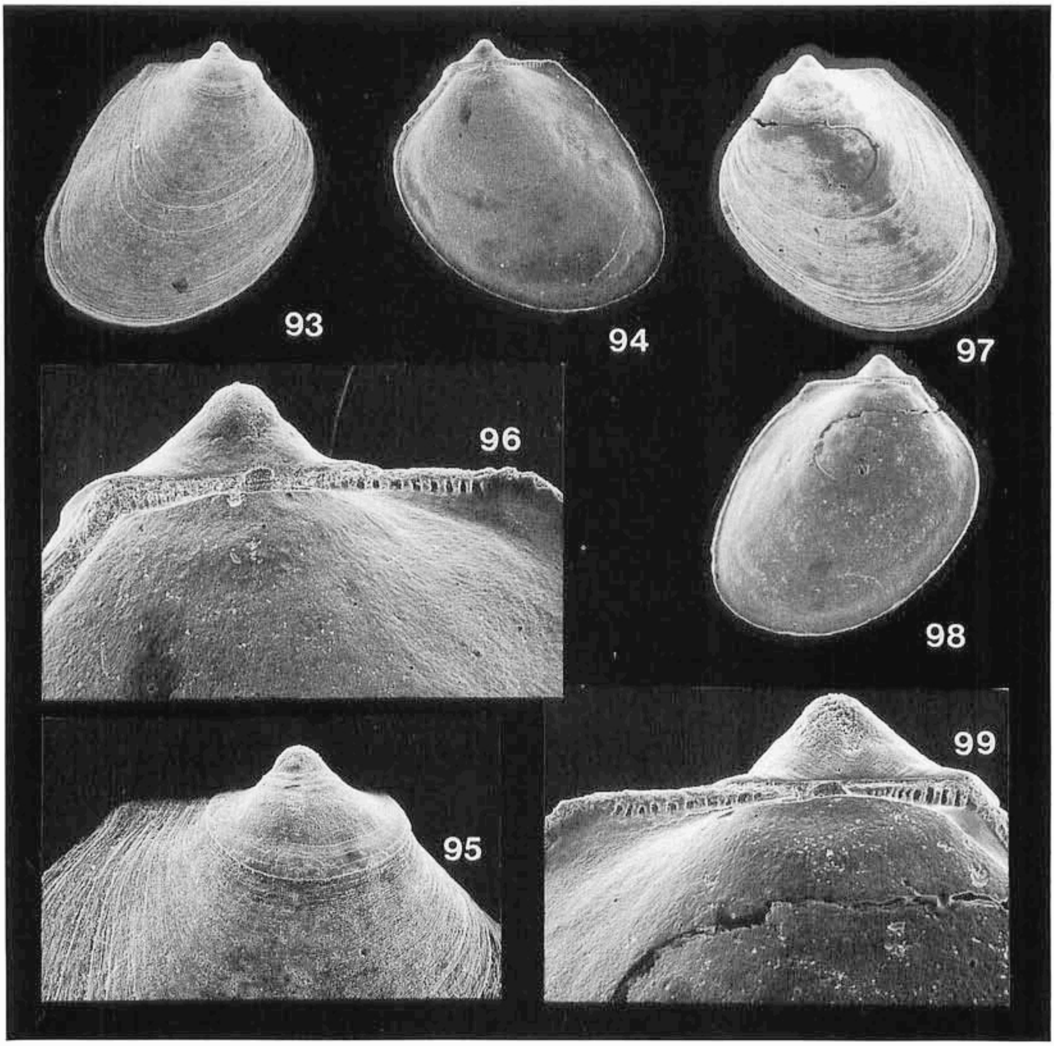
Distribution. — Common in several sublittoral caves of Ie, Shimoji and Irabu Islets, Ryukyu Islands. According to our preliminary survey, this species also occurs in "Balicasag cave" off Panglao Islet of Bohol Island, the Philippines, and "Chandelier cave" near Koror, Palau Islands.

Cosa uchimae sp. nov.

Figures 93–99

1992. *Cosa* sp. C, Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Type and material. — Holotype: RM19410a, a right valve from the bottom sedi-



Cosa uchimae sp. nov. ウチマシラスナガイモドキ (新称)
Figures 93–96: Holotype, RV, RM19410a, 0.85 × 0.90 mm, from "Shodokutsu" [93: exterior, 94: interior, 95: umbonal area (× 100), 96: hinge area (× 160)]. Figures 97–99: LV, RM19410b, 0.85 × 0.85 mm, from "Shodokutsu" [97: exterior, 98: interior, 99: hinge area (× 160)].

ments of "Shodokutsu" of Ie Islet, Okinawa. Paratypes: RM19410 from the same locality. No living specimen has been found.

Diagnosis. — Very small-sized, subovate species of *Cosa* characterized by short dorsal margin, absence of radial ribs, weak commarginal lamellae, entire inner margin, relatively short denticles of provinculum, and large hat-shaped Pd I which has a wide smooth brim.

Description. — Shell very small, scarcely exceeding 1.0 mm in length and height, subovate rather than quadrate, not carinate, with relatively weak convexity. Dorsal margin unusually short; anterior margin slightly concave; posterior and ventral margins hardly discriminated from each other. Umbo orthogyrous, situated anteriorly. Surface marked only with weak commarginal lamellae. Neither radial ribs nor marginal crenulations. Ligament pit triangular, acline, located about one-third of dorsal margin from anterior end. Denticles of provinculum persist until the latest growth stage but comparatively short; anterior and posterior series consist of about 11 and 13 denticles, respectively. Adult teeth do not appear. Pd I large, ranging 197–228 μm in maximum diameter, hat-shaped with round-topped central boss, gentle foot and non-frilled brim margin; Pd II absent.

Remarks. — The present species can be discriminated from other cave philobryids by its smaller adult size, shorter dorsal margin, subovate outline, absence of radial ornament, and weak commarginal lamellae, and the gentle foot of volcano-like Pd I. It shares undeveloped radial ribs with *Cosa kinjoi*, sp. nov., but is easily distinguishable from that species by the weaker shell convexity, shorter dorsal margin, undeveloped commarginal lamellae, shorter denticles of provinculum and hat-shaped Pd I.

The species name is dedicated to Miss M. Uchima, who kindly assisted us in our field work at Ie Islet in various ways.

Distribution. — Common in a sublittoral cave of Ie Islet, Ryukyu Islands. The present species has not been found in any cave of Miyako Islands.

Cosa sp. indet.

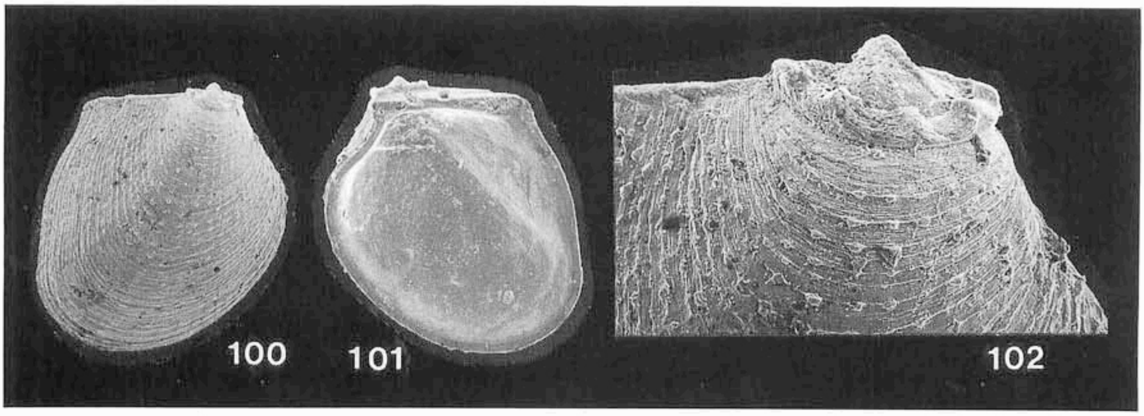
Figures 100–102

1991. *Cosa* (s. l.) sp. 1. Kaneko, 1991, *Venus*, vol.50, p.158, fig.I.

This species is represented by only a few empty valves from the bottom sediments of "Devil's Palace" (RM19413) and "Lunch Hole" (RM19414) of Shimoji-Irabu Islet, Miyako Islands.

In shape and size of shell it closely resembles *Cosa waikikia* from the same locality, but is distinguishable from that species in the more anteriorly located umbo, more prosoclinal ligament pit, entire valve margin, finely beaded radial ribs and coarsely frilled brim margin of Pd I. Unlike in other species of *Cosa* from Ryukyu Islands, the Pd I is slightly inclined forward, and its dorsal margin is considerably discordant with that of the adult shell (Figure 102).

On the other hand, all the observed features of this species are identical with those of an unnamed species, "*Cosa* (s. l.) sp. I", by Kaneko (1991, p.158, fig.I) from dredged sands of Okinawa Islands. These specimens as well as well as Kaneko's probably represent a new species, but the material at hand is still insufficient to propose a new name. It is also not clear whether this philobryid is an indigenous cryptic species or not.



Cosa sp. indet.
Figures 100–102: RV, RM19413a, 1.30 × 1.35 mm, from "Devil's Palace" [100: exterior, 101: interior, 102: umbonal area (× 100)].

Distribution. — The present species is, though rare, known in Okinawa and Miyako Islands. According to our preliminary observation, it occurs abundantly in "Balicasag Cave" off Panglao Islet of Bohol Island, the Philippines.

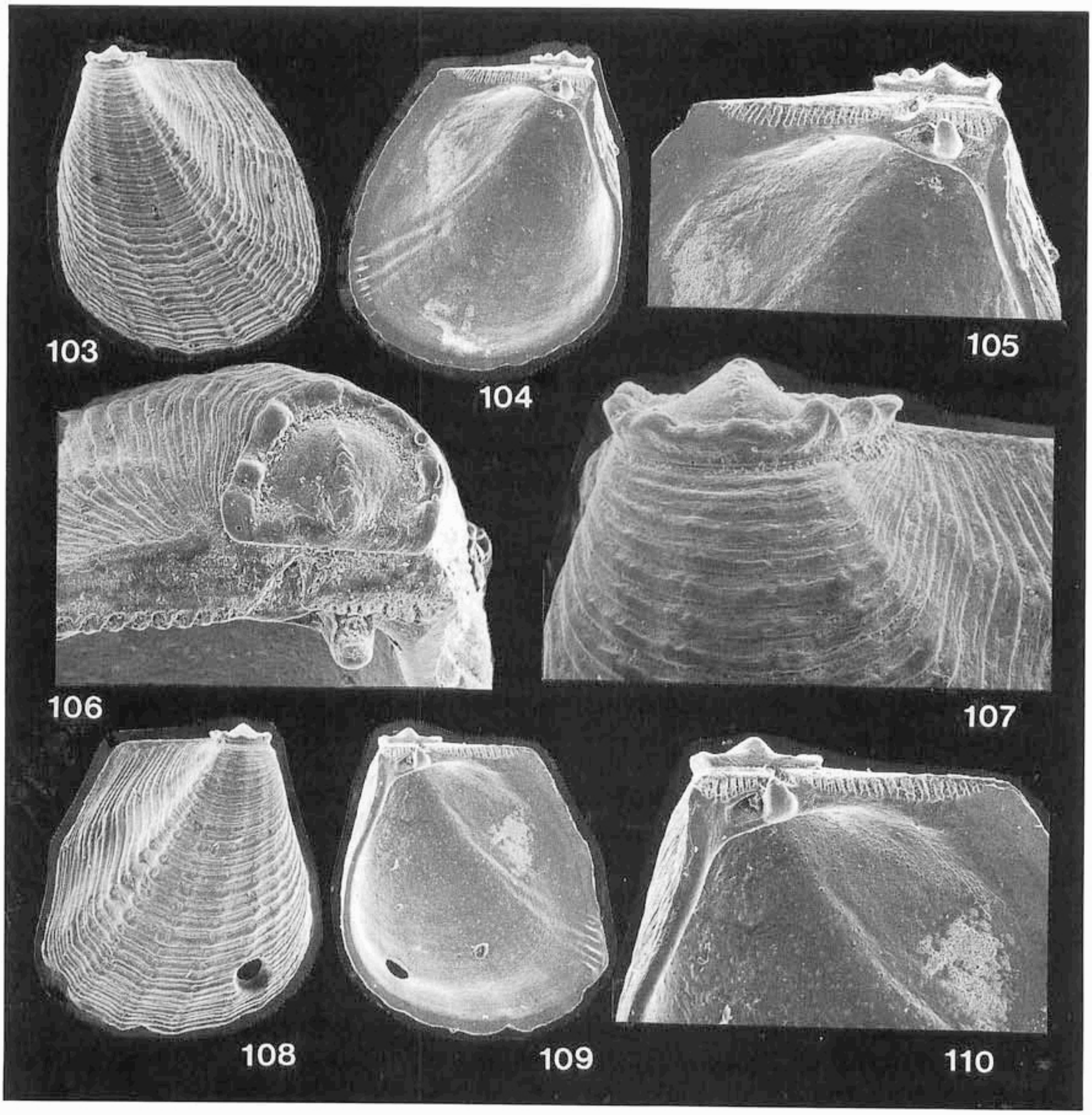
Genus **Cratis** Hedley, 1915

The genus *Cratis* has been represented by several lower sublittoral to bathyal species from Australia and New Zealand. Taxonomically, it has generally been treated as a group of the Philobryidae. Unlike *Cosa* and *Philobrya*, however, paedomorphic features are not very significant in *Cratis*; the denticles of provinculum are often restrictedly observed along the dorsal margin of Pd I, and a few anterior and posterior adult teeth occur on the hinge plate. As has been pointed out by Tevesz (1977) and some others, its similarity to some limopsids cannot be denied. For example, the genus *Nipponolimopsis* Habe, 1951 (type-species: *Limopsis nipponica* Yokoyama, 1922 = *Cyrilla decussata* A. Adams, 1862) is, as noted by Habe (1977a), similar to *Cratis* in shell shape, surface ornamentation and hinge teeth. *Limopsis dautzenbergi* Prashad, 1932, from the Celebes Sea, may also be a member of *Nipponolimopsis*. The only marked differences between *Cratis* and *Nipponolimopsis* are the shell size and the size and shape of Pd I. Yet, as clarified by Tanabe (1990), an undoubted limopsid, *Limopsis* (*Limopsis*) *azumana* Yokoyama, 1910, from the Pleistocene of central Japan is non-planktotrophic, because it is characterized by large Pd I (ranging 400–450 μm) and absence of Pd II. The features of Pd I, as interpreted by Matsui (1991), may be plastic in accordance with reproductive strategy. These lines of evidence indicate that *Cratis* is an intermediate genus between the Philobryidae and the Limopsidae.

Cratis kanekoi sp. nov.

Figures 103–110

1984. *Cosa* sp., Kaneko, Explanation of 11th special exhibition, Osaka City Museum of Natural History, p.23, pl.8, figs.6–7 (clearly illustrated but with no verbal description).



Cratis kanekoi sp. nov. カネコシラスナガイモドキ(新称)
Figures 103–107: Holotype, LV, RM19411a, 1.30 × 1.55 mm, from "Devil's Palace" [103: exterior, 104: interior, 105: hinge area (× 50), 106: umbonal area (× 125), 107: dorsal view of umbonal area (× 100)]. Figures 108–110: RV, RM19412a, 1.40 × 1.60 mm, from "Cross Hole" [108: exterior, 109: interior, 110: hinge area (× 50)].

1991. Philobryidae gen. and sp. III, Kaneko, *Venus*, vol. 50, p. 158, fig. III.

Type and material. — Holotype RM19411a, a left valve, from the bottom sediments of "Devil's Palace" of Shimoji Islet, Miyako Islands. Paratypes: RM19411 (dead) from the type locality, RM19412 (dead) from "Cross Hole" of Shimoji-Irabu Islet. No living specimens have been found.

Diagnosis. — Small-sized, tall, thick and polygonal species of *Cosa*, characterized by about eight beaded radial ribs, marginal crenulations restricted to postero-ventral portion, prosoclinal ligament pit, development of an adult tooth in anterior hinge plate in each valve, and hat-shaped Pd I with elevated and coarsely frilled brim margin.

Description. — Shell small, scarcely exceeding 1.7 mm in height, about 1.3 times as high as long, weakly carinated. Test considerably thick. Dorsal margin relatively short; anterior margin nearly straight; posterior and ventral margins polygonally angulate in accordance with external radial ribs. Umbo orthogyrous, located anteriorly. Surface ornamented with regular commarginal lamellae and about eight strong and beaded radial ribs; each interval of radials broadly concave. Marginal crenulations absent except for a few at postero-ventral portion. Ligament pit small, triangular, considerably prosoclinal, located about one-fourth of dorsal margin from anterior end. Provinculum persistent until the latest stage, consisting of about 8 anterior and about 15 posterior subvertical denticles. Adult hinge plate more or less developed in front of ligament pit, commonly producing a large tubercular adult tooth and a socket in each valve. Pd I large, hat-shaped, about 250 µm in maximum diameter, characterized by low conical central boss and thickly elevated and coarsely frilled brim margin.

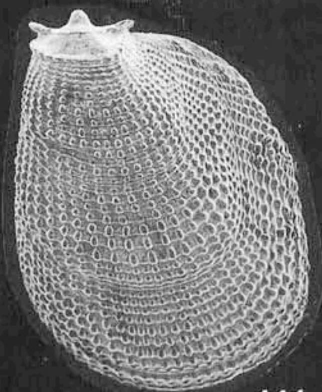
Remarks. — The present species is well characterized by a few widely spaced and beaded radial ribs, polygonal valve margin and the appearance of an adult tooth on the anterior hinge plate. A large socket is present behind the tooth in LV (Figure 105) and in front of the tooth in RV (Figure 110). Though the surface sculpture is similar to that of some species of *Cosa*, the presence of a large adult tooth in each valve indicates that the present species is better placed in the genus *Cratis*.

The present species is firmly identical with *Cosa* sp. by Kaneko (1984) and from Philobryidae gen. and sp. III from dredging sands at Nakagusuku-son, Okinawa. Hence the new species name. In view of the polygonal outline and strong radial ornaments, this species may be somewhat similar to *Hochstetteria costata* Bernard, 1896, the type species of *Cosa*, from Stewart Island, New Zealand. However, it differs from that species in its developed anterior adult teeth, less prosoclinal shell and much larger antero-dorsal angle. It may be closer to *Cosa serratocostata serratocostata* Powell, 1933, and *Cosa serratocostata dispar* Powell, 1937, from New Zealand, but differs from them in the fewer radial ribs and shorter dorsal margin. *Philobrya tatei* Hedley, 1901, from New South Wales, shows similar outline and hinge structure, but the radial ribs on the posterior area are finer and more numerous than those of the present species.

Distribution. — Rare in a few sublittoral cave of Shimoji and Irabu Islets, Ryukyu Islands. Kaneko (1984) recorded this species from the dredged sands from the sea

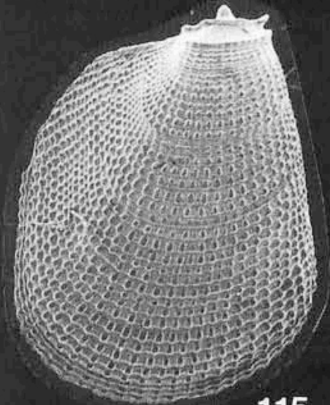
---

Cratis ohashii sp. nov. オオハシシラスナガイモドキ (新称)
Figures 111–114: Holotype, LV, RM19416a, 1.65 × 2.10 mm, from "Shodokutsu" [111: exterior, 112: interior, 113: umbonal area (× 85), 114: hinge area (× 50)]. Figure 115: RV, RM19416b, 2.10 × 2.60 mm, from "Shodokutsu". Figures 116–117: RV, RM19416c, 1.50 × 2.05 mm, from "Shodokutsu" [116: exterior, 117: hinge area (× 50)]. Figures 118–120: immature RV, RM19416d, 0.95 × 1.20 mm, from "Shodokutsu" [118: exterior, 119: interior, 120: umbonal area (× 85)].

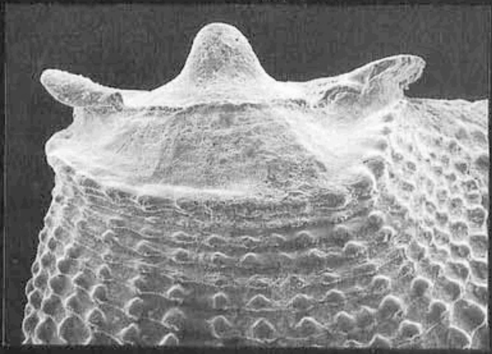


111

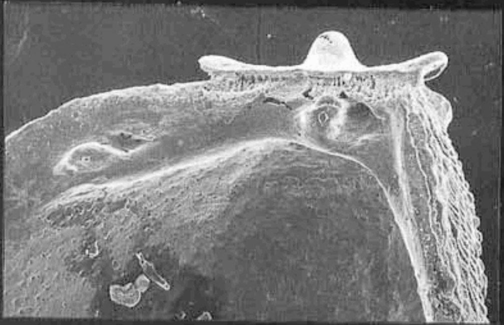
112



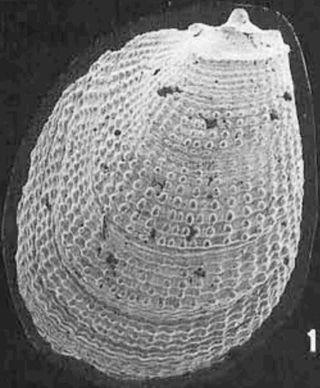
115



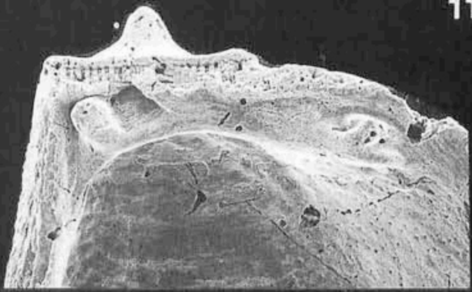
113



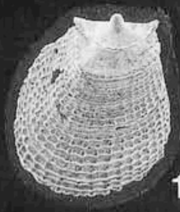
114



116

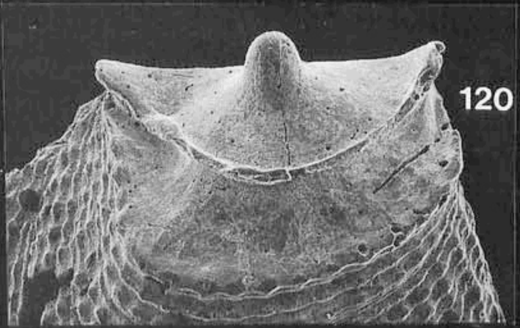


117



118

119



120

bottom of the Pacific coast of southern Okinawa. According to Dell (personal communication, March 25, 1993), the same species occurs in a number of areas in the southwestern Pacific. Therefore, it is unlikely that the habitat of the present species is restricted to cryptic environments.

Cratis ohashii sp. nov.

Figures 111–120

Compare 1991. Philobryidae sp. IV, Kaneko, *Venus*, vol.50, p.158, fig.IV.
1992. *Cratis* sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.
1993. *Cratis* sp., Hayami and Kase, *Univ. Mus. Univ. Tokyo, News*, no.27, p.3, fig.4.

Type and material. — Holotype: RM19416a, a left valve, from the bottom sediments of "Shodokutsu" of Ie Islet, Okinawa. Paratypes: RM19415 (dead) from "Fool's Palace" of Shimoji Islet, RM19416 (dead) from the type locality. No living specimens have been found.

Diagnosis. — Small-sized and subquadrate species of *Cratis*, characterized by incurved anterior margin, remarkably cancellate and beaded surface, one large anterior adult tooth and huge hat-shaped Pd I with mammilla-like central boss and flared brim margin.

Description. — Shell commonly smaller than 2.8 mm in height, roundly subquadrate, obscurely carinate, solid and strongly inflated. Ratio of height/length evidently increases with growth; about 1.0–1.2 in juvenile stage but larger than 1.3 in adult stage. Anterior peripheral area incurved, with nearly straight or slightly concave margin; posterior and ventral margins obscurely discriminated from each other. Umbo orthogyrous, located subcentrally in early growth stage but about one-fourth of dorsal margin from anterior end in adult. Surface marked with remarkably cancellate ornamentation consisting of regular commarginal lamellae and about 40 radial ribs, with numerous fine beads at their intersections. Inner margin weakly crenulated in accordance with radial ribs. Ligament pit triangular, slightly prosocline. Denticles of provinculum clearly observable along the dorsal margin of Pd I even in adult individual, but undeveloped along the hinge-line of dissoconch. Adult hinge teeth developed in later growth stages, commonly consisting of one subvertical anterior tooth and one or two opisthoclinal posterior teeth in each valve. Pd I extremely large, ranging 514–596 μm in maximum diameter, hat-shaped with mammilla-like central boss and widely flared subtriangular brim margin. Earliest part of dissoconch free from radials and marked only with faint commarginal lamellae.

Remarks. — This species is not much different from *Cratis progressa* Hedley, 1915, the type-species of this genus, from 100 fathoms off Port Macquarie, New South Wales. In view of the redescription by Tevesz (1977), however, the present species differs from the Australian species in its smaller size, less rounded (more quadrate) outline, incurved and concave anterior margin and more prominent posterior carina. In these respects it may be more closely related to *Cratis retiaria* Powell, 1937, from New Zealand, but the radial ribs are fewer and probably more strongly beaded in the present species.

According to Kaneko's personal communication (August 12, 1991), this species is possibly conspecific with his (1991) "Philobryidae sp. IV" from off Cape Shionomisaki (100 m deep) of Kii Peninsula, because the features of Pd I and dissoconch are very similar.

The species name is dedicated to Mr. S. Ohashi, a skilled professional diver, who cooperated in our field work in Okinawa and Miyako Islands and gave us invaluable information about cave organisms and submarine topography.

Distribution. — Common in a sublittoral cave of Ie Islet, Ryukyu Islands. The present species has been very rarely found from the caves of Shimoji Islet. Several specimens resembling the juveniles of this species have been found from the sediments near Gyuchaku-iwa, Kumomi, Izu Peninsula, Shizuoka Prefecture, central Honshu.

Limopsoidea? gen. and sp. indet.

Figures 121–128

This species is represented by a number of dead specimens from the bottom sediments of the submarine caves, namely, "Witch's House" (RM19417), "Wall Cave" (RM19587), "Toriike" (RM19418) of Shimoji Islet, "W-arch" (RM19419) and "Cross Hole" (RM19420) of Irabu Islet, Miyako Islands, and "Shodokutsu" (RM19421) of Ie Islet, Okinawa.

It has a minute translucent shell (smaller than 1.2 mm in length) revealing *Musculus*-like mytiliform outline with broadly concave antero-ventral margin, but seems to belong to the superfamily Limopsoidea instead of the Mytiloidea, because of the non-nacreous shell, the development of one or two tubercular prionodont teeth on the anterior and posterior parts of the hinge plate, and a subcentrally placed low-triangular ligament pit below the umbo. Unlike the species of *Musculus*, the anterior part of shell is not ornamented by radiating threads. It is also characterized by persistent denticles of provinculum, entire inner margin, several weak radial ribs on the posterior surface, and large, oblong and pockmarked Pd I ranging 200–230 μm in maximum diameter.

So far as we are aware, no comparable species has been described. It is likely that the present species represents an unnamed genus, but its taxonomic position is still obscure.

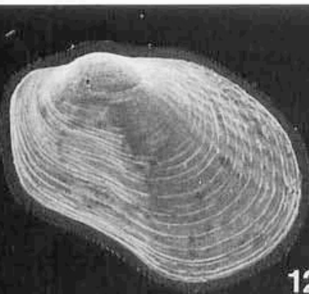
This species is common in many submarine caves of the Ryukyu Islands (Ie, Shimoji and Irabu Islets). According to our preliminary observation, it also occurs commonly in "Chandelier Cave" of Palau Islands, and "Balicasag Cave" off Panglao Islet of Bohol Island, the Philippines.

Order **Mytiloida** Férussac, 1822
Superfamily **Mytiloidea** Rafinesque, 1815
Family **Mytilidae** Rafinesque, 1815
Subfamily **Mytilinae** Rafinesque, 1815
Genus ***Brachidontes*** Swainson, 1840

Brachidontes sp. indet.

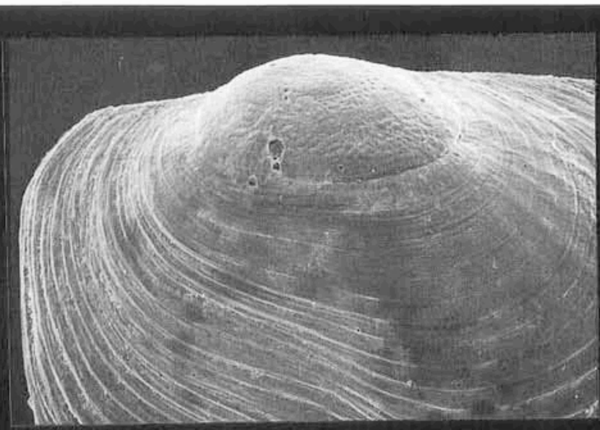
Figures 129–133

1992. *Brachidontes* sp. Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.


121

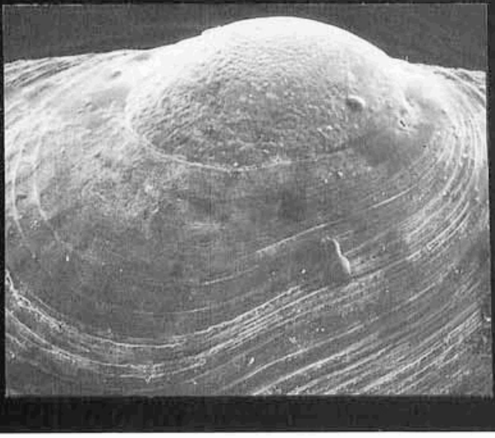

122

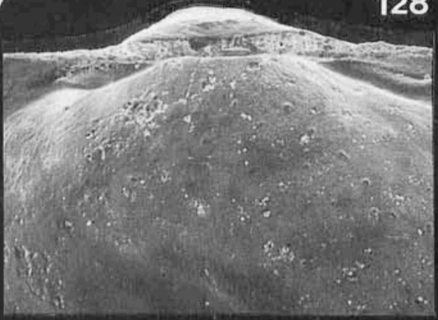

123


124

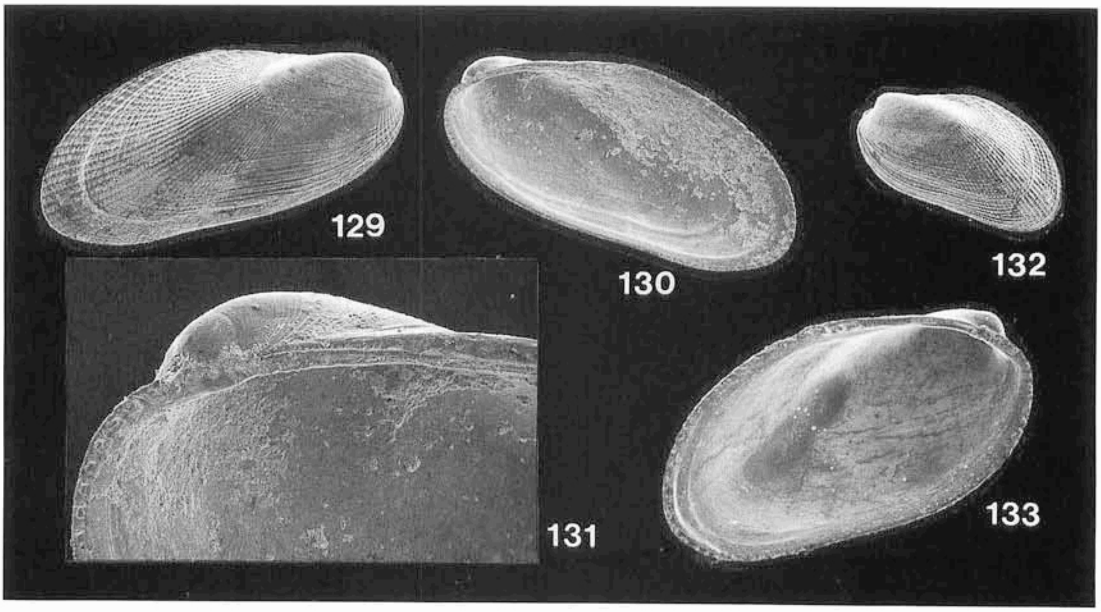

125


126


127


128

Limopsoidea? gen. et sp. indet.
Figures 121–124: LV, RM19418a, 0.90 × 0.65 mm, from "Toriike" [121: exterior, 122: interior, 123: hinge area (× 125), 124: umbonal area (× 125)]. Figures 125–128: RV, RM19418b, 0.95 × 0.75 mm, from "Toriike" [125: exterior, 126: interior, 127: umbonal area (× 125), 128: hinge area (× 125)].



Brachidontes sp. indet.
Figures 129–131: RV, RM19425a, 4.40 × 2.65 mm, from "Shodokutsu" [129: exterior, 130: interior, 131: hinge area (× 40)]. Figures 132–133: LV, RM19425b, 2.20 × 1.45 mm, from "Shodokutsu" [132: exterior, 133: interior].

This species is now represented by several empty valves from the bottom sediments of "Fool's Palace" (RM19422), "Coral Hole" (RM19588) of Shimoji Islet, "L-arch" (RM19423) and "Cross Hole" (RM19424) of Irabu Islet, Miyako Islands and "Shodokutsu" (RM19425) of Ie Islet, Okinawa.

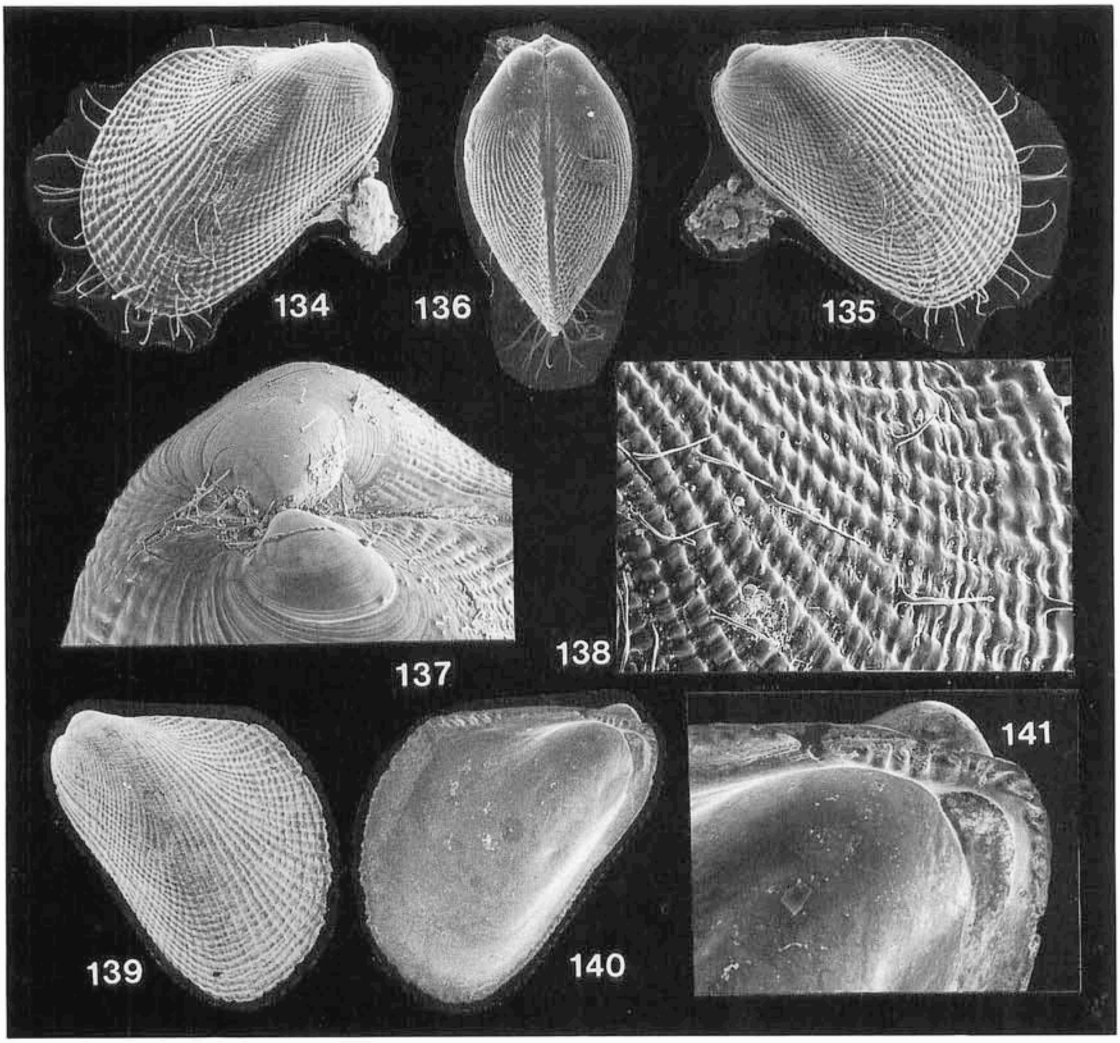
It is characterized by elongate-oval outline, non-terminal umbo, rounded anterior margin and numerous fine divaricate ribs, which cross densely spaced commarginal lamellae and give a cloth-like appearance to the later dissoconch. No subumbonal septum is observed. The dorsal margin is marked with numerous subvertical denticles. The inner valve margin is finely crenulated in accordance with the divaricate ribs. The Pd I is fairly large, ranging 101–148 μm; the veliconch (Pd I + Pd II) is 206–292 μm in maximum diameter, demarcated from the dissoconch. It may belong to a new species of *Brachidontes*, but the adult size is not clearly recognized because the shell-size of these specimens is quite variable.

Genus ***Septifer*** Récluz, 1848

Septifer sp. indet.

Figures 134–141

Diminutive specimens of *Septifer* occur, though rarely, in the bottom sediments of "Fool's Palace" (RM19426), "Wall Cave" (RM19589, partly living) of Shimoji Islet and "Cross Hole" (RM19427, partly living) of Irabu Islet, Miyako Islands.



Septifer sp. indet.

Figures 134–138: living specimen, RM19427a, 2.55 × 2.45 mm, from "Cross Hole" [134: left view, 135: right view, 136: dorsal view, 137: oblique view of umbonal area (× 50), 138: surface with hairy periostracum (× 50)]. Figures 139–141: LV, RM19426a, 2.40 × 2.40 mm, from "Fool's Palace" [139: exterior, 140: interior, 141: subumbonal septum (× 50)].

The shell is generally smaller than 3 mm in length and height, trigonally ovate, greenish when alive, and characterized by sparsely distributed bristles of periostracum, non-terminal umbo, many small denticles along the hinge line, crenulated inner margin, luniform subumbonal septum, and finely cancellate sculpture which consists of divaricate ribs and commarginal lamellae of similar strength. The Pd I is about 80 μm, and the veliconch (Pd I + Pd II) is about 390 μm in maximum diameter.

In view of the greenish coloration and hairy periostracum, we at first imagined that these specimens represent juveniles of *Septifer bilocularis* (Linnaeus, 1758) or *Septifer excisus* (Wiegmann, 1837), which are commonly distributed in rocky shores of this region. The triangular shell and shape of the subumbonal septum, however, are rather similar to those of a common Japanese species, *Septifer keenae* Nomura, 1936 [justified emendation by Habe (1951) for *Septifer keeni*, in accordance with ICZN Art. 32c], although the periostracum is black and not hairy in that species.

Unlike the above-mentioned species of *Septifer*, living individuals of the present species were found attached by byssus to small lumps of sediments on the soft bottom of the caves (Figures 134, 135). Because of its rare occurrence, it is not known whether the present species is indigenous to the cryptic environments or not.

According to our preliminary observation, the present species also occurs in "Balicasag Cave" off Panglao Islet of Bohol Island, the Philippines and "Chandelier Cave" near Koror, Palau Island.

Subfamily **Crenellinae** Gray, 1840

Genus ***Crenella*** Brown, 1827

Crenella sp. indet.

Figures 142–147

A few minute specimens of *Crenella* have been found from the bottom sediments of "Devil's Palace" (RM19428), "Fool's Palace" (RM19429), "Wall Cave" (RM19590, partly living on ceiling) and "Black Hole" (RM19430) of Shimoji Islet, and "Shodokutsu" (RM19431) of Ie Islet.

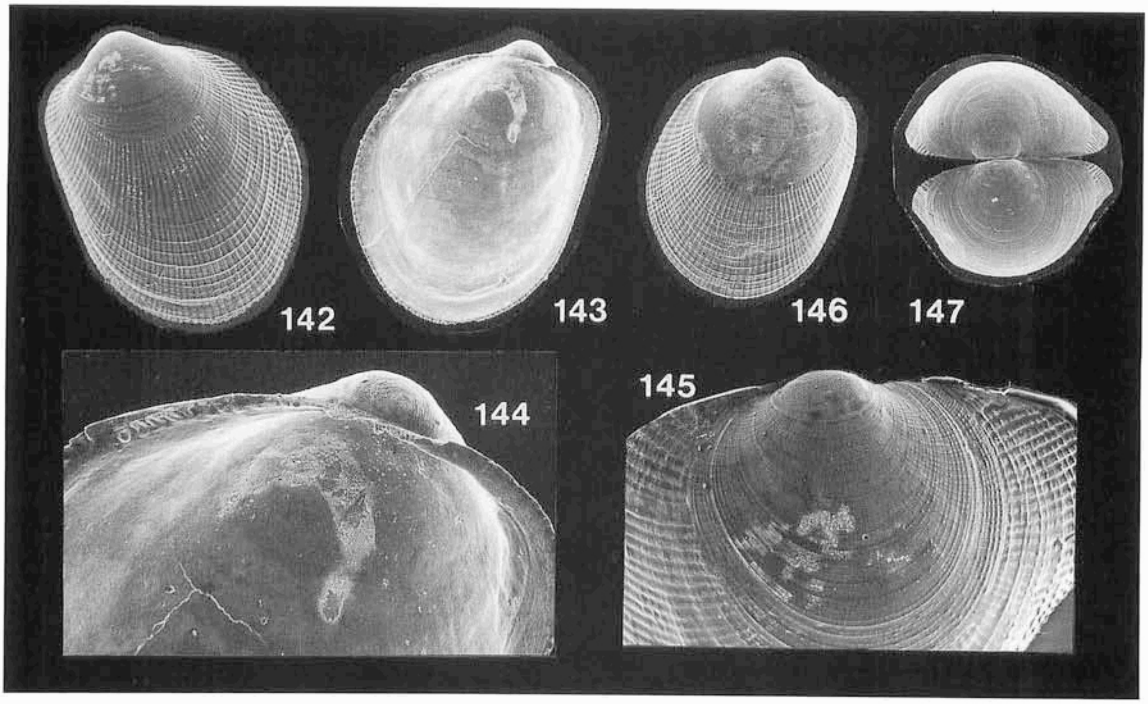
The shell is smaller than 2.0 mm in height, subovate, strongly convex, and characterized by a nearly smooth umbonal area and numerous fine divergent riblets of later dissoconch, about a dozen granular denticles along the postero-dorsal margin, and finely crenulated inner valve margin. The Pd I is very large, D-shaped, about 220 μm in maximum diameter; Pd II absent.

These specimens seem to belong to an undescribed species, but the material is still insufficient to estimate the adult size. A living specimen was found attached to the ceiling of a cave, but it is still uncertain that the present species is indigenous to cryptic environments.

Subfamily **Dacrydiinae** Ockelmann, 1983

Genus ***Dacrydium*** Torell, 1859

Dacrydium is a small-sized mytilacean genus, characterized by thin, hyaline and non-nacreous shell, a barely reduced anterior adductor and persistent denticles derived from provinculum that persist until the latest growth stage. It has been known mainly from bathyal and abyssal bottoms of the Pacific, Atlantic, Indian and Antarctic oceans (Knudsen, 1970; Okutani, 1975; Bernard, 1978; Ockelmann, 1983; Poutiers, 1989; Dell, 1990; etc.), though a few species are known from shallower waters of the East Pacific (Galapagos and California) and the Mediterranean. The abundant occur-



Crenella sp. indet.

Figures 142–145: LV, RM19428a, 1.60 × 1.80 mm, from "Devil's Palace" [142: exterior, 143: interior, 144: hinge area (× 50), 145: oblique view of umbonal area (× 50)]. Figure 146: RV, RM19430a, 1.40 × 1.60 mm, from "Black Hole". Figure 147: upper view of living specimen with broken ventral area, RM19590a, same magnification as other specimens, from "Wall Cave".

rence of a representative species of *Dacrydium* in sublittoral caves of a subtropical region is remarkable.

As pointed out by Ockelmann (1983), the hinge structure and non-nacreous shell homologous with nepioconch of other mytilids may be regarded as paedomorphic features. According to Le Pennec (1980) and Waller (1990), in many species of the Isofilibranchia initial fibrous ligament characterized by a primary subumbonal ligament pit appears only in the early growth stage immediately after the metamorphosis and becomes soon inactive by the development of posterior secondary ligament characterized by pseudonymphae. The initial ligament is active and persistent throughout growth in *Dacrydium* species, though incipient pseudonymphae may be observed in a few species.

Dacrydium zebra sp. nov.

Figures 148–158

1992. *Dacrydium* sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

1993. *Dacrydium* sp., Hayami and Kase, *Univ. Mus. Univ. Tokyo, News*, no.27, p.3, fig.7.

Type and material. — Holotype: RM19432a, a living specimen, from the bottom sediments of "Devil's Palace" of Shimoji Islet, Miyako Islands. Paratypes: RM19432 (living) from the type locality, RM19433 (living) from "Fool's Palace", RM19434 (living) from "Witch's House", RM19592 (living) from "Wall Cave", RM19435 (living) from "Toriike", RM19436 (living) from "Black Hole", RM19591 (dead) from "Coral Hole" of Shimoji Islet. RM19437 (dead) from "Lunch Hole", RM19438 (living) from "W-arch", RM19439 (dead) from "L-arch", RM19440 (living) from "Cross Hole" of Irabu Islet. RM19441 (living) from "Shodokutsu" of Ie Islet.

Diagnosis. — Small-sized brooding species of *Dacrydium*, characterized by pyriform outline, arcuate dorsal margin, straight or slightly concave anterior margin, persistent denticles derived from provinculum which are differentiated into pre-umbonal, post-umbonal and posterior series, dense commarginal lamellae and commonly whitish opaque spots.

Description. — Shell smaller than 2.3 mm in length and height, with maximum length about 1.4 times transverse breadth, obliquely pyriform, translucent, very thin, moderately inflated. Umbo moderately large, salient above dorsal margin. Anterior lobe obscurely discriminated. Dorsal margin broadly arcuate; anterior margin nearly straight or slightly concave, forming a near rectangle with anterior part of dorsal margin; ventral and posterior margins rounded, not discriminated from each other. Surface covered with numerous densely spaced commarginal lamellae. Early dissoconch marked faint divergent threads perpendicularly crossing growth lines. Later dissoconch often has several whitish opaque spots which are divergent from growth axis. Anterior adductor scar distinct, pear-shaped, not degenerated; posterior one obscurely impressed but probably smaller than anterior. Pre-umbonal denticles short but not much degenerated, numbering about 10. Post-umbonal denticles differentiated into two rows; denticles of the anterior row nearly vertical, short and disposed nearly symmetrically with the pre-umbonal denticles, while the posterior row consists of about 30 opisthoclinal denticles, increasing in length posteriorly, well developed on a plate between dorsal margin and internal ridge. Primary ligament persistent; pit acline, low and wide. Incipient secondary ligament probably present on the hinge plate between rows of post-umbonal and posterior denticles. Pd I large, ranging 176–225 μm in maximum diameter, with uneven surface; Pd II not demarcated.

Remarks. — Numerous individuals of the present species have been found attached by byssus on the sediment grains, polychaete tubes and walls in a number of caves of these islets.

More than a dozen species of *Dacrydium* have been known (Ockelmann, 1983; Poutiers, 1989). In the Japanese waters only a bathyal species, *Dacrydium nipponicum* Okutani, 1975 [=*D. pacificum* Okutani, 1968, non Dall, 1916], has been described, from which the present species differs in its smaller size, more sharply pointed anterior end and straight or feebly concave anterior margin. In these respects it may be closer to *Dacrydium occidentale* Smith, 1885, from the western Indian Ocean, and *D. rostriferum* Bernard, 1978, from the northeast Pacific.

Considering the intra- and interpopulational variations, the difference of shell shape from these bathyal-abyssal species is sometimes subtle. Yet the hinge structure of the present species may be unique; the denticles of the posterior series are well differentiated into two rows of different inclination (Figures 154, 157). According to Ockelmann (1983), however, similarly differentiated denticles are known in *Dacrydium viviparum* Ockelmann, 1983, from the northern Atlantic. In spite of the distant distributed areas, we regard the Atlantic species as closely related to the present species. Ockelmann interpreted the interruption of the posterior denticles as indicating the incipient development of a secondary ligament. Yoshida (1937, text-figs.3, 4) illustrated a somewhat similar hinge structure in the juvenile stage (0.6–1.0 mm in shell length) of *Brachidontes senhousia* (Benson, 1842), which is an ubiquitous embayment mussel in Japan.

In *Dacrydium viviparum* Ockelmann, 1983, suprabranchial incubation of a few embryos is known. This is also the case with the present species, though the Pd I is somewhat smaller than that of the Atlantic species. In the samples collected in late June of 1992 and mid April of 1993, several incubated embryos were seen through the translucent shell of many individuals generally larger than 1.5 mm in length. The divaricate whitish opaque spots are unfamiliar in *Dacrydium*. They look like a zebra pattern, when a disarticulated valve is placed on a dark stage (Figure 158).

Distribution. — Abundant or common in many sublittoral caves of Shimoji-Irabu and Ie Islets, Ryukyu Islands. This species also occurs in "Balicasag Cave" off Panglao Islet of Bohol Island, the Philippines.

Subfamily uncertain

Genus ***Urumella*** gen. nov.

Type-species. — *Urumella concava* sp. nov.

Diagnosis. — Small and uniquely distorted genus of Mytilidae, characterized by nacreous and very obliquely elongate shell, concave posterior margin, filmy periostracum, persistent denticles of provinculum, no adult teeth, and low-triangular primary ligament pit below umbo.

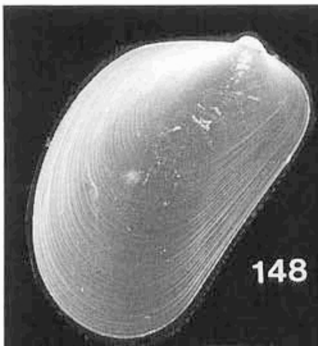
Etymology. — Uruma is another name of the Ryukyu Islands.

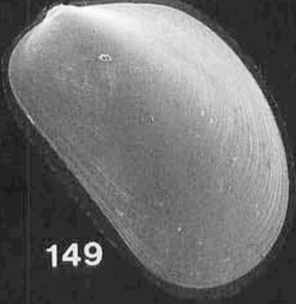
Remarks. — This new genus is proposed on the basis of a diminutive cave species, the posterior margin of which is characteristically concave and incurved. It may belong to the Crenellinae, if the system by Soot-Ryen *in* Cox et al. (1969) is accepted. Since there is no other species assignable to this new genus, the diagnoses for the genus and species are by no means clearly separable. The ligament and hinge structure of this type-species seems to be paedomorphic, resembling that of *Dacrydium*, but the shell is nacreous, unlike the members of the Dacrydiinae. The argenteous shell and persistent denticles derived from the provinculum resemble those of some species of the genus *Idas* Jeffreys, 1876 (= *Idasola* Iredale, 1915), from deep waters of the Atlantic and northern Pacific, but the periostracum is hairy and the secondary external

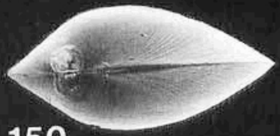
---

Dacrydium zebra sp. nov. ドウクツヒバリガイ (新称)

Figures 148–151: Holotype, living specimen, RM19432a, 1.75 × 1.95 mm, from "Devil's Palace" [148: right view, 149: left view, 150: dorsal view, 151: dorsal view of umbonal area (× 100)]. Figures 152–154: RV, RM19435a, 2.00 × 2.10 mm, from "Toriike" [152: exterior, 153: interior, 154: hinge area (× 65)]. Figures 155–157: LV, RM19435b, 1.85 × 2.05 mm, from "Toriike" [155: exterior, 156: interior, 157: hinge area (× 65)]. Figure 158: RV, RM19435c, 1.60 × 1.80 mm, from "Toriike" (optical photo with dark background).


148


149


150


151

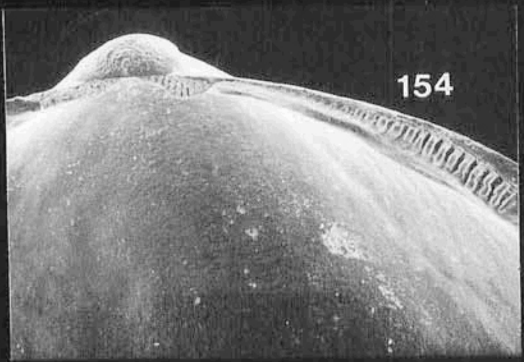

152


153


155


156


158


154


157

ligament is developed in *Idas*.

Urumella concava sp. nov.

Figures 159–166

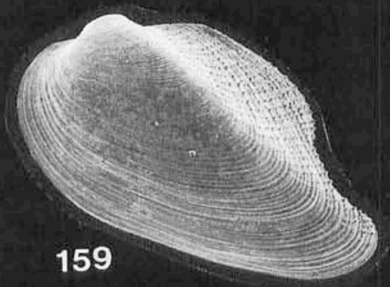
Type and material. — Holotype: RM19448a, a right valve, from the bottom sediments of "L-arch" of Irabu Islet, Miyako Islands. Paratypes: RM19442 (dead) from "Devil's Palace", RM19443 (dead) from "Fool's Palace", RM19444 (dead) from "Witch's House", RM19593 (dead) from "Wall Cave", RM19445 (dead) from "Toriike" of Shimoji Islet, RM19446 (partly living) from "Lunch Hole", RM19447 (dead) from "W-arch", RM19448 (dead) from the type locality, RM19449 (dead) from "Cross Hole" of Irabu Islet. No living specimens have been found except two juveniles from "Lunch Hole".

Diagnosis. — Very small-sized, uniquely distorted mytiliform species, characterized by very prosoclinal growth axis, remarkably concave posterior margin (only in adult stage), subcentrally placed umbo, densely spaced commarginal lamellae, thin filmy periostracum, numerous divergent riblets on posterior area and persistent denticles of provinculum.

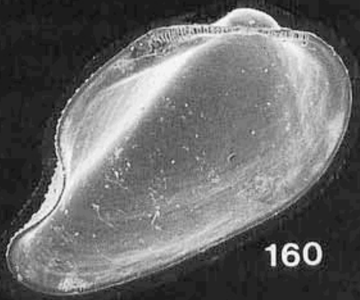
Description. — Shell very small, rarely exceeding 1.3 mm in length, translucent, argenteous, very prosoclinal, roundly carinate, much longer than high, strongly inflated. Periostracum thin, filmy, tinged with yellow. Dorsal margin straight, relatively short; anterior margin rounded, passing gradually into venter which is feebly indented in the middle; posterior margin remarkably concave in its lower half where the shell is strongly incurved, though this feature appears only in adult growth stage. Umbo slightly prosogyrous, located a little anteriorly from mid-point of dorsal margin. Surface wholly covered with fine regular commarginal lamellae; posterior area behind carina also marked with 20 or more curved radiating riblets which perpendicularly cross commarginal lamellae and produce minute tubercles at intersections. A few similar riblets occasionally observed on antero-dorsal area. No marginal crenulations. Primary ligament pit low-triangular, situated just below umbo, persistent throughout growth. Secondary outer ligament undeveloped. Denticles of provinculum persistent until latest growth stage; anterior series numbers about 10, nearly vertical, relatively short; posterior series numbers about 16, becoming gradually longer and more opisthocline toward posterior. Adult teeth not developed at all. Pd I large, D-shaped, about 160 μm in maximum diameter; Pd II not discriminated.

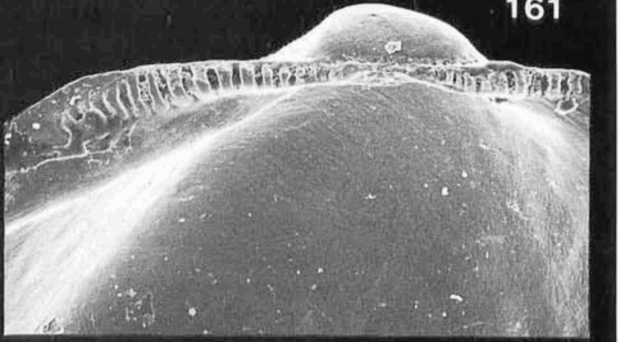
Remarks. — Several specimens are articulated and very fresh, bearing filmy periostracum. None of them, however, is living. The shape of the valves is so unique that no described species of mytilids is comparable with the present species. The concave and incurved posterior margin is not a malformed product because it is observed in all the adult specimens.

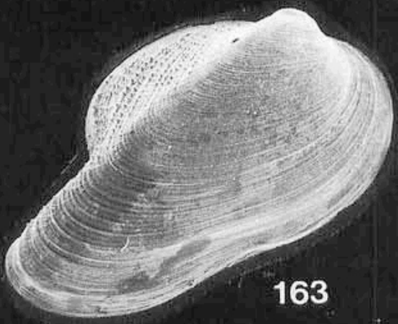
Urumella concava gen. et sp. nov. ウルマヒバリガイ (新称)
Figures 159–162: Holotype, LV, RM19448a, 1.10 × 0.90 mm, from "L-arch" [159: exterior, 160: interior, 161: oblique view of umbonal area (× 125), 162: hinge area (× 125)]. Figures 163–166: RV, RM19448b, 1.20 × 1.00 mm, from "L-arch" [163: exterior, 164: interior, 165: hinge area (× 125), 166: dorsal view of umbonal area (× 125)].

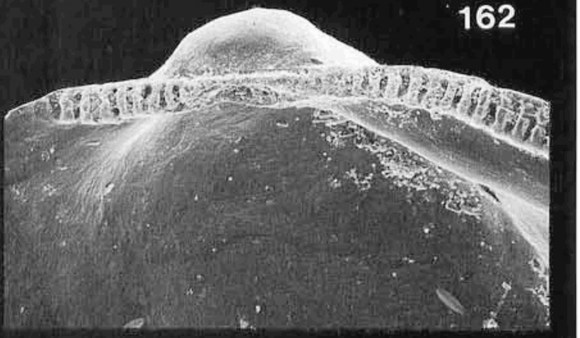

159

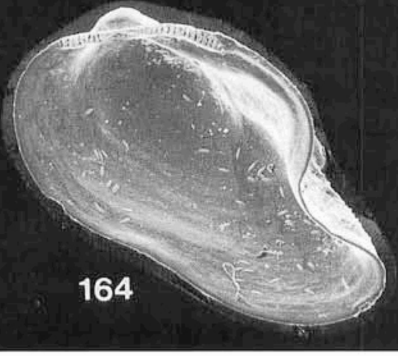

161

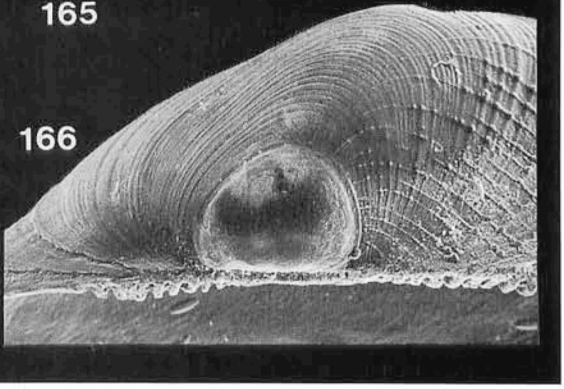

160


162


163


165


164


166

Distribution. — Common in many sublittoral caves of Shimoji and Irabu Islets, Miyako Islands. No specimen has been found in the cave of Ie Islet.

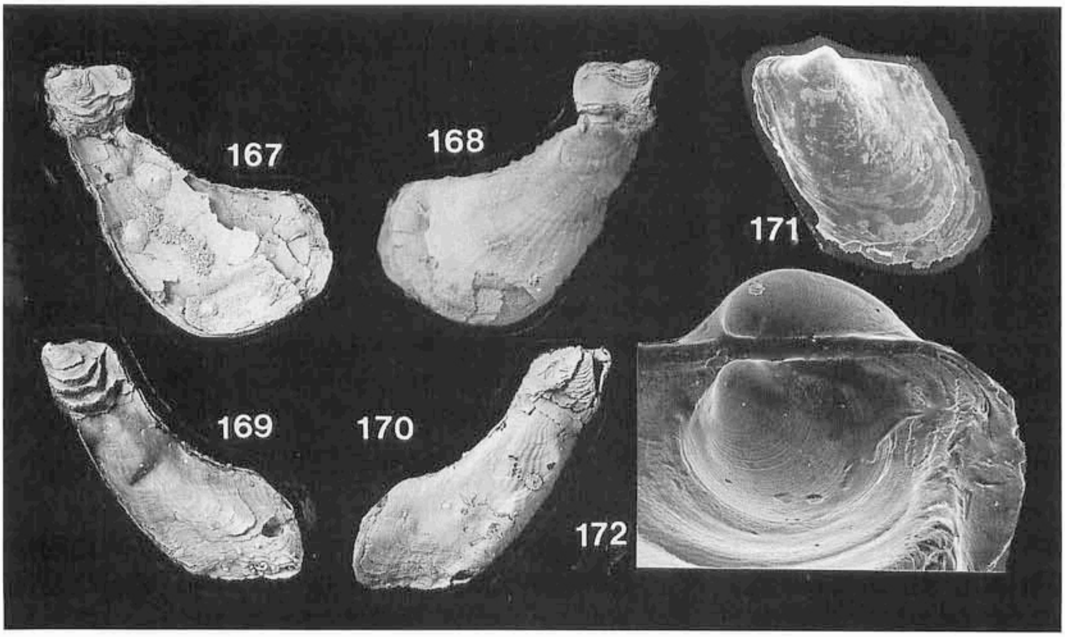
Order **Pterioida** Newell, 1965
Superfamily **Pterioidea** Gray, 1847
Family **Malleidae** Lamarck, 1819
Genus ***Malleus*** Lamarck, 1799
Subgenus ***Malvufundus*** de Gregorio, 1885

Malleus (***Malvufundus***) sp. indet.

Figures 167–172

The present species is represented by several living specimens collected from the following caves: "Witch's House" (RM19594), "Toriike" (RM19595) and "Coral Hole" (RM19596) of Shimoji Islet, and "Cross Hole" (RM19450) of Irabu Islet, Miyako Islands. According to divers, a number of individuals forming colonies attach themselves by the byssus to some narrow cavities on the cave walls. The byssus is so strong that one can hardly remove the individual without breaking the shell.

The shell is irregular in shape but generally elongated posteroventrally, very fragile



Malleus (*Malvufundus*) sp. indet.

Figures 167–168: living specimen, RM19596a, 26.0 × 24.7 mm, from "Coral Cave" [167: left view, 168: right view]. Figures 169–170: living specimen, RM19596b, 24.3 × 20.8 mm, from "Coral Cave" [169: left view, 170: right view]. Figures 171–172: immature living specimen, RM19450a, 1.50 × 1.40 mm, from "Cross Hole" [171: left view, 172: oblique view of umbonal area (× 75)]. (Figures 167–170 by optical photography) but commonly reinforced with an axial internal ridge, less than 45 mm in length, translucent, commonly yellowish in color but sometimes with brownish streaks. RV is moderately convex, while LV is nearly flat or a little concave. Weak irregular radial (or slightly divergent) costellae are often distributed on the surface. The simple prismatic outer layer is well developed, and each calcite prism both on the internal and external surface is about 30–50 μm in diameter. The nacreous inner layer is very thin and restricted to the early dissoconch.

The early dissoconch, commonly 4–7 mm in length and height, is always darkly colored and rather clearly delimited. Unlike the irregularly elongated later dissoconch, it is pteriform and subtrapezoidal with irregularly imbricated commarginal lamellae, anteriorly auriculated, inflated more strongly in LV. The primary ligament is alivincular with a subvertical triangular pit just below the umbo. A weak posterior tooth extends along the posterior part of the dorsal margin. Pd I is small and about 70 μm in diameter; veliconch (Pd I + Pd II) is about 380 μm in diameter and clearly marked. After the pteriform stage, the later dissoconch grows only posteroventrally to form an elongated valve.

The present specimens are probably related to *Malleus* (*Malvufundus*) *regula* (Forskål, 1775) and *Malleus* (*Malvufundus*) *irregularis* Jousseaume, 1894, from various shallow seas of the Indo-West Pacific. It shares many characters with the two species: especially the distribution of the nacreous inner layer and strong commarginal lamellae which are restricted to the pteriform early dissoconch. A similar axial internal ridge also occurs in *M.* (*M.*) *irregularis*. The shell is, however, much smaller and narrower, and the hinge line is shorter. The pteriform part of the early dissoconch commonly grows 10–20 mm in ordinary individuals of *M.* (*M.*) *regula* and *M.* (*M.*) *irregularis*, but rarely exceeds 6 mm in the present specimens.

It is still indeterminable whether these cave specimens represent a distinct species or only ecophenotypically stunted populations of *M.* (*M.*) *irregularis*. Similar shells occur in the bottom sediments of "Balicasag Cave" of Bohol Island, the Philippines.

Order **Ostreoida** Férussac, 1822
Suborder **Pectinina** Waller, 1978
Superfamily **Pectinoidea** Rafinesque, 1815

Family **Propeamussiidae** Abbott, 1954

Although some confusion arose as to the systematics of deep-sea translucent scallops, the contents and limits of the Propeamussiidae have become much clearer in recent years based on the characteristic shell microstructure (especially the simple prismatic outer layer of the disk of RV) and absence of tentacles and true ctenolium (Waller, 1972, 1984; Hayami, 1988a; Schein, 1989; Carter, 1990; etc.). The prismatic microstructure of RV dampens the development of surface sculpture except for dense commarginal lamellae and forms a flexible marginal apron in the Propeamussiidae. The shell of this family is therefore highly inequivalve.

All five unfamiliar minute scallops from the submarine caves of the Ryukyu Islands belong to the Propeamussiidae instead of the Pectinidae. Abraded valves of pectinids are occasionally found in association, but they are believed to have been accidentally transported from exposed environments. Four propeamussiids from these caves are assigned to cavernicolous species because they are commonly found alive in some caves. One species belongs to *Parvamussium*, one to *Cyclopecten*, and the remaining two to *Chlamydella*. All of these cave scallops are characterized by large Pd I and absence of Pd II, indicating non-planktotrophic development. Many dead specimens from a few caves of Shimoji Islet are attributable to another species of *Parvamussium*, which also inhabits the lower sublittoral hard bottom outside the caves.

Genus **Parvamussium** Sacco, 1897

Many Japanese malacologists and paleontologists (e.g. Habe, 1977a; Hayami, 1988a, b) have traditionally applied the generic name *Polynemamussium* Habe, 1951, [type species: *Pecten intuscostatus* Yokoyama, 1920] to byssate and internally ribbed propeamussiids from the northern Pacific, while such species are generally included in *Parvamussium* by European and American authors. Dautzenberg and Bavay (1912) described several species of byssate propeamussiids from the western tropical Pacific encountered by the Siboga Expedition, some of which closely resemble *Pecten intuscostatus*. The diagnostic characters of many minute propeamussiids in the Indonesian seas, including the Siboga species, became clear through Dijkstra's (1991) comprehensive study and accompanying SEM photomicrographs. The type-species of *Polynemamussium* may also be very close in every essential character to *Parvamussium holmesii* (Dall, 1886) from the lower sublittoral to bathyal waters of the West Indies. In view of these studies, we here regard *Polynemamussium* as a junior synonym of *Parvamussium*, as it was treated by Rombouts (1991). However, some supraspecific distinction may be needed for a few large-sized northern Pacific species such as *Parvamussium alaskensis* Dall, 1872, which have also been included in *Polynemamussium* by Japanese authors.

So far as we are aware, *Parvamussium*, except for the group of *P. alaskense* in boreal seas, had been known only from lower sublittoral and deeper substrata, and the following cryptic species may represent the first record of this genus from the upper sublittoral zone.

Parvamussium crypticum sp. nov.

Figures 173–181

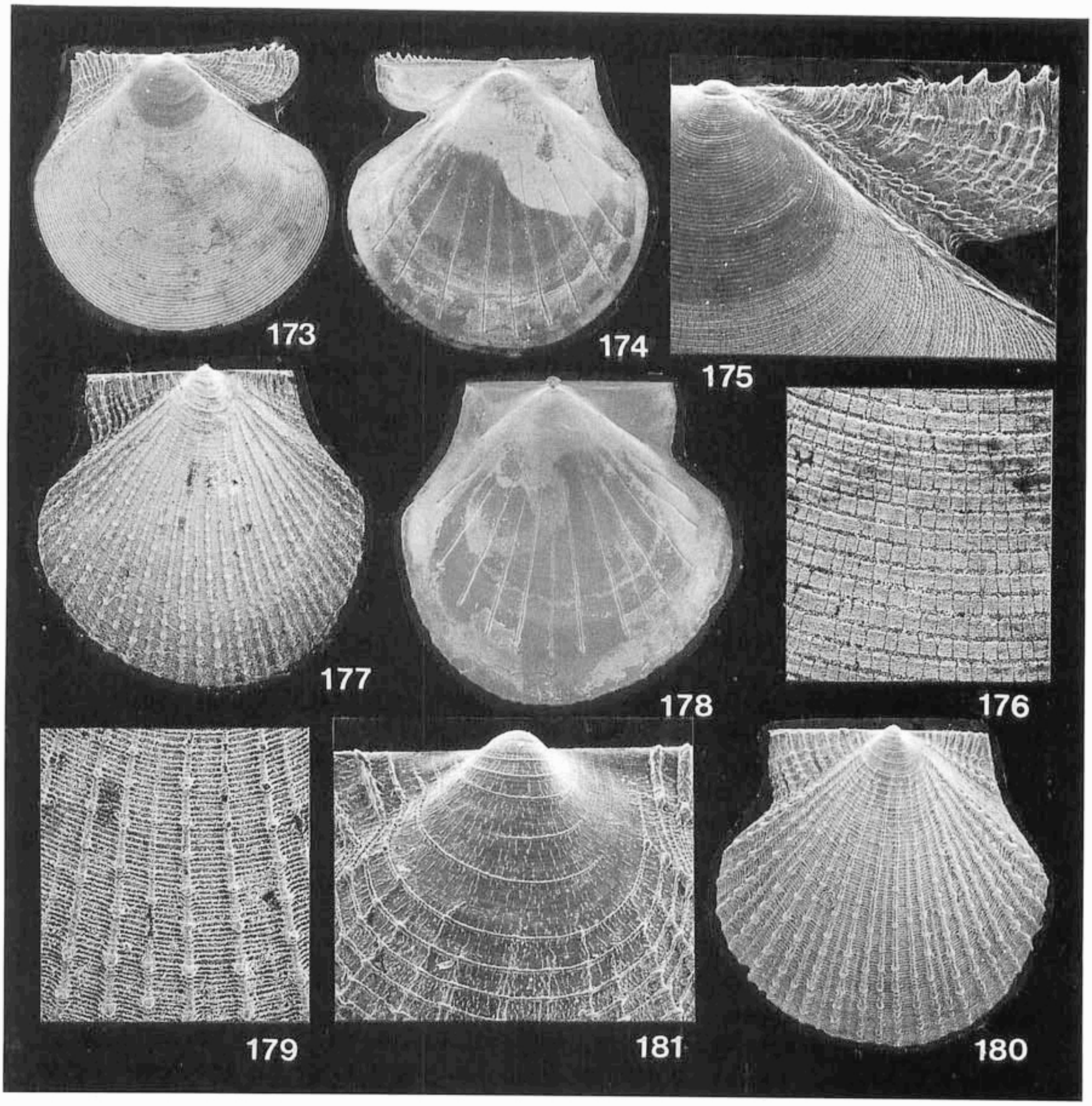
1992. *Parvamussium* sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

1993. *Parvamussium* sp., Hayami and Kase, *Univ. Mus. Univ. Tokyo, News*, no.27, p.3, fig.5.

Type and material. — Holotype: RM19451a, a living specimen, from cave wall of "Shodokutsu" of Ie Islet, Okinawa. Paratypes: RM19251 (partly living) from the type locality, RM19569 (partly living) from "Daidokutsu" of Ie Islet.

Diagnosis. — Small-sized cryptic species of *Parvamussium*, characterized by long antero-dorsal disk margin, deep byssal notch, clearly defined auricles, densely spaced commarginal lamellae of RV, more than 40 irregularly tuberculated radial costae of LV, cancellate ornaments on auricles of both valves, and 13–17 slender internal ribs.

Description. — Shell small and thin, rarely exceeding 5.0 mm in length and height, translucent with no color pattern, nearly acline, a little longer than high. Apical angle about 100 degrees. Antero-dorsal and postero-dorsal margins nearly straight; the former considerably longer than the latter. Byssal notch deep, with a strongly tubercu-



Parvamussium crypticum sp. nov.　　カクレツキヒガイ (新称)
Figures 173–179: Holotype, living specimen (separated valves), RM19451a, 4.65 × 4.70 mm, from "Shodokutsu" [173: exterior of RV, 174: interior of RV, 175: byssal area of RV (× 30), 176: surface of RV (× 75), 177: exterior of LV, 178: interior of LV, 179: middle surface of LV (× 30)]. Figures 180–181: living specimen, RM19451b, 4.55 × 4.40 mm, from "Shodokutsu" [180: left view, 181: left view of umbonal area (× 40)].

lated costa along lower margin of byssal auricle. Disk of RV covered with densely spaced commarginal lamellae, the interval of which essentially consists of rows of simple quadrate prisms. Disk of LV, in contrast, ornamented with more than 40 radial costae, which increase their number by occasional insertion, tuberculated at irregular intervals and crossed by dense commarginal lamellae, though early dissoconch of LV (less than 1mm in length) is free from radial ribs and marked with numerous *Camptonectes*-striae. Posterior auricle much larger than anterior; both auricles clearly demarcated in each valve, marked with coarse cancellate ornaments. Internal ribs 13–15 (14 on average) in number, slender but sharp. Resilium pit angular, situated about two-fifths of dorsal margin from anterior end. Denticles of provinculum observable, though obscurely, in adult. Pd I large, D-shaped, ranging 181–204 μm in maximum diameter; Pd II absent. No tentacles along mantle margin.

Remarks. — Several living specimens have been found attached to the wall, and numerous empty valves are contained in bottom sediments in the innermost part of "Shodokutsu" and "Daidokutsu", Ie Islet. The present species, however, does not seem to occur at any other localities.

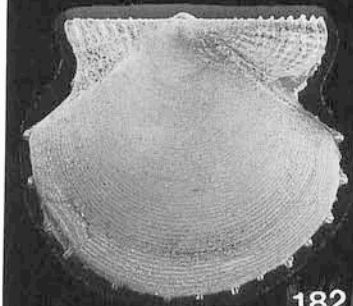
It is somewhat similar to *Parvamussium intuscostatum* (Yokoyama, 1920) from lower sublittoral to upper bathyal sandy substrates of central-south Japan and *Parvamussium holmesii* (Dall, 1886) from the similar depths of the Caribbean Sea, but the shell is characterized by much smaller size, longer postero-dorsal margin and absence of divaricate color pattern. In these respects it is closer to *Parvamussium carbaseum* Dijkstra, 1991, from the lower neritic to bathyal substrates of eastern Indonesia. Although the tuberculated radial ribs of LV and many other characters are similar, the byssal notch is decidedly deeper, and the ratio of length/height is a little larger than that of the Indonesian species. It is somewhat similar to *Parvamussium cristatellum* (Dautzenberg and Bavay, 1912) also from the Banda Sea, but the radial ribs and internal ribs are more numerous and commarginal lamellae of LV are denser in the present species.

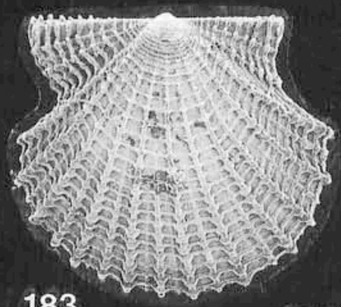
As usual in many propeamussiids, the ventral periphery of RV (called marginal apron by Hayami, 1988a), when the valves are tightly closed, is readily reflected along the internal surface of LV, because of the simple prismatic microstructure. The marginal apron is, however, extremely fragile in this species. Consequently, though only superficially, RV looks somewhat smaller than LV, and the internal ribs appear to reach the ventral margin only in RV.

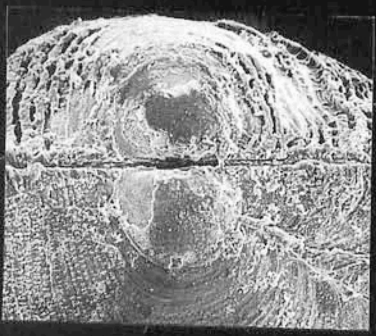
Distribution. — Very abundant in a sublittoral cave of Ie Islet, Ryukyu Islands. No specimen of this species has been found from the caves of Shimoji and Irabu Islets. A similar species occurs in the bottom sediments of "Chandelier Cave" near Koror of Palau Islands, but its internal ribs are generally weaker and more irregular in prominence.

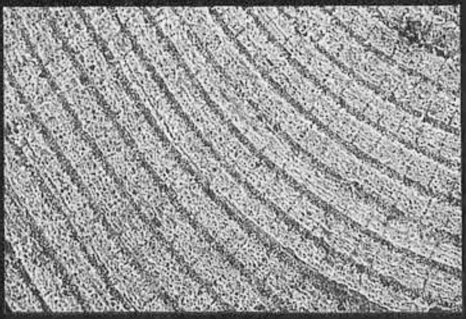
Parvamussium decoratum sp. nov. ミジンツキヒガイ (新称)

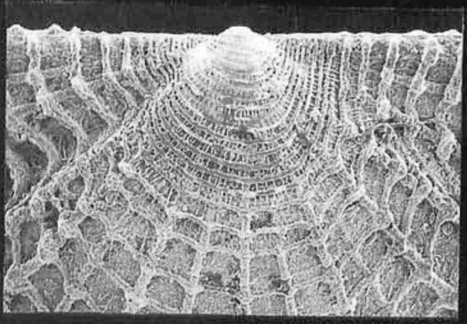
Figures 182–185: Holotype, living specimen, RM19572a, 4.40 × 3.90 mm, from off southern coast of Ie Islet (70 m deep) [182: right view, 183: left view, 184: dorsal view of corroded umbonal area (× 100), 185: umbonal area of LV (× 30)]. Figures 186–192: living specimen (separated valves), RM19572b, 3.95 × 3.75 mm, from the same locality [186: exterior of RV, 187: interior of RV, 188: exterior of LV, 189: interior of LV, 190: byssal area of RV (× 30), 191: umbonal area of RV (× 150), 192: surface of postero-ventral surface of RV (× 75)].

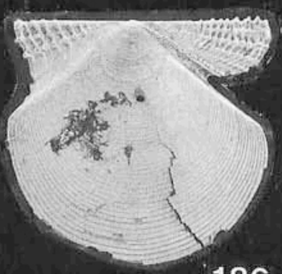

182


183

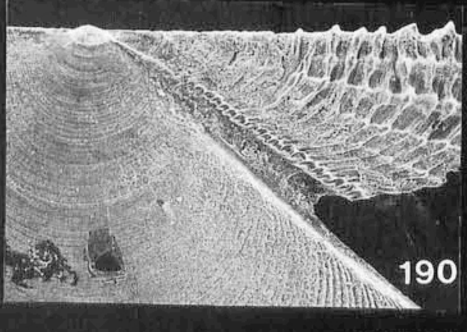

184

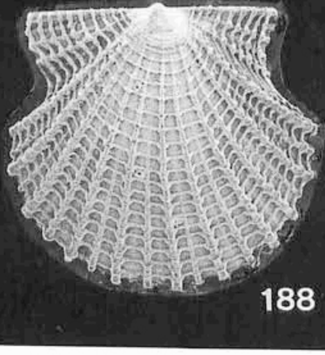

192

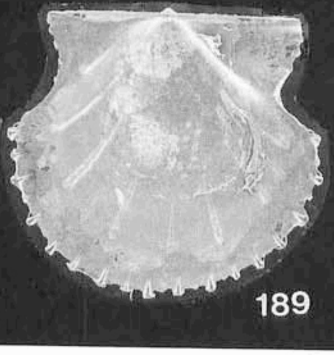

185

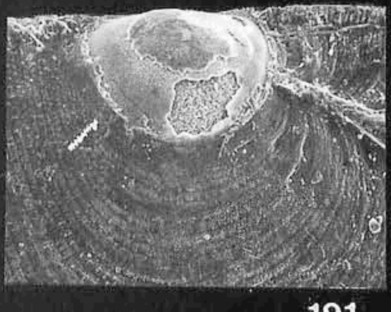

186


187


190


188


189


191

Parvamussium decoratum sp. nov.

Figures 182–192

Material. — Holotype: RM19572a, a living specimen attaching itself to algal balls by byssus, collected from the sublittoral bottom (about 70 m deep) off the southern coast of Ie Islet, Okinawa. Paratypes: RM19452 (dead) from "Devil's Palace", RM19453 (dead) from "Fool's Palace", RM19597 (dead) from "Toriike", RM19454 (dead) from "Black Hole" and RM19598 (partly living) from "Coral Hole" of Shimoji Islet. RM19455 (dead) from "Cross Hole" of Irabu Islet. RM19572 (living) from the type locality.

Diagnosis. — Small-sized, relatively low species of *Parvamussium*, characterized by nearly equilateral disk, clearly defined large auricles of subequal size, coarsely cancellate ornaments of LV consisting of strong radial ribs of two orders and prominent commarginal lamellae which become denser toward the umbo, and a few rudimentary internal ribs in each valve.

Description. — Shell small for genus, scarcely exceeding 5.0 mm in length, dirty white, opaque, longer than high. Disk nearly equilateral, with slightly concave antero- and postero-dorsal margins. Apical angle about 100°. Byssal notch deep, with comparatively weak radial costae. Posterior auricle relatively large, acutely angulated, subequal to anterior in size; umbo placed near mid-point of dorsal margin. Disk of LV and auricles of both valves possess coarsely lattice ornaments. Radial ribs on disc of LV consist of two orders: primary ribs about 10 in number, very stout, starting about 1 mm from the umbo; secondary ribs alternate almost regularly with primary, also giving digitations to ventral margin. Commarginal lamellae a little weaker than radial ribs, densely spaced in early dissoconch where *Camptonectes*-striae are distinct. Disk of RV nearly smooth except for densely spaced commarginal lamellae. Flexible marginal apron occupies about a sixth of shell height. Internal ribs only a few, rudimentary, appear earlier in anterior and posterior parts than in central part in each valve. Pd I, though commonly corroded even in living specimens from outside the caves, D-shaped, about 140 μm in maximum diameter; Pd II not discriminated.

Remarks. — This is not necessarily a cavernicolous species, because the living specimens described here were obtained from algal balls on exposed sublittoral bottom. In Shimoji Islet, however, empty shells are sometimes abundantly contained in the cave sediments, and one living specimen was found on an empty shell of *Spondylus varius* in a dark cave ("Coral Hole").

In view of the rudimentary internal ribs, the present species is regarded as intermediate between *Parvamussium* and *Cyclopecten*. In the lattice ornaments and many other characters of LV it resembles *Cyclopecten cancellus* Dijkstra, 1991, from the lower neritic and upper bathyal bottoms of the Banda Sea. Because the internal ribs appear in the present species only near the ventral margin, in the juvenile stage it seems to be closely related to the Indonesian species. The RV of the Indonesian species was neither illustrated nor described by Dijkstra (1991), but we consider that it is distinct from *C. cancellus*, because the shell is a little lower and because the commarginal lamellae of LV are more densely spaced near the umbo in the present species. It is also somewhat similar to *Cyclopecten secundus* (Finlay, 1927), but the primary and secondary ribs look more numerous in the present species. The present species clearly differs from *Parvamussium crypticum* sp. nov. in the subequilateral disk, strongly cancellate ornaments, fewer and more rudimentary internal ribs, and smaller prodissoconch I.

Distribution. — The present species has been known from the exposed sublittoral bottom of Okinawa (off Ie Islet) and several caves of Shimoji and Irabu Islets, Miyako Islands.

Genus ***Cyclopecten*** Verrill, 1897

A large number of species belonging to *Cyclopecten* have been described in the world. Though some confusion arose as to the relation to *Delectopecten* and other hyaline deep-sea pectinids (Hertlein *in* Cox et al., 1969; Knudsen, 1970; Habe, 1977a; Bernard, 1978; Rombouts, 1991), the type-species of *Cyclopecten*, *Pecten pustulosus* Verrill, 1893, is an undoubted propeamussiid, whereas *Delectopecten* is a pectinid.

The bathymetric distribution of *Cyclopecten* is very wide, ranging from subtidal to abyssal. Soot-Ryen (1960) recorded a tiny species from the subtidal zone of Tristan da Cunha. As noticed by Waller (1984: 214), some shallow-water subtropical species of *Cyclopecten* are "cryptic" (presumably interstitial) organisms, because their shell-size is nearly the same as sand and *Halimeda* grains. Some specialized life habits may be required to enable such a fragile scallop to survive on shallow-water substrata in low latitudinal regions. In the Galapagos Islands a few species of this genus also have been known from shallow waters (Bernard, 1983). Most species of *Cyclopecten* in the Pacific, however, are deep-water inhabitants, as indicated by Habe (1977a) and Bernard (1983).

The morphologic difference between *Parvamussium* and *Cyclopecten* appears to be gradational. In some western Pacific species, e. g., *Parvamussium araneum* Dijkstra, 1991, and *Parvamussium decoratum* sp. nov., rudimentary internal ribs appear at first in the later growth stage. No other essential character seems to be applicable to clearly distinguish the two genera. It is suggested that *Cyclopecten* may have been derived from *Parvamussium* through paedomorphic evolution.

Cyclopecten ryukyuensis sp. nov.

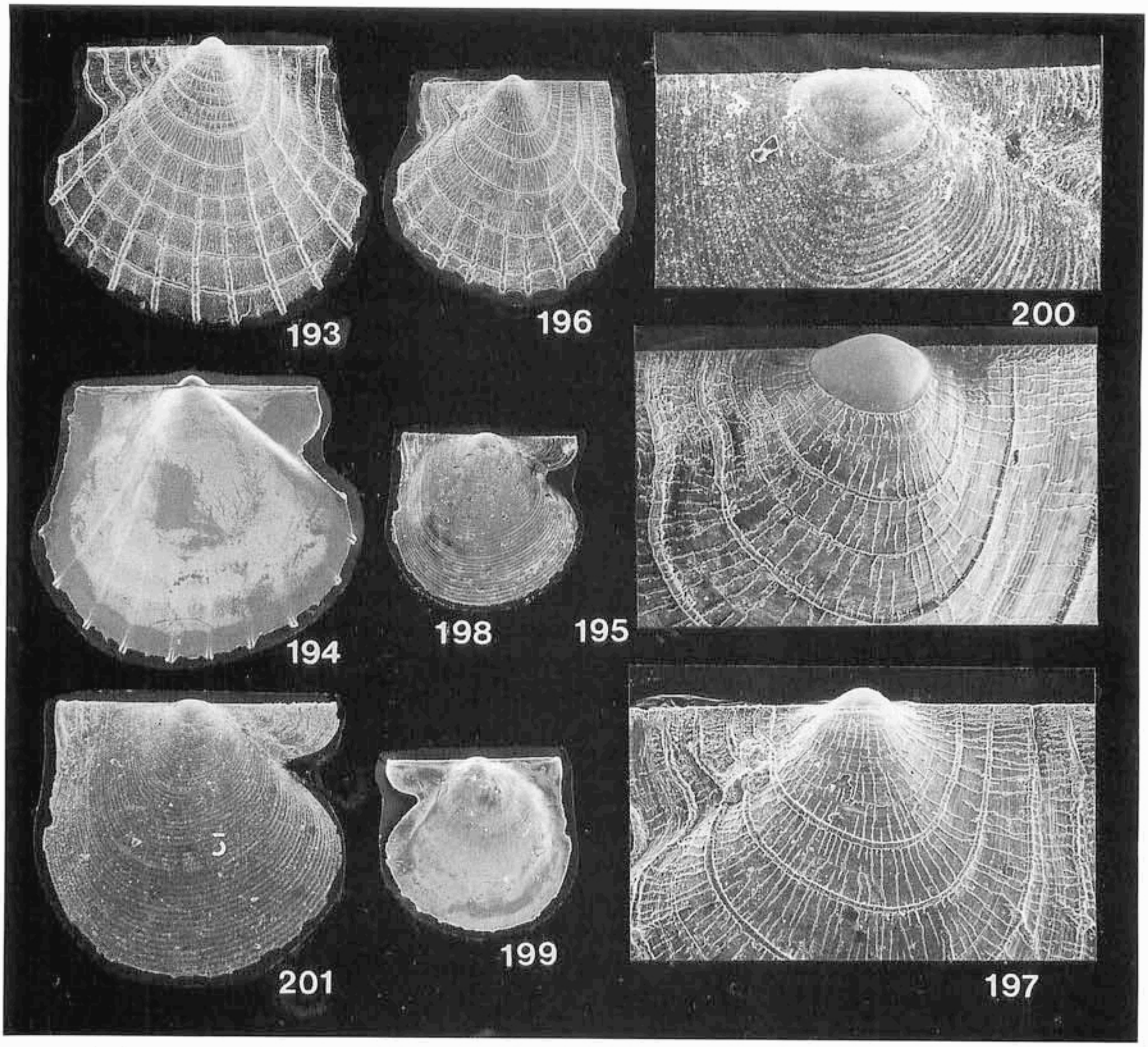
Figures 193–201

1992. *Cyclopecten* sp. A and B, Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Type and material. — Holotype: RM19463a, a living specimen, from the bottom sediments of "Cross Hole" of Irabu Islet, Miyako Islands. Paratypes: RM19456 (dead) from "Devil's Palace", RM19457 (dead) from "Fool's Palace", RM19458 (dead) from "Witch's House", RM19459 (dead) from "Toriike", RM19460 (dead) from "Black Hole", RM19599 (dead) from "Coral Hole" of Shimoji Islet. RM19461 (dead) from "W-arch", RM19462 (dead) from "L-arch", RM19463 (living) from the type locality of Irabu Islet. RM19464 (dead) from "Shodokutsu", RM19570 (dead) from "Daidokutsu" of Ie Islet.

Diagnosis. — Small-sized, comparatively low and paedomorphic species of *Cyclopecten*, characterized by deep byssal notch, long dorsal margin, poorly defined posterior auricle, and coarsely cancellate ornaments in addition to persistent *Camptonectes*-striae in LV.

Description. — Shell small, rarely exceeding 2.5 mm in length, very thin, translu-



Cyclopecten ryukyuensis sp. nov. ケシハリナデシコ (新称)
Figures 193–195: LV, RM19463b, 1.95×1.75 mm, from "Cross Hole" [193: exterior, 194: interior, 195: oblique view of umbonal area (× 100)]. Figures 196–197. Holotype, living specimen, RM19463a, 1.50 × 1.40 mm, from "Cross Hole" [196: left view, 197: umbonal area of LV (× 50)]. Figures 198–200: RV, RM19463c, 1.15 × 1.10 mm, from "Cross Hole" [198: exterior, 199: interior, 200: umbonal area (× 120)]. Figure 201: RV, RM19464a, 1.60 × 1.50 mm, from "Shodokutsu".

cent, nearly acline, weakly convex, a little longer than high. Umbo located near midpoint of dorsal margin. Dorsal margin long, occupying nearly the whole shell length. Byssal notch deep. Posterior auricle large, rectangularly truncated but poorly defined from disk. Disk of RV covered with dense commarginal lamellae and numerous fine rectangular interstitial threads representing regular arrangement of simple quadritic prismatic crystals of outer layer. Byssal auricle bears several weak radial ribs, while posterior auricle often has a strong radial rib and coarse commarginal lamellae. Disk and both auricles of LV marked with widely spaced and strong commarginal lamellae and several irregular radial ribs. *Camptonectes*-striae of LV persistent until later dissoconch. No internal ribs. Resilium pit spoon-shaped, projecting downward. Numerous denticles of provinculum persistent throughout growth. Pd I large, D-shaped, ranging 165–204 μm in maximum diameter; Pd II absent.

Remarks. — In a preliminary study (Kase and Hayami, 1992), we identified two unnamed species of *Cyclopecten* in the bottom sediments of "Shodokutsu"; a strong radial ribs occurs on the middle of the posterior auricle in one species and not in the other. However, the difference between the two forms is actually gradational and is regarded here as due to intrapopulational variation. The morphology of this species is somewhat similar to that of the juvenile stage of *Parvamussium crypticum* sp. nov. but is clearly distinguishable from it by fewer radial ribs, more persistent *Camptonectes* striae in LV (at similar size) and absence of internal ribs throughout growth.

The long dorsal margin, poorly defined posterior auricle and coarse cancellate ornaments at a glance constitute criteria for characterizing this species, but these features are shared by juvenile specimens of many species of *Cyclopecten* (and *Parvamussium*).

Distribution. — Common in many sublittoral caves of Ie, Shimoji and Irabu Islets, Ryukyu Islands. This species also occurs in "Balicasag Cave" off Panglao Islet of Bohol Island, the Philippines.

Genus ***Chlamydella*** Iredale, 1929

Chlamydella was proposed by Iredale (1929) for a diminutive, hyaline pectinacean species, *Cyclopecten favus* Hedley, 1902, from lower sublittoral substrata of eastern Australia. As originally described in detail, the type species seems to be well characterized by the pteriform shell and honeycomb-like shell microstructure of RV. Another Hedley's species, *Cyclopecten obliquus*, may be congeneric or even conspecific with the type species (Cotton and Godfrey, 1938). No additional species, so far as we are aware, was described under this generic name, but *Cyclopecten hexagonalis* Powell, 1958, has similar honeycomb structure, as clearly illustrated by Dell (1990). This genus also may include *Pecten aviculoides* Smith, 1885, from the sea off Prince Edward Island, *Pecten* (*Pseudamusium*) *meleagrinus* Thiele *in* Thiele and Jackel, 1931, from the sea around the Kerguélen Islands, and a few species of "*Cyclopecten*" (listed by Dell, 1990) from the Subantarctic seas. Detailed features of these species, however, are now difficult to recognize from their original descriptions.

Recently, we unexpectedly discovered numerous living specimens of two pteriform propeamussiids in the cave sediments of the Ryukyu Islands. One has strongly cancellate ornaments on the surface of LV, while the other shows nearly a smooth surface and much thinner test. The two species reveal characteristic honeycomb structure of RV (Figures 202, 216). They are brooding species, and their Pd I is unusually large and strange in shape for pectinaceans. Through the courtesy of the staff of the Australian Museum, we were able to examine the holotype (C13231) of *Chlamydella favus* (Hedley). Although the shell structure and other essential characters are similar to the cave species, the Pd I of *C. favus* is much smaller and normal in shape. We think that the discrepancy of Pd I indicates only different developmental strategy instead of generic or subgeneric difference.

As the result of our comparative study by SEM observations, it is concluded that *Chlamydella* should be taxonomically placed near *Cyclopecten*, as treated by Hertlein *in* Cox et al. (1969), but is distinguishable from *Cyclopecten* by the commarginally elongate hexagonal (honeycomb-like) simple calcitic prisms of the outer layer of RV as well as the pteriform outline of both valves with undifferentiated auricles (except the byssal auricle of RV). The outer layer of RV of *Cyclopecten bistriatus* (Dall, 1916), *Cyclopecten nakaii* Okutani, 1962, and *Cyclopecten ryukyuensis* sp. nov., for example, also consists of simple prismatic calcite, but the prisms are subquadrate (not hexagonal) and regularly arranged along the growth lamellae.

Cyclochlamys Finlay, 1927 [type-species: *Pecten transennus* Suter, 1913, from New Zealand] is generally regarded as synonymous with *Cyclopecten* (Dell, 1956; Hertlein *in* Cox et al., 1969; Dijkstra, 1991). The LV of the New Zealand species, as described by Dell (1956), exhibits remarkably cancellate ornaments and poorly defined auricles and is similar to that of one of the present cave species. Though the shell structure of *C. transennus* has not been described, there is a possibility that *Chlamydella* falls into a junior synonym of *Cyclochlamys*. The outline of RV of *C. transennus*, however, is more pectiniform than and differs in other ways from that of the type and present species of *Chlamydella*.

Chlamydella incubata sp. nov.

Figures 202–212

1984. *Cyclopecten* sp., Kaneko, Explanation of 11th special exhibition, Osaka City Museum of Natural History, p.23, pl.8, figs.11,12 (clearly illustrated but with no verbal description).

1992. Propeamussiidae sp. A and B, Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.447, figs.1E,F, p.448, listed.

1993. *Chlamydella* sp., Hayami and Kase, *Univ. Mus. Univ. Tokyo, News*, no.27, p.3, fig.6.

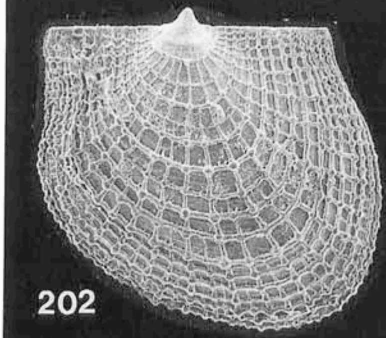
Type and material. — Holotype: RM19473a, a living specimen, from the bottom sediments of "Cross Hole" of Irabu Islet, Miyako Islands. Paratypes: RM19465 (living) from "Devil's Palace", RM19466 (living) from "Fool's Palace", RM19467 (living) from "Witch's House", RM19601 (living) from "Wall Cave", RM19468 (living) from "Toriike", RM19469 (living) from "Black Hole", RM19600 (living) from "Coral Hole" of Shimoji Islet. RM19470 (living) from "Lunch Hole", RM19471 (living) from "W-arch", RM19472 (living) from "L-arch", RM19473 (living) from the type locality of Irabu Islet. RM19474 (dead) from "Shodokutsu" and RM19570 (dead) from "Daidokutsu" of Ie Islet.

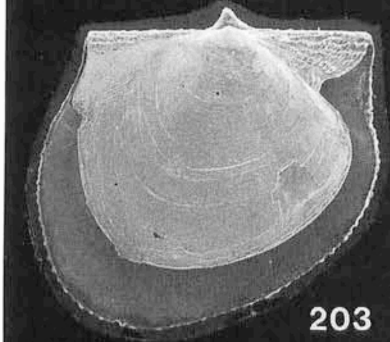
Diagnosis. — Small-sized brooding species of *Chlamydella*, characterized by nearly

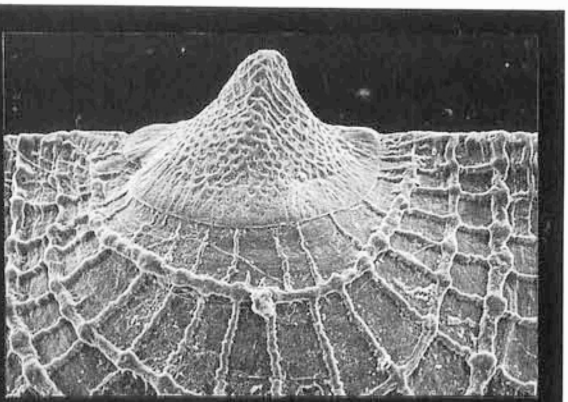
---

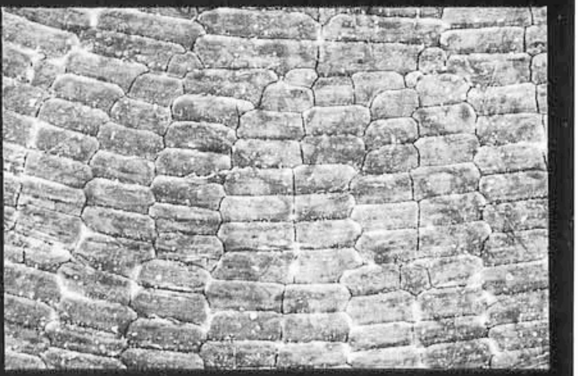
Chlamydella incubata sp. nov. コモチハリナデシコ (新称)

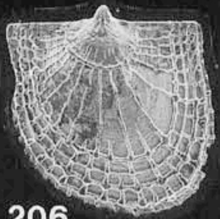
Figures 202–205: Holotype, living specimen, RM19473a, 1.80 × 1.65 mm, from "Cross Hole" [202: left view, 203: right view, 204: umbonal area of LV (× 125), 205: middle surface of RV, honeycomb-like shell structure (× 400)]. Figures 206–207: immature living specimen, RM19473b, 1.10 × 1.05 mm, from "Cross Hole" [206: left view, 207: right view]. Figure 208: immature living specimen, RM19473c, 0.90 × 0.80 mm, from "Cross Hole". Figures 209–210: RV, RM19473d, 1.80 × 1.60 mm, from "Cross Hole" [209: exterior, 210: umbonal area (× 100)]. Figure 211: incubated juvenile, left view, RM19473e, 0.25 × 0.20 mm, from "Cross Hole". Figure 212: RM19473f, living specimen adhered to an annelid tube (× 18), from "Cross Hole".


202

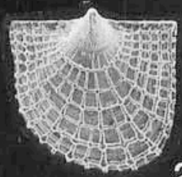

203


204

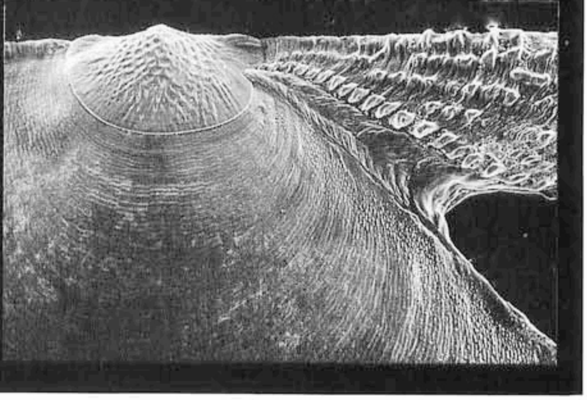

205

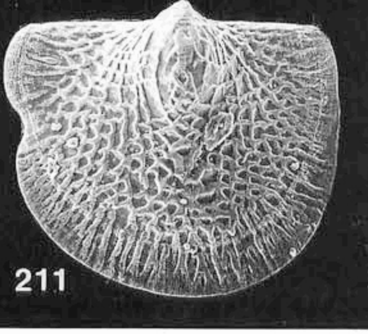

206

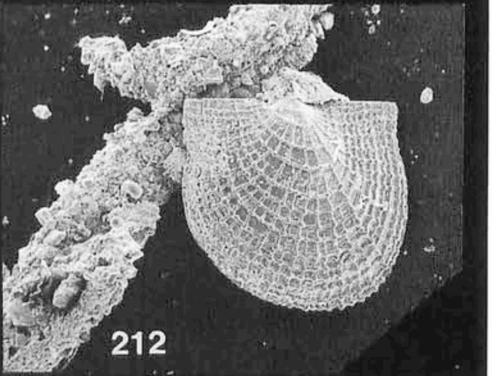

207


208


209


210


211


212

acline and sometimes considerably thickened shell, large and radially ornamented byssal auricle, honeycomb-like prismatic structure in RV and remarkably cancellate sculpture in LV, and large Pd I which is highly conical especially in LV, ornamented with diagonal riblets and characterized by rudimentary byssal notch.

Description. — Shell very small, scarcely exceeding 2.2 mm in length and height, nearly as high as long, whitish, nearly acline or slightly prosocline, highly inequivalve. Shell thickness somewhat variable (probably thickened in late growth stage). LV more strongly convex than RV. Dorsal margin long, extends over almost whole shell length. Auricles except for byssal one not clearly differentiated from disk, but anterior and posterior margins of LV usually slightly concave. Byssal auricle large, provided with a few radial rows of granules, the lowest of which is the strongest. Byssal fasciole relatively wide. Marginal apron of RV, consisting of simple prismatic outer layer, is relatively wide, about one fifth of height. Disk and auricles of LV wholly covered with remarkably cancellate sculpture which consists of more than 30 increasingly divergent ribs and widely spaced commarginal lamellae. Divergent ribs orthogonally cross commarginal lamellae, producing small tubercles at the intersections. Disk of RV nearly smooth but microscopically reveals radial arrangement of commarginally elongated hexagonal (honeycomb-like) prisms; each prism about 50 μm long and about 10 μm high). Resilium pit low-triangular, located near mid-point of dorsal margin. Denticles of provinculum observable until adult stage. Pd I very large, ranging 246-279 μm in maximum diameter, hat-shaped, highly elevated in LV, with diagonally decussate ornament and distinct rudimentary byssal notch in each valve; prodissoconch II absent.

Remarks. — Numerous living individuals of this species have been found attached to the sediment grains, gravels, polychaete tubes and walls in many caves of Shimoji and Irabu Islets.

This species is most certainly conspecific with *Cyclopecten* sp. by Kaneko (1984) from the beach sand at Kubokawa of southern Shikoku, because every essential character is similar. The illustrated specimen by Kaneko shows a little longer outline and probably less salient Pd I than the most of the present specimens, but these may be due to geographic variation within one and the same species.

As listed in our preliminary study (Kase and Hayami, 1992), two forms may exist in the present species; one has thicker test with robust cancellate ornaments, and the other is vice versa. The diagonally decussate ornaments of Pd I may be more delicate in the former than in the latter. Because some specimens reveal intermediate features, taxonomic distinction of the two forms is difficult, and it is more reasonable to consider a wide range of intrapopulational variation in these characters.

The ecology and developmental strategy of this species appears unique for pectinaceans. Near the entrance of these submarine caves, many individuals attach themselves to the surface of the exposed part of polychaete tubes (Figure 212), though living specimens also occur on the sediment surface and cave wall. Moreover, many adult specimens collected there on June 27–30, 1992, and April 13–19, 1993, reveal suprabranchial incubation of a few (commonly three to seven) embryos. The prereleased larvae (e.g. Figure 211) are of course coincident with the Pd I (plus the earliest dissoconch) in every character. Such incubation of juveniles as well as hat-shaped Pd I probably has not been described in the Pectinacea. The central boss of Pd

I is more highly elevated in LV than in RV, and the anterior margin of Pd I exhibits a clear notch in each valve. The position of this notch in RV is followed by the byssal notch of dissoconch (Figure 210). We presume that pre-released larvae attach themselves to parent ctenidia by means of incipient byssus.

Distribution. — Abundant in many sublittoral caves of Shimoji, Irabu and Ie Islets, Ryukyu Islands. The present species is not necessarily indigenous to submarine caves, because empty shells are often found in beach sands of southern Japan. In addition to Kaneko's record of an identical species from southern Shikoku, we have found abundant dead specimens of this species at the following localities: 1) beach of Tsuchihama, Kasari Town, Amami-Oshima Island, Kagoshima Pref., 2) beach of Okuda-no-hama, near Kushimoto, Kii Peninsula, Wakayama Pref., 3) bottom sediments near Gyuchaku-iwa of Kumomi, western Izu Peninsula (coll. by H. Nabeshima) and 4) beach sand at Heta, Izu Peninsula, Shizuoka Pref.

Chlamydella tenuissima sp. nov.

Figures 213–220

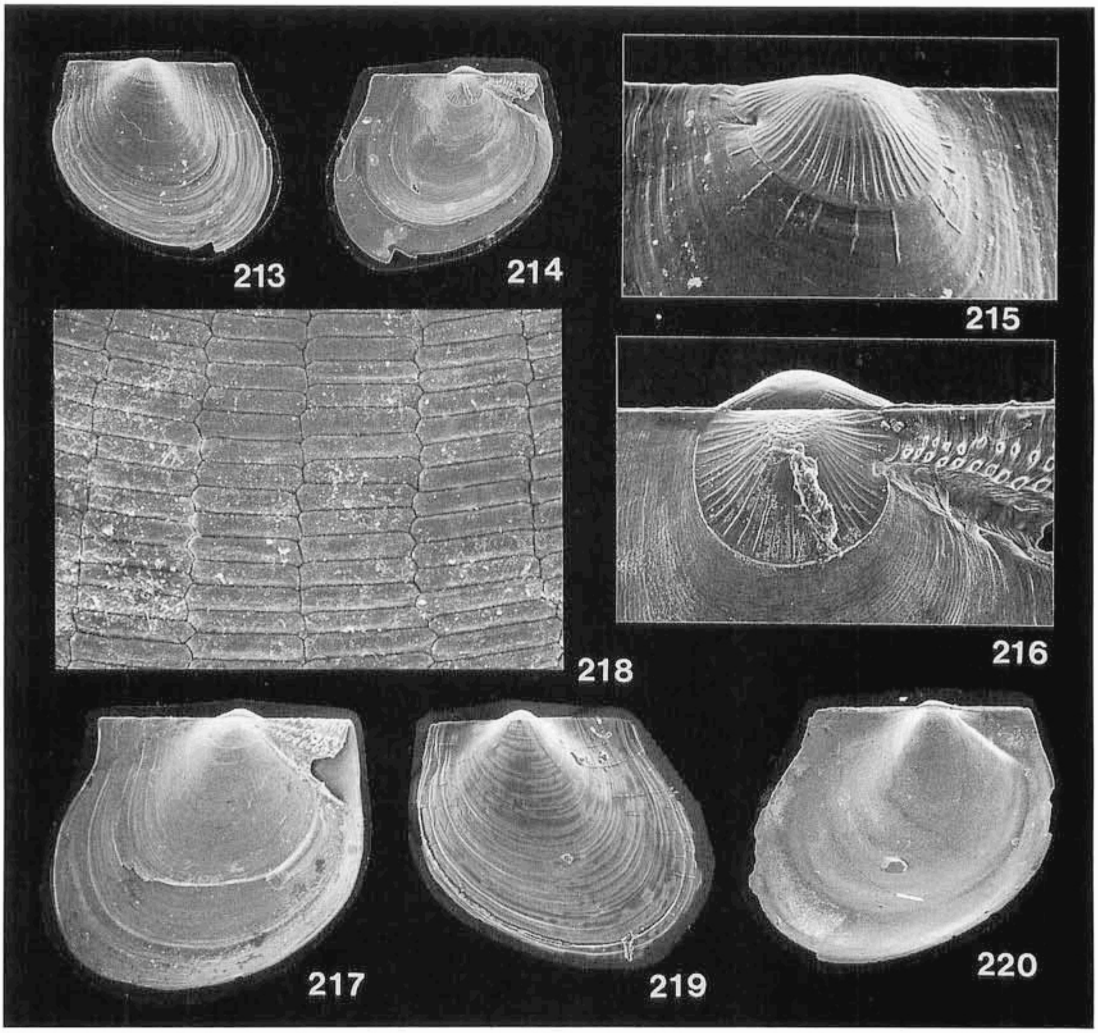
1992. *Chlamydella* sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Type and material. — Holotype: RM19483a, a living specimen from the bottom sediments of "Cross Hole" of Irabu Islet, Miyako Islands. Paratypes: RM19475 (living) from "Devil's Palace", RM19476 (living) from "Fool's Palace", RM19477 (dead) from "Witch's House", RM19603 (living) from "Wall Cave", RM19478 (living) from "Toriike", RM19479 (living) from "Black Hole", RM19602 (living) from "Coral Hole" of Shimoji Islet. RM19480 (dead) from "Lunch Hole", RM19481 (living) from "W-arch", RM19482 (dead) from "L-arch", RM19483 (living) from the type locality of Irabu Islet. RM19484 (dead) from "Shodokutsu" of Ie Islet.

Diagnosis. — Small-sized brooding species of *Chlamydella*, characterized by very thin, hyaline and prosoclinal shell, granular ornaments on byssal auricle, nearly smooth surface of LV except for a few sparse divergent striae, and large low-conical Pd I which is radially striated and possesses rudimentary byssal notch in each valve.

Description. — Shell very small, scarcely exceeding 2.2 mm in length, highly inequivalve, prosocline, hyaline, translucent, extremely thin, longer than high. Auricles (except for byssal one) not clearly delimited from disk. LV more strongly convex than RV. Dorsal margin long, occupying almost whole length of shell. Byssal auricle relatively short, supported by a wide byssal fasciole. Disk and auricles of LV nearly smooth, but commonly with several sparse divergent striae which are irregular in prominence and intervals but always perpendicularly cross growth lines. Disk and posterior auricle of RV apparently smooth, and microscopically revealing commarginally elongated honeycomb-like hexagonal calcitic prisms of outer layer. Surface of byssal auricle exhibits three (or four) radial rows of tubercles which occur at intersections with commarginal lamellae. Resilium pit low-triangular, located near mid-point of dorsal margin. Pd I very large, ranging 261–298 μm in maximum diameter, low-conical, characterized by rudimentary byssal notch in each valve as well as pitted proximal part and radially striated distal part; Pd II absent.

Remarks. — The present species is found attached by byssus to the sediment particles, polychaete tubes and wall surface in many caves. It is also a brooding species; many specimens collected in late June of 1992 and middle April of 1993 bear several



Chlamydella tenuissima sp. nov. ウスハリナデシコ (新称)
Figures 213–216: Holotype, living specimen, RM19483a, 1.40 × 1.20 mm, from "Cross Hole" [213: left view, 214: right view, 215: umbonal area of LV (× 100), 216: umbonal area of RV (× 100)]. Figures 217–218: living specimen, RM19483a, 1.55 × 1.40 mm, from "Cross Hole" [217: right view, 218: middle surface of RV, honeycomb-like shell structure (× 400)]. Figures 219–220: LV, RM19483b, 1.85 × 1.65 mm, from "Cross Hole" [219: exterior, 220: interior].

embryos which seem to attach themselves to parent ctenidia.

It is somewhat similar to *Cyclopecten favus* Hedley, 1902, the type species of *Chlamydella*, from the lower neritic substrata of New South Wales. The radially disposed honeycomb-like prismatic microstructure of the external surface of RV agrees well with that of the Australian species. If compared with the holotype of *C. favus*, however, the present specimens show somewhat smaller shell, longer dorsal margin and stronger sculpture of byssal auricle. Moreover, divergent striae on LV are not seen, and the Pd I is much smaller and not radially striate in Hedley's specimen.

The relation between the present species and *Chlamydella incubata* sp. nov. is another problem. The two species often occur sympatrically in many submarine caves of the Ryukyu Islands, though the relative frequency is significantly different among localities. They share nearly the same microhabitats, poorly defined auricles, wide marginal apron and commarginally elongate honeycomb-like prismatic microstructure of RV. The present species, however, is distinguishable from *C. incubata* by the 1) more translucent, hyaline and prosoclinal shell, 2) undeveloped cancellate sculpture in LV, 3) somewhat shorter byssal auricle, 4) less salient Pd I with radially (not diagonally) striate surface and finely pitted central part, and 5) more commarginally elongated simple prisms in RV. Although the outline and surface sculpture show wide ranges of intrapopulational variation, there is a clear morphological gap between the two species.

Distribution. — Locally abundant in some sublittoral caves of Shimoji, Irabu and Ie Islets, Ryukyu Islands.

Suborder **Ostreina** Férussac, 1822
Superfamily **Ostreoidea** Rafinesque, 1815
? Family **Gryphaeidae** Vyalov, 1936
Subfamily **Pycnodonteinae** Stenzel, 1959
Genus ***Pycnodonte*** Fischer de Waldheim, 1835
Subgenus ***Pycnodonte*** Fischer de Waldheim, 1835

Pycnodonte* (*Pycnodonte*) *taniguchii Hayami and Kase

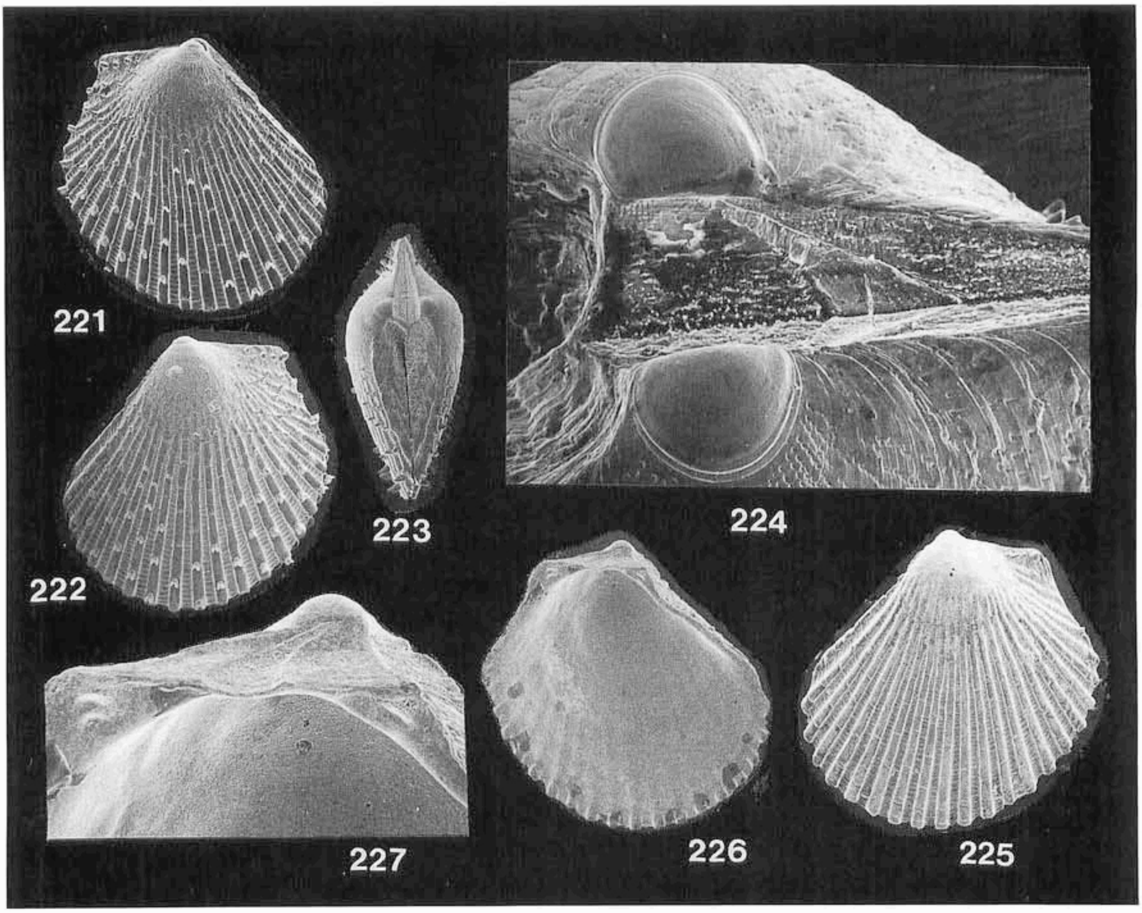
Frontispiece (figures 1–2)

1992. *Pycnodonte (Pycnodonte) taniguchii* Hayami and Kase, *Trans. Proc. Palaeont. Soc. Japan*, n. s., no.165, p.1076, figs.2-7.

1993. *Pycnodonte (Pycnodonte) taniguchii*, Hayami and Kase, *Univ. Mus. Univ. Tokyo, News*, no.27, p.1, 2 figs.

As fully described by us, this species is a significantly bradytelic "living fossil" oyster. Until now, the present oyster has been found alive on the gloomy walls and ceilings of "W-arch" (type locality), "L-arch" and "Cross Hole" of Irabu Islet, "Devil's Palace", "Toriike", "Black Hole" and "Coral Hole" of Shimoji Islet, "Daidokutsu" of Ie Islet, and below an overhang at Seragaki Beach of Okinawa. The largest colony (more than 100 living individuals) has been found on the ceiling near the entrance of "Coral Hole" (RM19604). Thus, this oyster is regarded as an important constituent of the sclerosponge fauna, at least in this region.

Color dimorphism exists in the present species, as shown in the frontispiece. One phenotype is characterized by a purplish brown shell, and the other has an ivory white shell. No intermediate individual has been found, though a few ivory individuals have dark streaks. Brownish individuals are more abundantly found than ivory individuals, according to divers who observed the colonies at "Coral Hole" and "Toriike". As preliminarily assumed, they should be regarded as due to genetic dimorphism, because the two phenotypes occur strictly sympatrically at every locality.



Lima sp. indet.
Figures 221–224: living specimen, RM19487a, 2.35 × 2.50 mm, from "Cross Hole" [221: right view, 222: left view, 223: dorsal view, 224: oblique view of umbonal area (× 100)]. Figures 225–227: LV, RM19488a, 2.80 × 2.95 mm, from "Shodokutsu" [225: exterior, 226: interior, 227: hinge area (× 40)].

Order **Limoida** Waller, 1978
Superfamily **Limoidea** Rafinesque, 1815

Family **Limidae** Rafinesque, 1815

All the limids from these submarine caves are extremely small in size, commonly exhibiting large prodissoconch I and paedomorphic features.

Genus ***Lima*** Bruguière, 1797

Lima sp. indet.
Figures 221–227

The present species is represented by a few specimens from the bottom sediment of

"Cross Hole" (RM19487, including a living individual), "Fool's Palace" (RM19485) and "Black Hole" (RM19486) of Shimoji-Irabu Islet, Miyako Islands, and a few dead specimens (RM19488) from "Shodokutsu" of Ie Islet, Okinawa.

It is characterized by small size (less than 3.5 mm in height), about 25 simple radial ribs with sparsely and quincuncially disposed small scales, very anteriorly located umbo, large posterior auricle, narrow, prosoclinal and curved ligament pit, and one or two incipient teeth on the anterior and posterior parts of the hinge plate. The outline and ornamentation strongly remind us of those of *Lima* (s. s.), but the anteriorly located umbo, large posterior auricle and narrowly curved ligament pit are similar to those of some species of *Acesta*. Moreover, unlike many shallow-water limids, the present species has large Pd I (about 260 μm in maximum diameter) and no Pd II.

These specimens seem to belong to a new species, but it is still uncertain whether the material contains adult individuals or not. The distribution pattern of scales on the external surface is essentially similar to that of *Lima tomlini* Prashad, 1932, from the lower sublittoral and bathyal depths in Indonesia, the Philippines and southern Japan, but the radial ribs are decidedly fewer, the posterior auricle is larger and the shell size is much smaller in the present species.

Genus ***Divarilima*** Powell, 1958

Divarilima elegans sp. nov.

Figures 228–235

1992. *Divarilima* aff. *iwaotakii*, Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Type and material. — Holotype: RM19489a, a right valve, from the bottom sediments of "Shodokutsu" of Ie Islet, Okinawa. Paratypes: RM19489 (dead) from the type locality. No living specimens have been found.

Diagnosis. — Small-sized, semicircular species of *Divarilima*, characterized by *Plagiostoma*-like outline, strong shell convexity, relatively short and excavated anterior margin, numerous punctations arranged in irregularly divaricate or zigzag rows, and narrowly elongate prosoclinal ligament pit.

Description. — Shell small, rarely exceeding 3.5 mm in length and height, very thin, translucent, remarkably opisthocline, semicircular, strongly convex. Dorsal margin relatively short, occupying about two-fifths of shell length, bearing numerous denticles of provinculum. Anterior auricle is very small; posterior one is moderate in size. Anterior umbonal ridge sharp, very opisthoclinal, overhanging wide and deeply excavated "lunule". Anterior margin relatively short, concave in dorsal part. Ventral and posterior margins broadly arcuate. Surface of dissoconch wholly marked with delicate punctations which are quincuncially arranged and apparently form numerous divaricate or zigzag rows. Cardinal area very wide, triangular, divided into subequal areas by ligament pit which is unusually narrow, curved and remarkably prosoclinal. Umbo located anteriorly from mid-point of dorsal margin. Pd I large, D-shaped, ranging 200–226 μm in maximum diameter; Pd II absent entirely.

Remarks. — The quincuncially arranged punctations on the surface (Figure 233), which look like divaricate or zigzag striae to the naked eye, indicate that the present species belongs to *Divarilima*. Actually, it closely resembles *Acesta iwaotakii* Habe, 1961a, from lower sublittoral substrata at several localities of south-central Japan, which was referred to *Divarilima* by Habe (1977a). Though the original line-drawing illustration of *A. iwaotakii* may look dissimilar, the actual outline and surface sculpture of that species are almost identical with those of the present species. However, the shell-size is smaller by half (the length and height exceed 6 mm in the holotype and many other specimens of *D. iwaotakii*), the ligament pit more prosoclinal, the "lunule" somewhat wider and the Pd I distinctly larger in the present species.

The anterior umbonal ridge, as defined by Cox (1943: 156), forms an obtuse angle of about 145° with the hinge axis in the present species. This value may be larger than that of *D. iwaotakii* and probably most other extant limids. The present species may also be comparable with *Lima sydneyensis* Hedley, 1904, from New South Wales, the type species of *Divarilima*, a specimen of which was recently well illustrated by Lamprell and Whitehead (1992). The shell of the present species, however, is much smaller and broader, and the ligament pit more prosoclinal. *Lima albicoma* Dall, 1886 (its illustration first appeared in Dall (1902)), from Florida and Barbados, which shares hemicircular outline and delicate divaricate striae with the present species, is certainly another congener, though the shell size of the Caribbean species is also more than twice as large.

In the shell shape, particularly the excavated anterior margin, strong and very opisthoclinal anterior umbonal ridge and wide triangular cardinal area, *Divarilima* together with *Acesta* in deep waters seems to represent a primitive group of the Limidae, which includes *Plagiostoma* and some other genera in the Mesozoic. *Divarilima* seems to be represented by a few vicariate species separately distributed in the western Pacific and Caribbean Sea, and these extant species were probably derived from a common ancestral stock before the mid-Tertiary closure of the Tethyan Ocean.

Distribution. — Empty valves occur very abundantly in the bottom sediments of a sublittoral cave of Ie Islet. No specimen has been found in the caves of Shimoji and Irabu Islets.

Genus ***Ctenoides*** Mörch, 1853

Ctenoides minimus sp. nov.

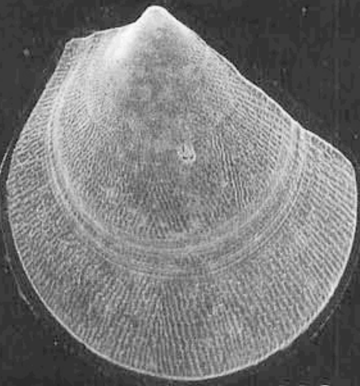
Figures 236–246

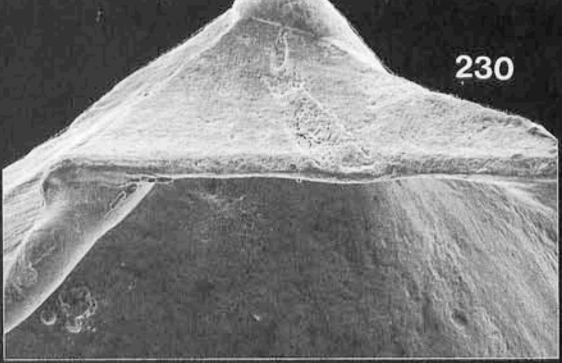
1992. *Ctenoides* sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Type and material. — Holotype: RM19495a, a right valve, from the bottom sediments of "L-arch" of Irabu Islet, Miyako Islands. Paratype: RM19490 (dead) from "Devil's Palace", RM19491 (dead) from "Fool's Palace", RM19492 (dead) from "Toriike", RM19493 (dead) from "Black Hole", RM19606 (dead) from "Coral Hole" of Shimoji Islet. RM19494 (dead) from "Lunch Hole", RM19605 (partly living) from

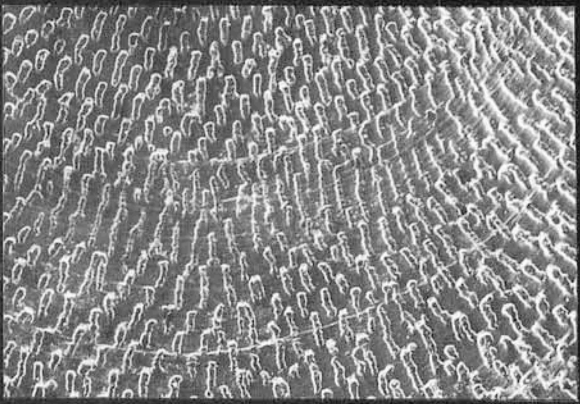
---

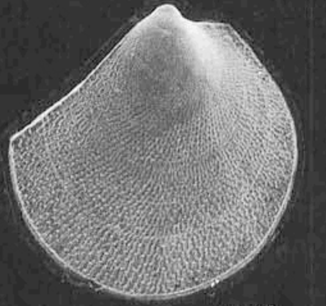
Divarilima elegans sp. nov. ヒメタキハネガイ (新称)
Figures 228–230: Holotype, RV, RM19489a, 3.10 × 3.10 mm, from "Shodokutsu" [228: exterior, 229: interior, 230: hinge area (× 65)]. Figures 231–235: LV, RM19489b, 2.55 × 2.40 mm, from "Shodokutsu" [231: exterior, 232: interior, 233: middle surface (× 65), 234: hinge area (× 65), 235: oblique view of umbonal area (× 130)].

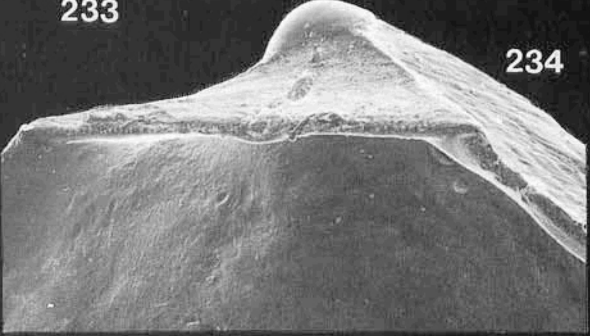

228


230

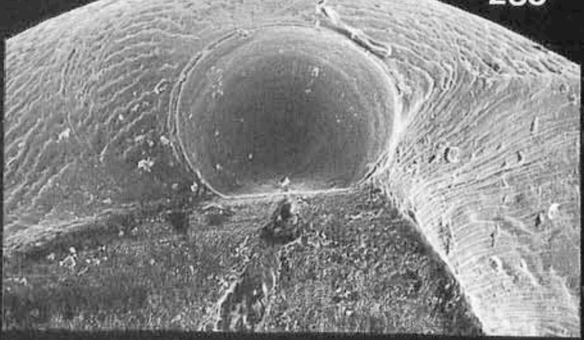

229

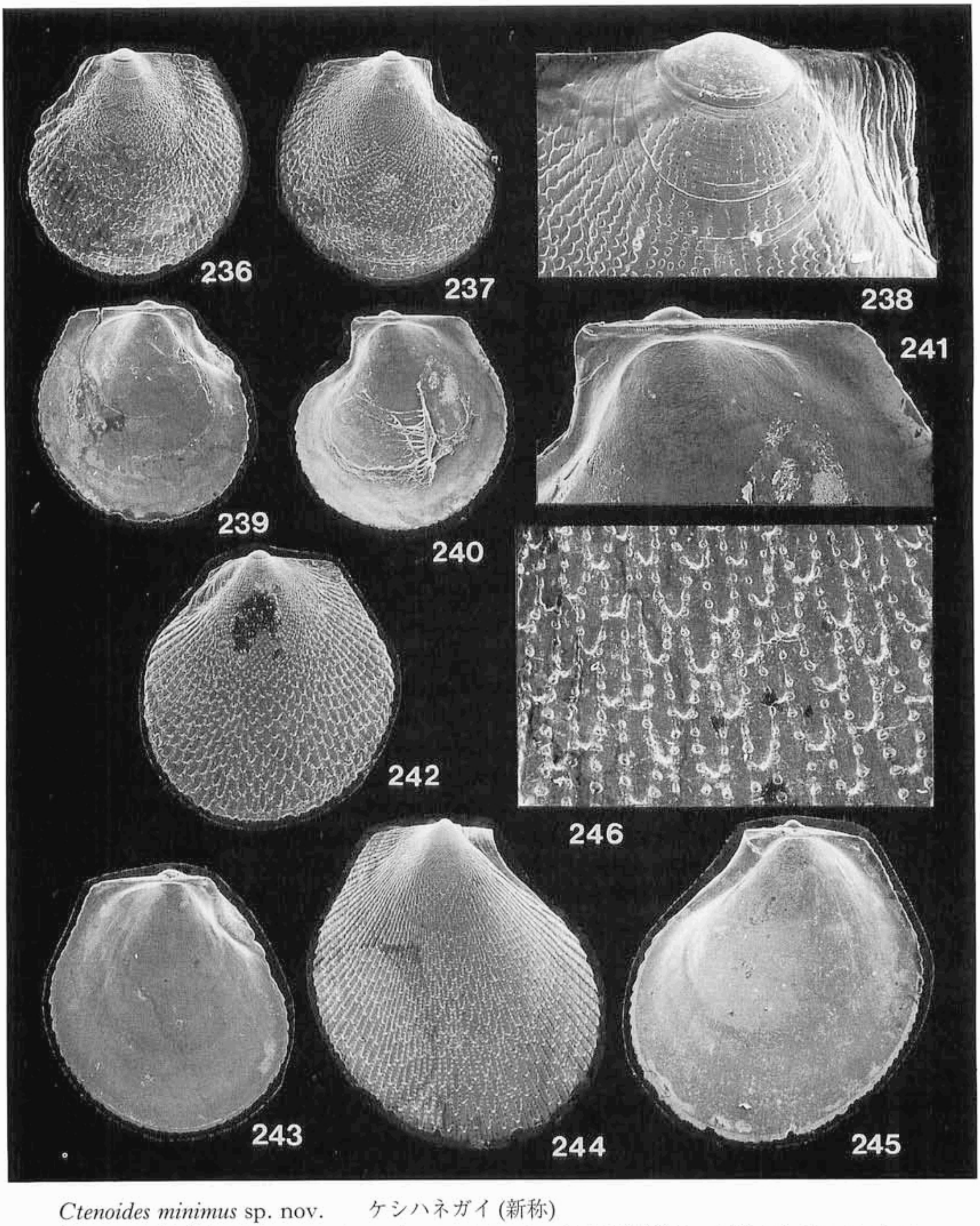

233


231


234


232


235



Ctenoides minimus sp. nov. ケシハネガイ (新称)
Figures 236–241: living specimen (separated valves), RM19605a, 1.50 × 1.55 mm, from "W-arch" [236: exterior of LV, 237: exterior of RV, 238: umbonal area of RV (× 100), 239: interior of LV, 240: interior of RV, 241: hinge area of RV (× 50)]. Figures 242–243: LV, RM19495b, 1.95 × 2.10 mm, from "L-arch" [242: exterior, 243: interior]. Figures 244–246: Holotype, RV, RM19495a, 4.00 × 4.35 mm, from "L-arch" [244: exterior, 245: interior, 246: ornaments of middle surface (× 50)].

"W-arch", RM19495 (dead) from the type locality, RM19496 (dead) from "Cross Hole" of Irabu Islet. RM19497 (dead) from "Shodokutsu" of Ie Islet.

Diagnosis. — Very small-sized and considerably inequivalve species of *Ctenoides*, characterized by opisthoclinal shell, reflected anterior auricle of LV, deeply excavated anterior margin of RV, quincuncial arrangement of punctations on early dissoconch, and numerous radial ribs with alternating scales on later dissoconch.

Description. — Shell extremely small, about 5 mm high in the largest individual, very thin, inequivalve, more or less opisthocline, subovate, not much elongated. Form ratio (height/length) 1.1–1.3, becoming larger with growth. Dorsal margin relatively long; umbo located far anteriorly from its midpoint. Anterior auricle well delimited, swollen, marked with irregular growth lamellae in LV, while its anterior margin is deeply concave in RV. Anterior umbonal ridge not developed at all. Posterior auricle not clearly demarcated but somewhat flattened. Early dissoconch marked with quincuncially disposed punctations, followed by more than 50 radial ribs with alternating scales in later dissoconch (except anterior auricle). Radial ribs not divergent, but alternating scales give an impression of diagonally oriented sculpture. Cardinal area narrow, with subvertical low-triangular ligament pit. Denticles of provinculum commonly persistent, but a rudimentary tooth observed near anterior and posterior end of hinge plate. Pd I D-shaped, large, ranging 177–203 μm in maximum diameter; Pd II absent.

Remarks. — In most caves this species is represented by empty shells, but an immature individual has been found attached pleurothetically to the surface of a rock fragment at "W-arch". The shape of anterior auricles differs remarkably between LV and RV, but a similarly asymmetric feature of this part is commonly observed in the early growth stage of the species of *Ctenoides* and Jurassic *Ctenostreon*, probably indicating pleurothetic living orientation.

The shell size of available specimens may be unusually small for *Ctenoides*, but every character suggests that it is a diminutive and paedomorphic species of this genus. The adult size is still difficult to estimate from the size frequency distribution, but abundant occurrence of empty valves in the cave sediments suggests that this is a cavernicolous species.

Distribution. — Common in many sublittoral caves of Shimoji, Irabu and Ie Islets, Ryukyu Islands. This species also occurs in "Balicasag Cave" off Panglao Islet of Bohol Island, the Philippines.

Genus ***Isolimea*** Iredale, 1929

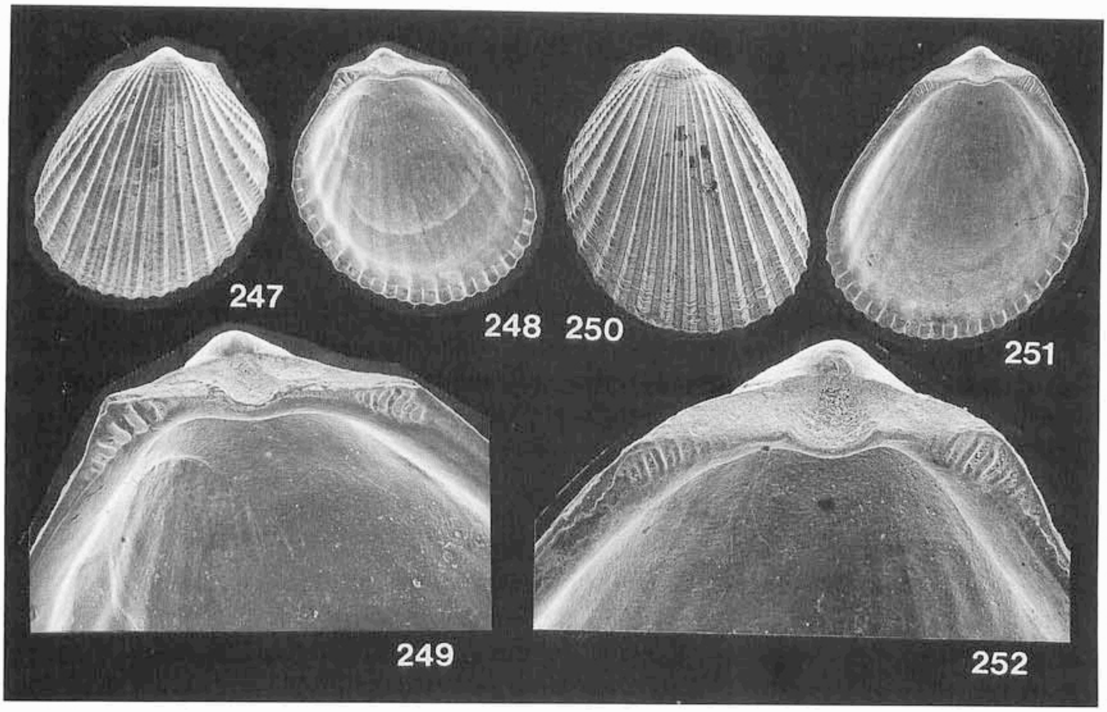
Isolimea limopsis (Nomura and Zinbo, 1934)

Figures 247–252

1934. *Lima (Limea) limopsis* Nomura and Zinbo, *Sci. Rep. Tohoku Imp. Univ.*, 2nd ser., vol.16, no.2, p.154, pl.5, figs.11–12.

1943. *Limatula (Notolimea) limopsis* (Nomura and Zinbo), Oyama, Conchologia Asiatica, vol.1, p.12, pl.1, figs.4–5.

1977. *Isolimea limopsis* (Nomura and Zinbo), Habe, Systematics of Mollusca in Japan, Bivalvia and Scaphopoda, p.103.

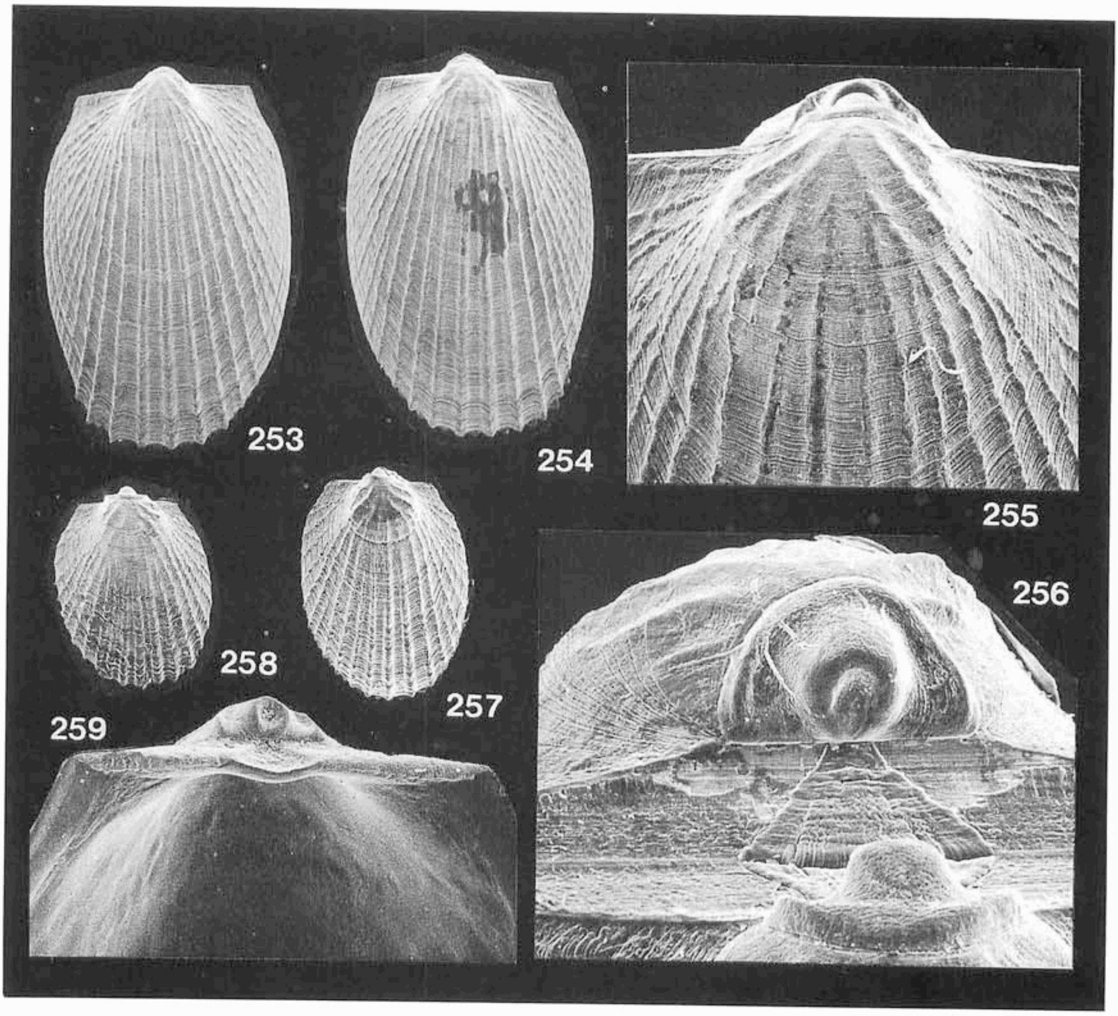


Isolimea limopsis (Nomura and Zinbo)　シラスナユキミノガイ
Figures 247–249: LV, RM19498a, 2.90 × 3.10 mm, from "Fool's Palace" [247: exterior, 248: interior, 249: hinge area (× 30)]. Figures 250–252: RV, RM19498b, 3.35 × 3.65 mm, from "Fool's Palace" [250: exterior, 251: interior, 252: hinge area (× 30)].

A few empty valves from the bottom sediments of "Fool's Palace" (RM19498) of Shimoji Islet are referable to *Lima* (*Limea*) *limopsis* Nomura and Zinbo, 1934, which was later referred to *Isolimea* by Habe (1977a). Lamprell and Whitehead (1992) treated the type species of *Isolimea*, *Limea parvula* Verco, 1908, as belonging to *Gemellima* which was proposed in the same paper by Iredale (1929). Though the distinction between *Isolimea* and *Gemellima* at the generic or subgeneric level may be controversial, the present species seems to be more closely related to the type species of *Isolimea* than that of *Gemellima*.

The shell is small, thick, higher than long, not exceeding 5.0 mm in height, subovate and opisthocline, characterized by several oblique denticles of *Limea*-type on the anterior and posterior parts of the hinge plate and about 20 radial ribs which are much narrower than their intervals. Ventral margin coarsely crenulated in accordance with radial ribs. Though the umbonal area is somewhat abraded in every observed specimen, Pd I may be about 170 μm in diameter, and Pd II seems to be absent.

The present species was first described by Nomura and Zinbo from the Pleistocene Ryukyu Limestone at Kikai Island, Kagoshima Prefecture, and later recorded from lower sublittoral substrata between Yaku Island and Miyako Islands (Habe, 1977a). Because only a few specimens have been found in the cave sediments, it is rather unlikely that the habitat is confined to cavernicolous environments.



Limatula kinjoi sp. nov. キンジョウユキバネガイ (新称)
Figures 253–256: Holotype, living specimen, RM19506a, 1.55 × 2.30 mm, from "Cross Hole" [253: left view, 254: right view, 255: umbonal area (× 70), 256: oblique view of umbonal area (× 120)]. Figure 257: immature living specimen, RM19506b, 1.15 × 1.60 mm, from "Cross Hole". Figure 258: immature RV, RM19502a, 1.10 × 1.50 mm, from "Toriike". Figure 259: hinge area of RV, RM19507a, from "Shodokutsu" (× 50).

Genus ***Limatula*** Wood, 1839

Limatula kinjoi sp. nov.

Figures 253–259

1992. *Limatula* sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.447, figs.1G,H, p.448, listed.

Type and material. — Holotype: RM19506a, a living specimen, from the bottom sediments of "Cross Hole" of Irabu Islet, Miyako Islands. Paratypes: RM19499 (dead) from "Devil's Palace", RM19500 (dead) from "Fool's Palace", RM19501 (dead) from "Witch's House", RM19502 (dead) from "Toriike", RM19503 (dead) from "Black Hole" of Shimoji Islet. RM19504 (dead) from "Lunch Hole", RM19607 (partly living) from "W-arch", RM19505 (dead) from "L-arch", RM19506 (partly living) from the type locality of Irabu Islet. RM19507 (dead) from "Shodokutsu" of Ie Islet.

Diagnosis. — Small-sized species of *Limatula*, characterized by narrow cardinal area, divaricated ribs on early dissoconch, centrally strengthened and weakly tuberculated radial ribs on later dissoconch, persistent denticles of provinculum, and large hat-shaped Pd I.

Description. — Shell very small, rarely exceeding 3.0 mm in height, nearly equilateral in young stage but slightly opisthocline in adult, about 1.7 times higher than long (though the ratio is much smaller in juveniles), white and opaque, strongly inflated. Umbo orthogyrous, situated near midpoint of dorsal margin. Dorsal margin moderate in length, truncated by anterior and posterior margins. Both auricles moderately wide, sharply angulated. Early dissoconch marked with a few irregularly divaricate ribs; later dissoconch with coarser growth lamellae and 25–30 weakly tuberculated radial ribs which are somewhat strengthened and widely spaced in the central part. Cardinal area relatively narrow, provided with relatively small low-triangular ligament pit. Adult teeth undeveloped. Denticles of provinculum persistent until the late growth stage. Pd I, large, ranging 233–265 μm in maximum diameter, hat-shaped with depressed summit of central boss and somewhat thickened brim; Pd II absent.

Remarks. — The weakly tuberculated radial ribs, persistent provinculum and relatively short shell in juvenile stage may remind one of those of the subgenus *Notolimea*, but in the adult stage the present species shares many characters with *Limatula* (s. s.) species. In addition to the unusually small adult size, the irregularly divaricate sculpture on the early dissoconch (Figure 255) seems to characterize this species. The large hat-shaped Pd I (Figures 256, 259) is also unique, because such a feature has not been recorded in any species of *Limatula*. We presume that the drastic change of ornamentation in the early dissoconch indicates the releasing stage of incubated juveniles.

Oyama (1943) described hitherto known species of *Notolimea* and *Limatula* (s. s.) in the Indo-West Pacific region. Fleming (1978) listed about 150 named fossil and extant species of *Limatula*. He classified the Pacific and southern ocean species into four subgenera: *Limatula* (s. s.), *Limatuletta* Fleming, 1978, *Stabilima* Iredale, 1939, and *Squamilima* Fleming, 1939 [an objective synonym of *Antarctolima* Habe, 1977b]. The present material, however, is not referable to any species of these subgenera in view of the unique prodissoconch shape and early dissoconch sculpture.

This species is named after Mr. S. Kinjo, a shell-collecting skilled diver of Itoman City of Okinawa, who assisted our field work and supplied many samples for study.

Distribution. — Common in many sublittoral caves of Shimoji, Irabu and Ie Islets of the Ryukyu Islands.

Genus ***Limaria*** Link, 1807

Limaria sp. indet.

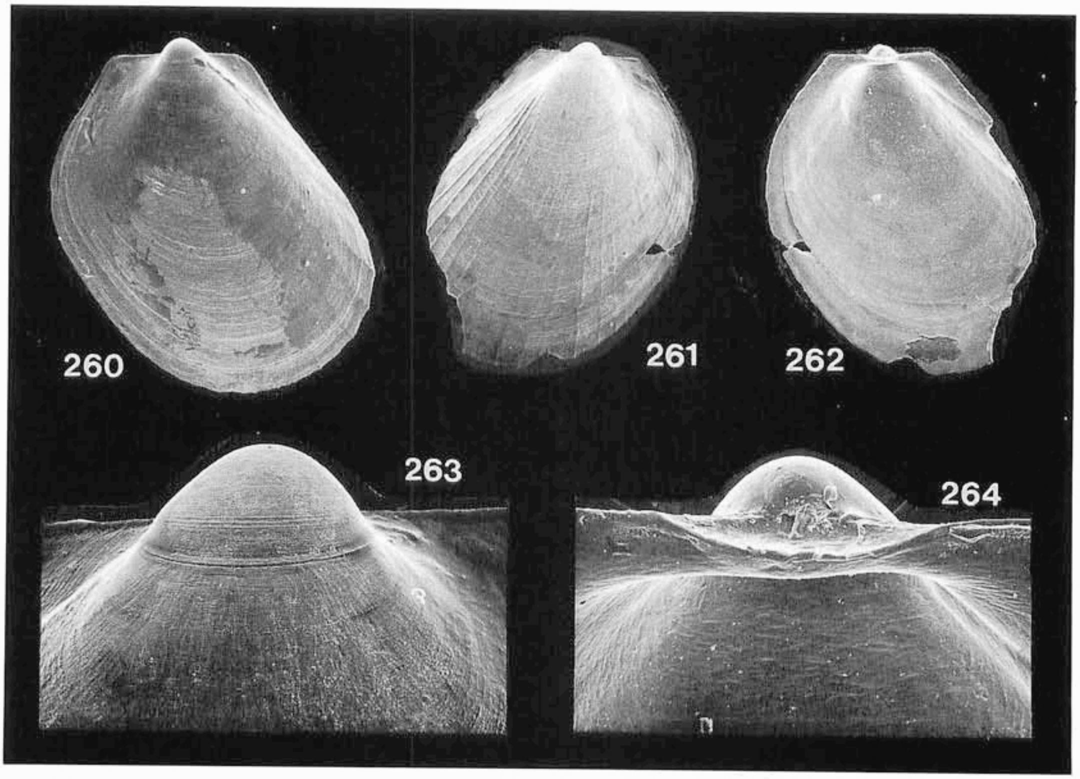
Figures 260–264

1992. *Limaria* sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

This species is represented by a few living specimens from "Cross Hole" (RM19511) in addition to many dead specimens from "Fool's Palace" (RM19508), "Black Hole" (RM19509) and "L-arch" (RM19510) of Shimoji-Irabu Islets, and also from "Shodokutsu" (RM19512) of Ie Islet.

The shell is small (though adult size cannot be estimated at present), opisthocline, translucent and very thin. The surface is nearly smooth except for about 30 irregular weak radial threads and faint *Camptonectes*-striae. The Pd I is moderate in size, ranging 84–114 μm in maximum diameter, and the Pd II, ranging 258–281 μm, is also discriminated.

This species is certainly a member of *Limaria*, and the weak radial sculpture suggests its subgenus *Limatulella* Sacco, 1898. *Limaria* (*Limatulella*) *kawamurai* Masahito and Habe, 1972, from Tosa Bay of Shikoku has a similar outline and sculpture, but is much larger than the present species. We cannot yet determine whether this is an



Limaria sp.

Figure 260: living specimen (right view), RM19511a, 1.90 × 2.20 mm, from "Cross Hole". Figures 261–264: LV, RM19512a, 2.15+ × 2.65+ mm, from "Shodokutsu" [261: exterior, 262: interior, 263: umbonal area (× 100), 264: hinge area (× 100)].

indigenous species to cryptic environments or represents only some juvenile stage of a non-cryptic species.

It also occurs in "Balicasag Cave" of Bohol Island, the Philippines.

Subclass **Heterodonta** Neumayr, 1884
Order **Lucinoida** Dall, 1889
Superfamily **Lucinoidea** Fleming, 1828
Family **Lucinidae** Fleming, 1828
Subfamily **Lucininae** Fleming, 1828
Genus ***Epicodakia*** Iredale, 1930

Epicodakia pygmaea sp. nov.

Figures 265–274

1992. *Epicodakia* sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

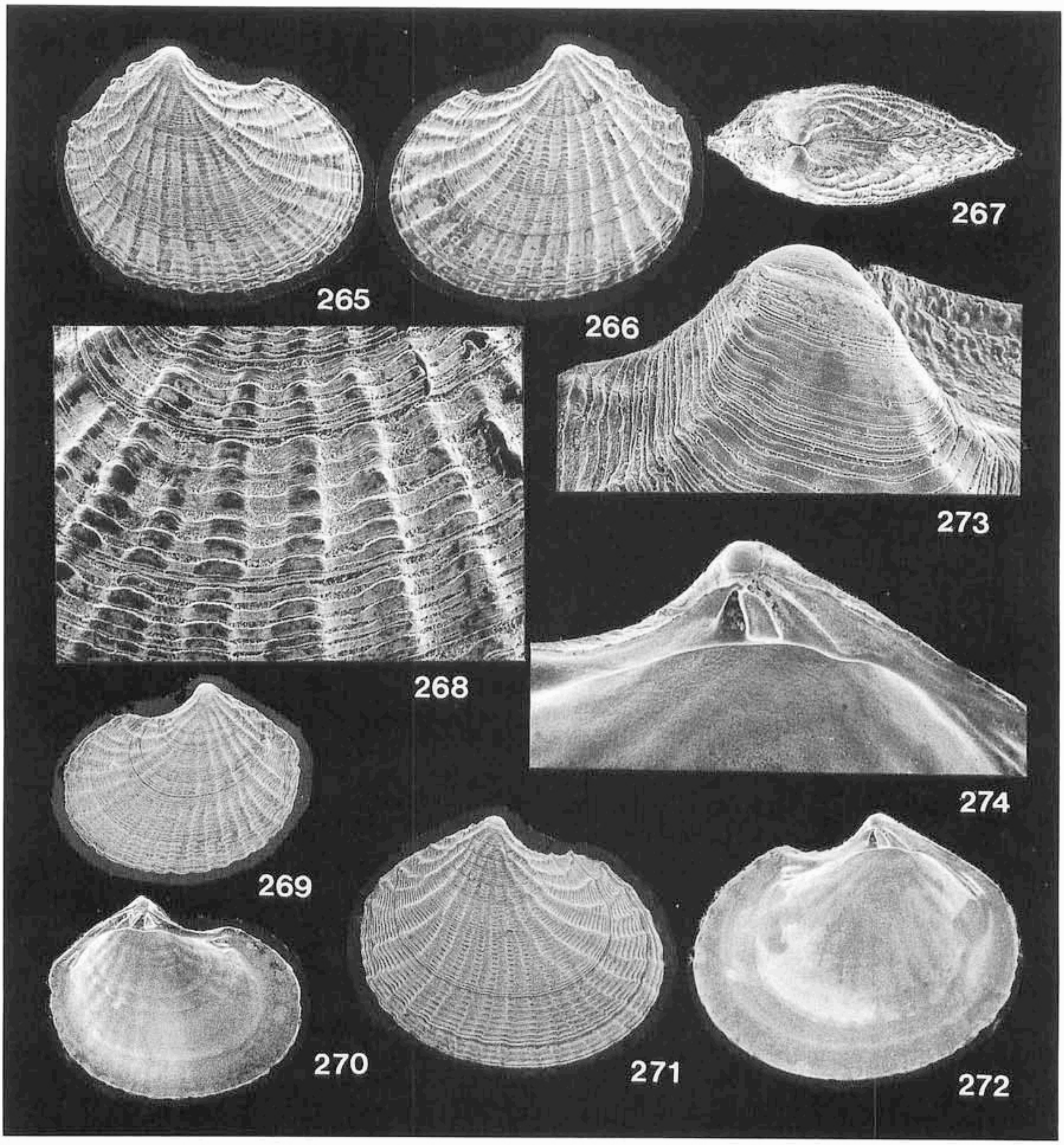
Type and material. — Holotype: RM19514a, a living specimen, from the bottom sediments of "Fool's Palace" of Shimoji Islet, Miyako Islands. Paratypes: RM19513 (living) from "Devil's Palace", RM19514 (living) from the type locality, RM19515 (dead) from "Black Hole" of Shimoji Islet. RM19516 (living) from "Lunch Hole", RM19517 (dead) from "W-arch", RM19518 (living) from "Cross Hole" of Irabu Islet. RM19519 (dead) from "Shodokutsu" of Ie Islet.

Diagnosis. — Very small-sized species of *Epicodakia*, characterized by anteriorly expanded shell, posteriorly located umbo, deeply concave pre-umbonal margin, irregularly increased divaricate ribs, well-developed commarginal lamellae, and hinge teeth typical of the genus.

Description. — Shell minute, rarely exceeding 4.0 mm in length, about 1.2 times longer than high, reddish brown when alive, comparatively thick, anteriorly expanded, not strongly inflated. Umbo small, salient, slightly prosogyrous, placed at about three-fifths of shell length from anterior end. Antero-dorsal margin deeply concave, forming an obtuse angle with anterior margin. Postero-dorsal margin very short, nearly straight, forming a rounded angle with ventral margin. Lunule indistinct. Surface wholly covered with numerous regularly spaced commarginal lamellae which are interrupted by irregularly increasing slender divaricate ribs. Marginal crenulations undeveloped. Ligament external but inframarginal. Hinge teeth typical of *Epicodakia*, as formulated: AIII (AI) (3a) 3b PIII/AIV AII 2 4b PII PIV ; 2 and 3b triangular; 4b thin, 3a not clearly separated from nymph margin, and lateral teeth tubercular, distant, located near antero-dorsal and postero-dorsal angulations. Pd I relatively large, about 150 μm in maximum diameter, though Pd II is also distinct.

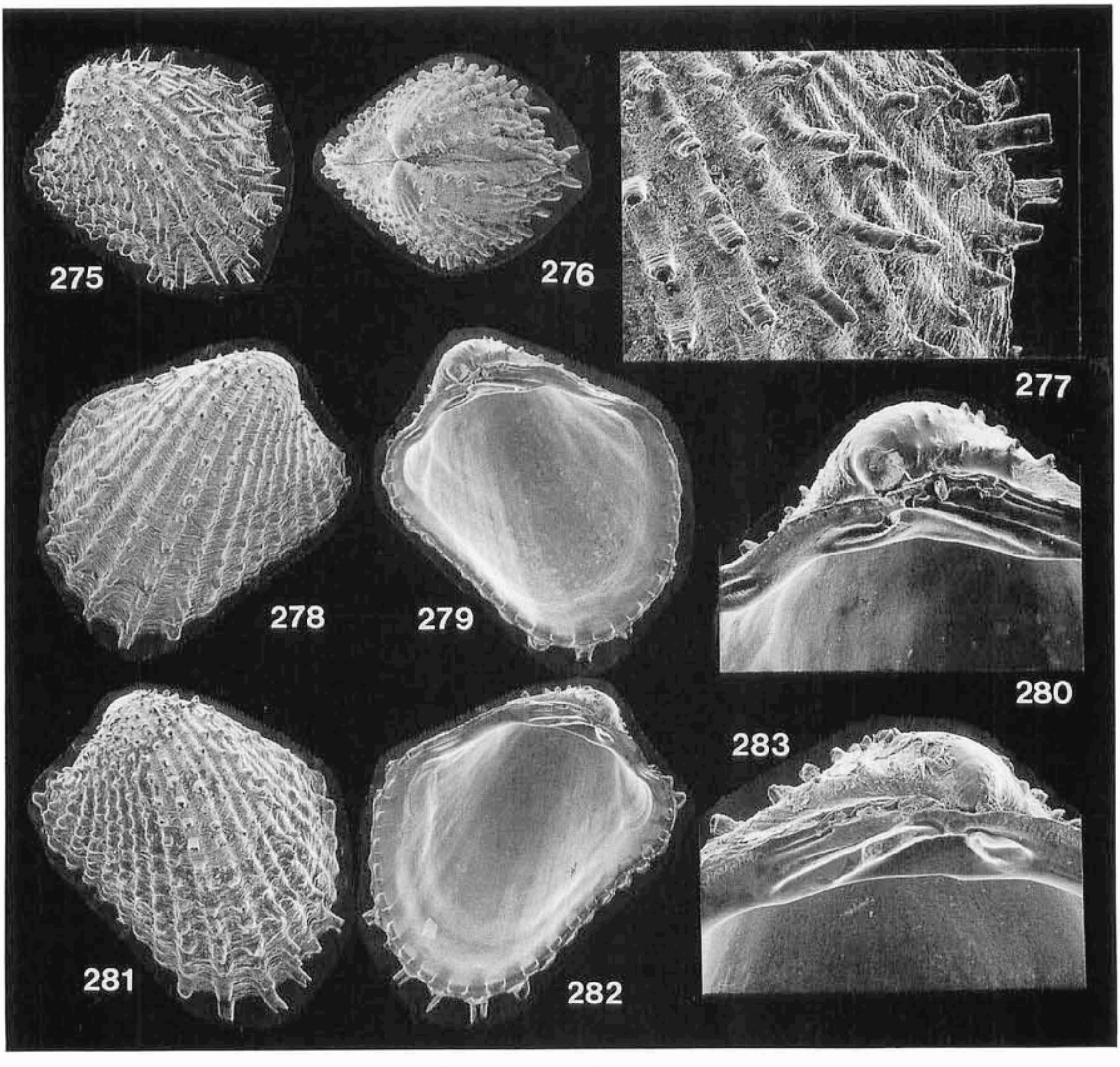
Remarks. — Although the adult shell may be unusually small, the present species is referable to *Epicodakia* by the divaricate ornaments and hinge structure typical of the genus. However, the anteriorly expanded shell, posteriorly located umbo, delicate commarginal lamellae, slender divaricate ribs and remarkably concave antero-dorsal margin seem to constitute diagnostic characters for distinguishing the present species from hitherto described species of this genus.

Distribution. — Rare in several sublittoral caves of Ie, Shimoji and Irabu Islets, Ryukyu Islands.



Epicodakia pygmaea sp. nov. コビトウミアサガイ (新称)
Figures 265–268: Holotype, living specimen, RM19514a, 3.30 × 2.75 mm, from "Fool's Palace" [265: right view, 266: left view, 267: dorsal view, 268: middle surface of LV (× 50)]. Figures 269–270: LV, RM19519a, 2.90 × 2.35 mm, from "Shodokutsu" [269: exterior, 270: interior]. Figures 271–274: RV, RM19519b, 3.75 × 3.40 mm, from "Shodokutsu" [271: exterior, 272: interior, 273: umbonal area (× 120), 274: hinge area (× 35)].

Order **Veneroida** Adams and Adams, 1856
Superfamily **Carditoidea** Fleming, 1828
Family **Carditidae** Fleming, 1828
Subfamily **Carditinae** Fleming, 1828
Genus ***Cardita*** Bruguière, 1792



Cardita uruma sp. nov. イガトマヤガイ (新称)
Figures 275–277: Holotype, living specimen, RM19523a, 3.30 × 3.40 mm, from "Cross Hole" [275: left view, 276: dorsal view, 277: surface of LV (× 30)]. Figures 278–280: RV, RM19521a, 4.00 × 4.35 mm, from "Devil's Palace" [278: exterior, 279: interior, 280: hinge area (× 25)]. Figures 281–283: LV, RM19521b, 4.20 × 4.60 mm, from "Devil's Palace" [281: exterior, 282: interior, 283: hinge area (× 30)].

Cardita uruma sp. nov.

Figures 275–283

Type and material. — Holotype: RM19523a, a living specimen, from the bottom sediments of "Cross Hole" of Irabu Islet, Miyako Islands. Paratypes: RM19521 (dead) from "Devil's Palace", RM19522 (living) from "Fool's Palace", RM19608 (living) from "Toriike" of Shimoji Islet. RM19523 (living) from the type locality of Irabu Islet. RM19524 (living) from "Shodokutsu" of Ie Islet.

Diagnosis. — Small-sized, trapezoidal, relatively short and brownish species of *Cardita*, characterized by about 20 spiniferous radial ribs, very strong shell convexity, long posterior cardinal tooth in each valve, and strongly crenulated inner margin.

Description. — Shell rarely exceeds 5.0 mm in length, commonly yellowish with brownish posterior part, trapezoidal, relatively short, strongly inflated, weakly carinate, with reduced anterior part and broadened posterior part. Umbo very prosogyrous, incurved, situated very anteriorly. Antero-dorsal margin short, deeply concave, while postero-dorsal margin is long, forming an obtuse angle with posterior margin. Ventral margin almost straight or a little concave to form byssal indentation. Surface ornamented with about 20 strong radial ribs on which a number of long half-tubular spines occur. Ligament opisthodetic, external. Dentition of *Cardita*-type, formulated as: AI 3a 3b PI/AII 2 4b PII; 3a and 2 short, subparallel to pre-umbonal margin, 3b and 4b long, very oblique, lateral teeth remote and rather weak. Pd I D-shaped, moderate in size, about 120 μm in maximum diameter. Veliconch (PdI + PdII) about 260 μm in diameter.

Remarks. — The present species has been found alive mainly on the cave walls and ceilings. In view of the external features and hinge structure the present species is undoubtedly referable to *Cardita.* It seems to be characterized by a relatively short shell, small shell size, strongly crenulated inner margin and about 20 spinose radial ribs. The spines are almost identical with those of the Japanese species generally referred to *Cardita nodulosa* Lamarck, 1819, but the shell is much smaller and shorter, and the radial ribs are more numerous in the present species.

Distribution. — This species occurs, though rather rarely, in some sublittoral caves of Ie, Shimoji and Irabu Islets, Ryukyu Islands.

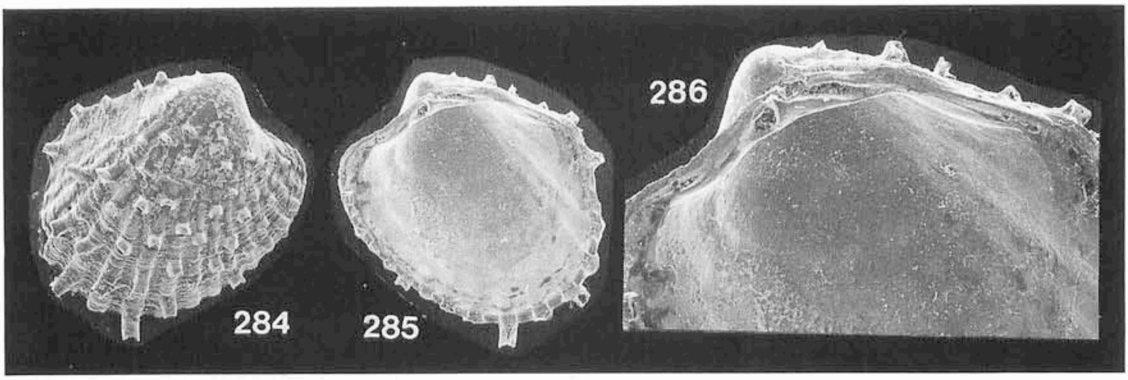
Cardita sp. indet.

Figures 284–286

1992. Carditidae sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Several dead specimens (UMUT RM19525) of another carditid were obtained from the bottom sediments of "Shodokutsu" of Ie Islet of Okinawa.

In the spinose radial ribs this species resembles *Cardita uruma* sp. nov. but is easily distinguishable from that species by the weaker shell convexity, subovate outline, absence of ventral indentation, broader radial ribs, smaller umbo and shorter cardinal teeth 3b and 4b. It is possible that they represent juvenile individuals of some non-cryptic species of *Cardita*, but the shell convexity is weaker and the Pd I is larger (ranging 165–176 μm in maximum diameter) than the known *Cardita* species around this cave.



Cardita sp. indet.
Figures 284–286: RV, RM19525a, 1.70 × 1.75 mm, from "Shodokutsu" [284: exterior, 285: interior, 286: hinge area (× 40)].

Subfamily **Carditellinae** Iredale and McMichael, 1962

Genus ***Carditella*** Smith, 1881

Carditella, as defined by Chavan *in* Cox et al. (1969), seems to include several small carditids mainly from lower sublittoral substrata of the Indo-Pacific low-middle latitudinal regions. Recently numerous individuals of two minute species, which probably belong to this genus, have been found alive on calcareous muddy sediments in the innermost part of sublittoral caves of Okinawa.

Carditella iejimensis sp. nov.

Figures 287–294

1992. *Carditella* sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.
1993. *Carditella* sp., Hayami and Kase, *Univ. Mus. Univ. Tokyo, News*, no.27, p.3, fig.8.

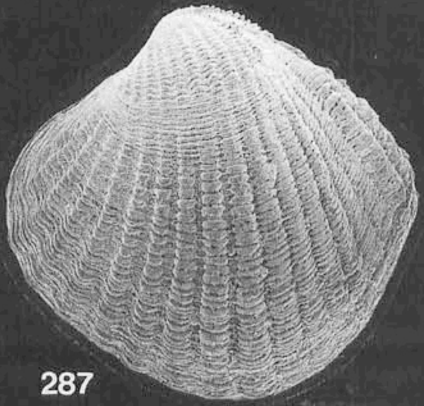
Type and material. — Holotype: RM19526a, a living specimen, from the bottom sediments of "Shodokutsu" of Ie Islet, Okinawa. Paratypes: RM19526 (living) from the type locality, RM19571 (living) from "Daidokutsu" of Ie Islet.

Diagnosis. — Small-sized cryptic species of *Carditella*, characterized by subquadrate outline, considerably developed resilium, clearly delimitted lunule and escutcheon, lucinoid teeth typical of the genus, and 16–20 granulated radial ribs, two of which are scaly and stronger than others in early dissoconch and delimit posterior area and escutcheon.

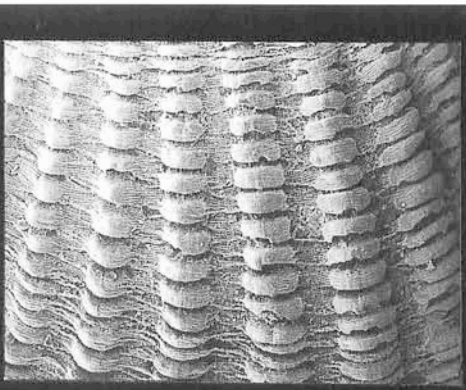
Description. — Shell very small, rarely exceeding 3.3 mm in length and height,

---

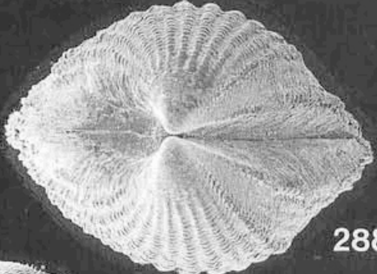
Carditella iejimensis sp. nov. イエジマケシザルガイ (新称)
Figure 287: Holotype, living specimen (left view), RM19526a, 2.75 × 2.65 mm, from "Shodokutsu". Figure 288: living specimen (dorsal view), RM19526b, 2.40 × 2.35 mm, from "Shodokutsu". Figures 289–292: LV, RM19526c, 3.15 × 3.05 mm, from "Shodokutsu" [289: exterior, 290: interior, 291: middle surface (× 50), 292: hinge area (× 70)]. Figures 293–294: RV, RM19526d, 3.20 × 3.05 mm, from "Shodokutsu" [293: interior, 294: hinge area (× 70)].



287

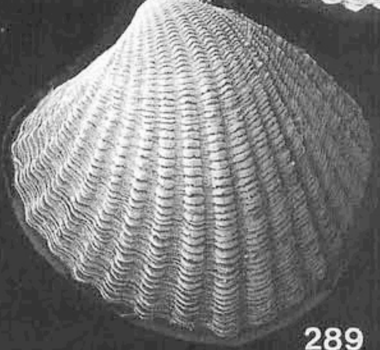


291

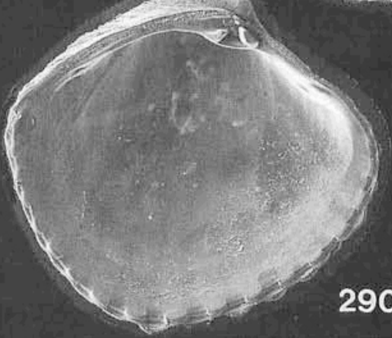


288

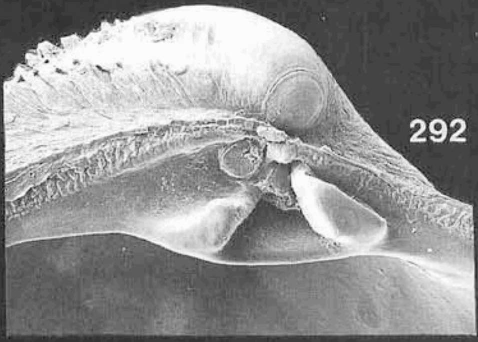
293



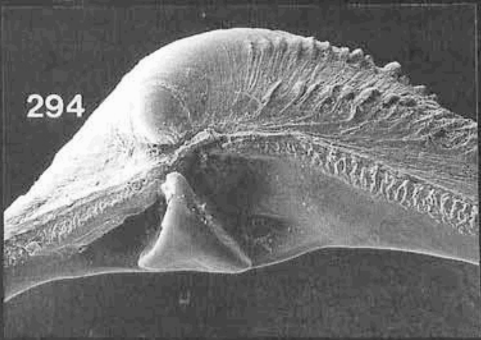
289



290



292



294

subquadrate, translucent but light-brownish when alive, slightly longer than high, moderately thick, strongly inflated. Umbo prosogyrous, contiguous, located about two-fifths of shell length from anterior end. Antero-dorsal margin long, a little concave; postero-dorsal margin feebly convex, turning somewhat abruptly into posterior margin. Lunule and escutcheon wide, distinct, not ornamented. Surface covered with 16–20 (18 on average) radial ribs which appear granular owing to numerous strong commarginal lamellae; on early dissoconch two radials are scaly and more prominent than others, corresponding to small posterior and escutcheon carinae, though the difference in prominence becomes insignificant with growth. Marginal crenulations distinct. Ligament external but continuous to a developed resilium just behind beak. Hinge teeth typical of the genus, as formulated: AIII (3a) 3b PIII/AII 2 4b PII; 3a not clearly separated by valve margin, 3b triangular, very thick, 2 and 4b also stout, and lateral teeth lamellar and weak. Dorsal margin retains numerous denticles of provinculum. Pd I comparatively large, suborbicular, ranging 130–157 μm in maximum diameter; Pd II not discriminated.

Remarks. — Numerous living individuals were found on the sediment surface of a totally dark cave "Shodokutsu". The present species is somewhat similar to *Carditella infans* Smith, 1885, from the south of New Guinea in its small shell size, granulated radial ribs and persistent denticles along dorsal margin. Such granulated surface are also known in many described species of *Carditella*; the subquadrate shell and two stronger radial ribs defining the posterior area and escutcheon in the early dissoconch are so characteristic that none of them seems to be closely related to the present species. Some species of the genus *Pleuromeris* Conrad, 1867, exhibit a similarly granulated surface, but its type-species, *P. decemcostata* Conrad, 1867, possesses the more obliquely elongated cardinal tooth 3a.

Venericardia quadriangulata Nomura and Zinbo, 1934, from the Upper Pleistocene fore-reef sediments of Kikai Island, Kagoshima Prefecture, resembles the present species in the subquadrate outline, but the fossil species is characterized by much larger shell size and fewer radial costae than the present species.

Distribution. — This carditid is the most dominant molluscan species in the caves of Ie Islet, but no specimen has been found from any cave of Shimoji and Irabu Islets of Miyako Islands.

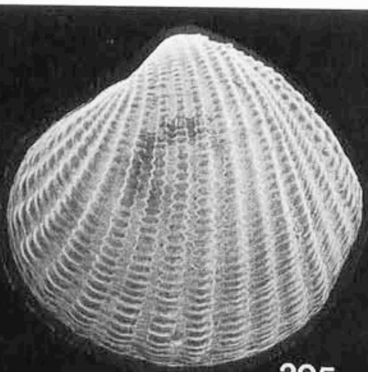
Carditella shimojiensis sp. nov.

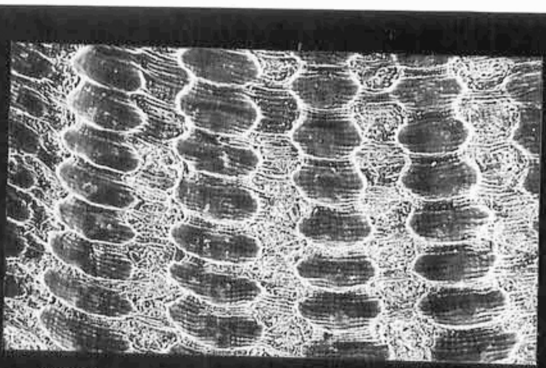
Figures 295–303

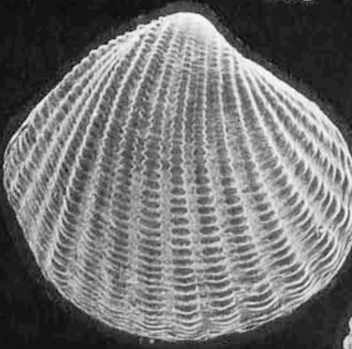
Type and material. — Holotype: RM19527a, a living specimen, from the bottom sediments of "Fool's Palace" of Shimoji Islet, Miyako Islands. Paratypes: RM19527 (living) from the type locality, RM19528 (dead) from "Black Hole", RM19609 (dead) from "Toriike" of Shimoji Islet.

Carditella shimojiensis sp. nov. シモジケシザルガイ (新称)

Figures 295–298: Holotype, living specimen, RM19527a, 2.95 × 2.80 mm, from "Fool's Palace" [295: left view, 296: right view, 297: dorsal view, 298: middle surface of RV (× 50)]. Figures 299–301: LV, RM19527b, 3.20 × 3.10 mm, from "Fool's Palace" [299: exterior, 300: interior, 301: hinge area (× 70)]. Figures 302–303: RV, RM19527c, 3.20 × 3.15 mm, from "Fool's Palace" [302: interior, 303: hinge area (× 70)].

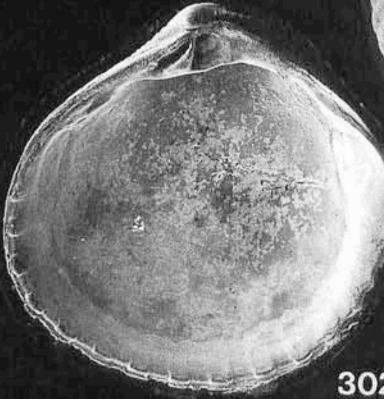

295


298

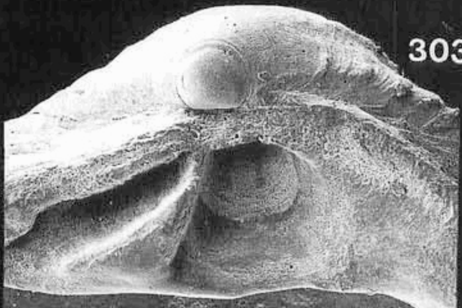

296

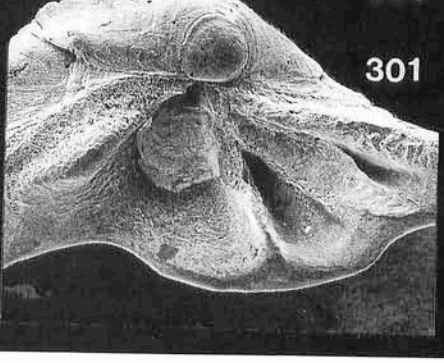

299


297


302


300


303


301

Diagnosis. — Small-sized cryptic species of *Carditella*, characterized by subovate outline, large triangular resilium below umbo, opisthoclinal cardinal teeth, and about 18 radial costae which are somewhat finer on posterior area.

Description. — Shell small, rarely exceeding 3.3 mm in length, subovate in outline, white, pink or yellow (probably due to polymorphism) when alive, slightly longer than high, moderately inflated. Umbo prosogyrous, contiguous, located near mid-length of shell. Antero-dorsal margin long, nearly straight; postero-dorsal margin feebly convex, turning abruptly to posterior margin. Lunule and escutcheon distinct, not ornamented. Surface covered with 16–19 broad radial costae, which become somewhat finer on posterior area and are marked with numerous densely spaced commarginal lamellae. Ventral margin coarsely crenulated in accordance with radial costae. On early dissoconch two radials scaly and more prominent than others, corresponding to small posterior and escutcheon carinae, though the prominence becomes insignificant with growth. Resilium unusually large, triangular, situated below beak, whereas external ligament seems to be poorly developed. Lucinoid cardinal teeth pushed in front of resilium pit; all of 2b, 3b and 4b opisthocline and relatively thin. A small tooth-like ridge commonly developed behind resilium pit in LV. Pd I D-shaped, relatively large, about 130 μm in maximum diameter; Pd II absent.

Remarks. — The present species is very similar to *Carditella iejimensis* sp. nov. in the surface sculpture, but is easily distinguishable from that species by the narrower posterior area, weaker shell convexity and more centrally placed umbo. Moreover, the hinge structure is considerably different; the resilium pit is much larger, the outer ligament undeveloped, cardinal teeth much thinner and more opisthocline, and lateral teeth better developed.

Thiele (1935) regarded *Carditella* as belonging to the Condylocardiidae, probably because of the subinternal ligament in the type and other constituent species. The presence of a large resilium pit below the umbo and a small post-resilial tooth in LV suggest that the *C. shimojiensis* is actually intermediate between *Carditella* of the Carditidae and *Carditopsis* of the Condylocardiidae. If the *C. iejimensis* and *C. shimojiensis* are phylogenetically related to each other, it may be strongly suggested that evolutionary change of ligament from external to internal (or vice versa) has occurred rather easily.

Distribution. — The present species occurs only in two caves of Shimoji Islet, Miyako Islands.

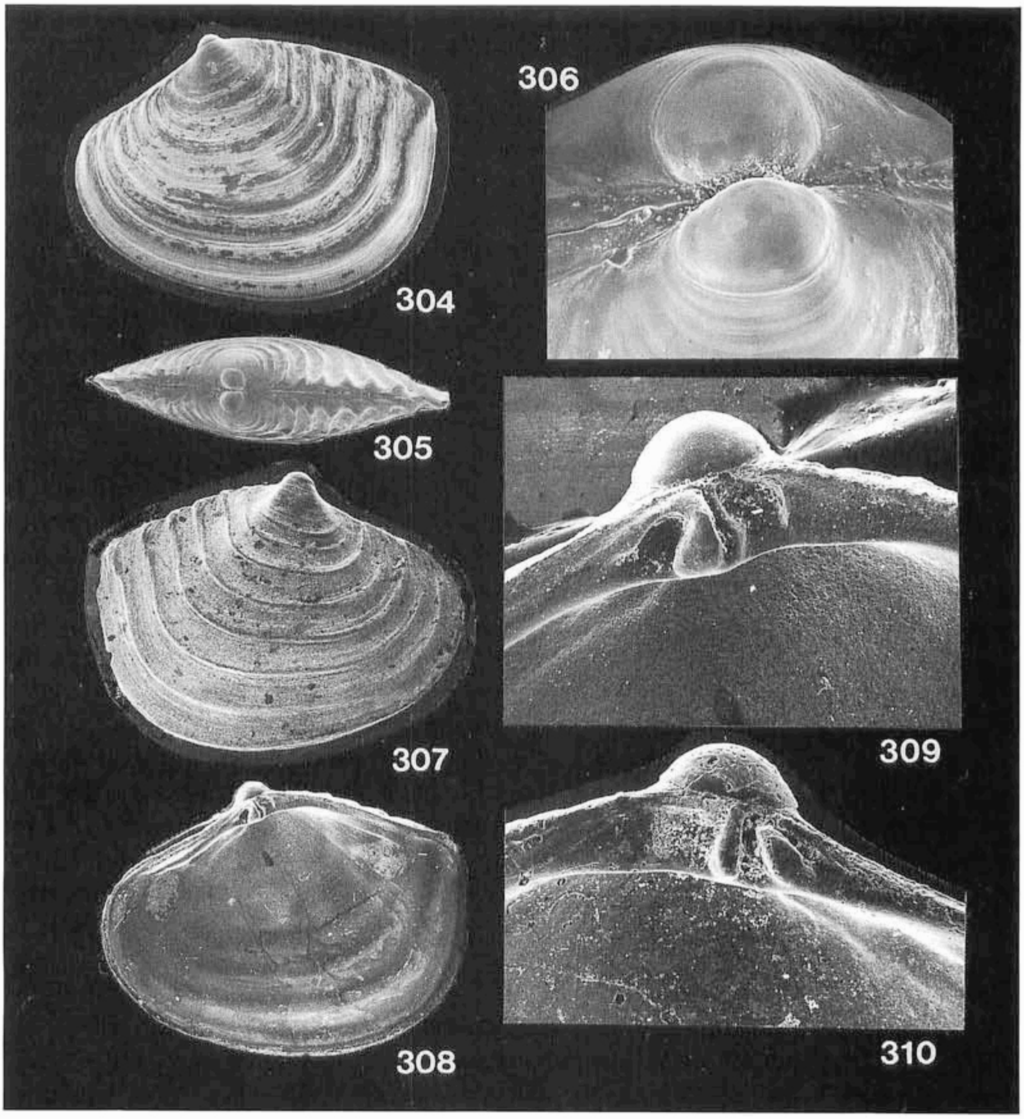
Superfamily **Crassatelloidea** Férussac, 1822
Family **Crassatellidae** Férussac, 1822
Subfamily **Crassatellinae** Férussac, 1822
Genus ***Salaputium*** Iredale, 1924

Salaputium unicum sp. nov.

Figures 304–310

1992. *Salaputium*? sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Type and material. — Holotype: RM19530a, a living specimen, from the bottom sediments of "Fool's Palace" of Shimoji Islet, Miyako Islands. Paratypes: RM19529



Salaputium unicum sp. nov.　チビモシオガイ (新称)
Figures 304–306: Holotype, living specimen, RM19530a, 2.85 × 2.25 mm, from "Fool's Palace" [304: left view, 305: dorsal view, 306: oblique view of umbonal area (× 100)]. Figures 307–309: RV, RM19532a, 2.25 × 1.65 mm, from "Shodokutsu" [307: exterior, 308: interior, 309: hinge area (× 100)]. Figure 310: hinge area of LV (× 100), RM19532b, from "Shodokutsu".

(living) from "Devil's Palace", RM19530 (living) from the type locality of Shimoji Islet. RM19531 (living) from "Cross Hole" of Irabu Islet. RM19532 (dead) from "Shodokutsu" of Ie Islet.

Diagnosis. — Small-sized crassatellid, characterized by the truncated posterior area, highly salient umbo, widely spaced and sharp commarginal lamellae, non-crenulated margin, two cardinal teeth and long lateral teeth in each valve, and large hemispherical

Pd I.

Description. — Shell very small, rarely exceeding 3.0 mm in maximum length, colorless and opaque, trigonally ovate, weakly convex, about 1.3 times longer than high. Umbonal angle about 130 degrees, comparatively large for crassatellids. Umbo slightly prosogyrous, conically salient, located near mid-length. Antero-dorsal margin long and a little concave; postero-dorsal margin slightly convex, almost rectangularly truncated by posterior margin. Lunule defined by a ridge but very narrow. Surface ornamented with widely spaced and sharp commarginal lamellae, the interval of which is marked with faint growth lamellae. No marginal crenulations. Hinge plate comparatively narrow. Dentition formulated as: (AI) AIII 3a 3b PIII/AII 2 4b PII; 3a rudimentary, 3b rounded triangular, 2 opisthocline, 4b thin and nearly vertical, both lateral teeth elongated along valve margin. Resilium adjacent to posterior cardinal tooth. Pd I large, hemispherical, ranging 193–201 μm in maximum diameter; Pd II absent.

Remarks. — Because the posteriorly truncated shell and highly salient umbonal area are unique, the generic reference of the present species is by no means convincing. The hinge structure, however, is almost identical with that of the type species of *Salaputium*. No comparable species has been described from Japanese waters.

It is somewhat similar to *Crassatella rhomboides* Smith, 1885, from the shallow-sea of south New Guinea and near Cape York, but the umbonal angle is much larger, the umbo is more centrally placed, and the interval of commarginal lamellae lacks radial threads. Cotton and Godfrey (1938) regarded three crassatellids from south Australia as belonging to *Salaputium*. Among others, the specimen of *Salaputium micrum* (Verco, 1895) from the depth of 16–110 fathoms off Fremantle somewhat resembles the present species in outline. The shell-size of the present specimens is, however, much smaller.

Distribution. — Rare in sublittoral caves of Ie, Shimoji and Irabu Islets, Ryukyu Islands.

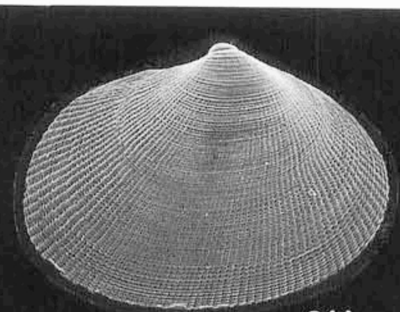
Superfamily **Mactroidea** Lamarck, 1809
Family **Mesodesmatidae** Gray, 1839
Subfamily **Erviliinae** Dall, 1895

Genus ***Rochefortina*** Dall, 1924

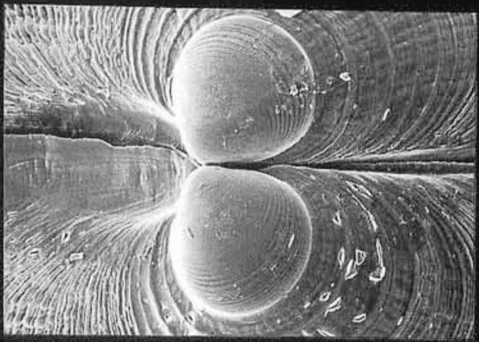
Rochefortina has been regarded as belonging to the Mesodesmatidae, but its taxonomic position is still ambiguous, because of the unique hinge structure and microscopically wrinkled and pitted surface. Its type species, *Ervilia sandwichensis*, was

---

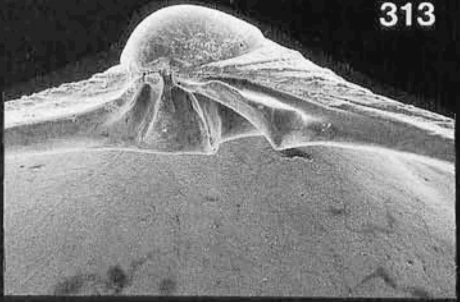
Rochefortina sandwichensis (Smith) ハコベノハナガイ
Figures 311–313: living specimen, RM19540a, 3.00 × 2.20 mm, from "Cross Hole" [311: left view, 312: dorsal view, 313: dorsal view of umbonal area (× 75)]. Figures 314–316: RV, RM19540b, 3.25 × 2.35 mm, from "Cross Hole" [314: exterior, 315: interior, 316: hinge area (× 75)]. Figures 317–320: LV, RM19540c, 3.10 × 2.35 mm, from "Cross Hole" [317: exterior, 318: interior, 319: oblique view of umbonal area (× 150), 320: hinge area (× 75)].


311

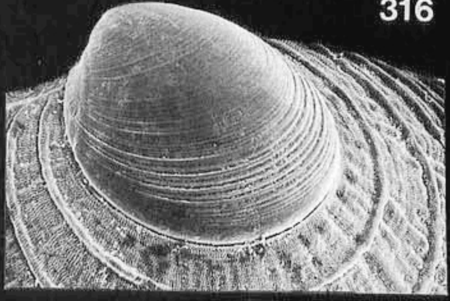

312


313

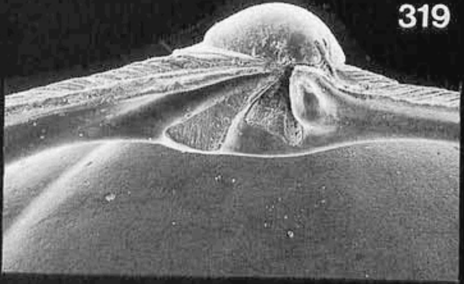

314


316


315


319


317


320


318

originally described from Hawaii, and has been widely known from the upper sublittoral sandy bottom of southern Japan, as recorded by Sakurai and Habe (1973).

Rochefortina sandwichensis (Smith)

Figures 311–320

1885. *Ervilia sandwichensis* Smith, *Rep. Sci. Res. Voy. H. M. S. Challenger*, Zool., vol.13, p.81, pl.25, figs.5–5b.
1924. *Rochefortina semele* Dall, *Proc. Biol. Soc. Wash.*, vol.37, p.88.
1938. *Rochefortina sandwichensis*: Dall, Bartsch and Rehder, *Bernice P. Bishop Mus., Bull.* 153, p.169, pl.44, figs.9–12.
1953. *Spondervilia rubra* Laseron, *Rec. Austr. Mus.*, vol.23, p.52.
1973. *Rochefortina sandwichensis*: Sakurai and Habe, *Venus*, vol.32, p.7.
1979. *Ervilia sandwichensis*: Kay, *Hawaiian Marine Shells*, sec.4, p.558.
1992. *Rochefortina* cf. *sandwichensis*: Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Material. — RM19533 (dead) from "Devil's Palace", RM19534 (living) from "Fool's Palace", RM19535 (living) from "Witch's House", RM19536 (dead) from "Toriike", RM19537 (dead) from "Black Hole" of Shimoji Islet. RM19538 (dead) from "Lunch Hole", RM19539 (living) from "L-arch", RM19540 (living) from "Cross Hole" of Irabu Islet. RM19541 (dead) from "Shodokutsu" of Ie Islet.

Description. — Shell small, scarcely exceeding 3.5 mm in length, variable in coloration (white, yellow and pink) when alive, oblong, moderately thick and convex, 1.3–1.4 times longer than high, commonly whitish or yellowish but sometimes tinted with three brownish or pinkish radiating bands. Umbo slightly prosogyrous, located a little posterior from mid-length of shell. Antero-dorsal margin long, a little concave in front of umbo; postero-dorsal margin comparatively short, roundly arcuate, passing gradually into posterior margin. Escutcheon depressed, narrow but distinct. Surface covered with numerous crowded, increasingly radial riblets and fine commarginal lamellae which reveal cancellate appearance. Numerous microscopic wrinkles and punctations distributed on whole surface of dissoconch. Inner margin not crenulated. Resilium situated in a depressed triangular pit just below umbo, bordered by a pair of ridges in RV. A narrow prosoclinal cardinal tooth present in RV; a tubercular tooth in front of the resilium and a thick triangular tooth behind the resilium in LV. Lateral tooth, if present, weak and indistinct. Pd I small, 75–85 μm in maximum diameter, followed by Pd II which is hemispherical, brownish or pink in color; veliconch (Pd I + Pd II) 240–248 μm in maximum diameter.

Remarks. — In every macroscopic characteristic and shell size the present material is indistinguishable from *Ervilia sandwichensis* Smith, 1885, the type-species of *Rochefortina*, from the Hawaiian Islands, though we have not yet done SEM observations of the Hawaiian specimens. The holotype of this species, in the British Museum (Natural History), is a left valve collected from the bottom (40 fathoms) off the reefs at Honolulu, Oahu Island. Dall, Bartsch and Rehder (1938) and Kay (1979) gave more detailed descriptions of this species. Moreover, Smith (1885) and Dall, Bartsch and Rehder (1938) noticed the presence of well-demarcated and colored prodissoconch, which corresponds well with the features of the Pd II in the present material. The maximum shell size and polymorphic coloration of the shell are also comparable with those of the Hawaiian specimens.

Spondervilia rubra Laseron, 1953, from New South Wales, as pointed out by Sakurai and Habe (1973), is probably identical with *Rochefortina sandwichensis*, though detailed comparison should be based on SEM observation of original specimens.

The present species is not necessarily an indigenous cryptic bivalve, because abraded valves have been found occasionally in beach sand in southern Japan. The abundant occurrence of living specimens in these caves, however, is remarkable.

Distribution. — Common in many sublittoral caves of Ie, Shimoji and Irabu Islets, Ryukyu Islands. This species also occurs in "Balicasag cave" off Panglao Islet of Bohol Island, the Philippines. It has been recorded from many localities (Amami, Goto and Hachijo Islands and Kii Peninsula) of southern Japan in addition to the Hawaiian Islands and Australia.

Superfamily **Arcticoidea** Newton, 1891

Family **Kelliellidae** Fischer, 1887

Genus ***Kelliella*** Sars, 1870

The genus *Kelliella* is represented by about a dozen minute species, most of which have been known from abyssal to hadal depths in three major oceans (Knudsen, 1970; Bernard, 1989), even though it seems to have inhabited shallower waters until the Middle Miocene (Studencka, 1987). The occurrence of a representative of this genus from an upper sublittoral cave in subtropical region is, therefore, very remarkable. The cave species, as well as *Kelliella nakayamai* Habe, 1953, from the Holocene fossil bed of Kyushu, shares the cyprinoid hinge teeth, well-demarcated lunule and other diagnostic characters of this genus with deep-water species. Knudsen (1970) mentioned the presence of a fine furrow running along the circumference of valves in *Kelliella brunni* (Filatove, 1969) and *K. indica* Knudsen, 1970. Such a furrow is clearly observed in RV of the type species of *Kelliella* (Warén, 1989) and the present cave species (Figures 312, 319).

Kelliella japonica sp. nov.

Figures 321–330

1992. *Kelliella* sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Type and material. — Holotype: RM19543a, a right valve, from the bottom sediments of "Shodokutsu" of Ie Islet, Okinawa. Paratype: RM19542 (dead) from "Fool's Palace", RM19610 (dead) from "Coral Hole" of Shimoji Islet and RM19543 (dead) from the type locality. No living specimens have been found.

Diagnosis. — Small-sized species of *Kelliella* characterized by suborbicular outline, densely spaced commarginal lamellae, a sharp groove clearly delimiting wide lunule and giving a distinct notch to antero-dorsal margin, a fine furrow along the circumference of RV and a corresponding ridge in LV, and cyprinoid hinge consisting of two subparallel teeth in RV and a tubercular and a winding lamellar tooth in LV.

Description. — Shell generally smaller than 2.5 mm in length, suborbicular but slightly longer than high, strongly inflated, white and shiny. Umbo prosogyrous, located about two-fifths of shell length from anterior end. Antero-dorsal and postero-dorsal margins gently arcuate without umbonal angulation. A narrow sharp groove delimits wide lunule, giving a distinct small notch to the antero-dorsal margin. Surface marked with fine irregular commarginal lamellae, the interval of which becomes denser toward ventral margin. Internal surface shiny, without marginal crenulations. A fine internal furrow and a corresponding ridge run along the whole circumference (except for the hinge plate) in RV and LV, respectively. Ligament opisthodetic, external. Hinge teeth of cyprinoid-type, as formulated: 3a (1) 3b/2a–2b 4b; 3a lamellar and nearly horizontal, 1 distant from umbo (might better be called AI), 2a–2b forming a winding subhorizontal tooth, 3b and 4b tubercular; lateral teeth undeveloped. Pd I relatively small, D-shaped, ranging 75–120 µm in maximum diameter; Pd II distinct; veliconch (Pd I + Pd II) ranging 158–199 µm in diameter, commarginally striated.

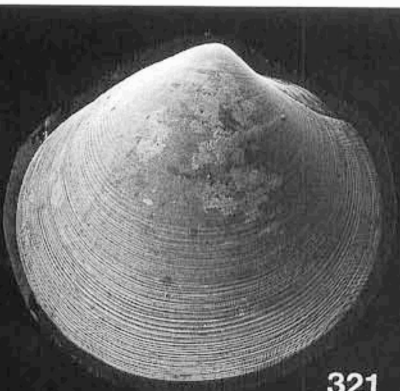
Remarks. — The present species is represented only by several disarticulated valves. Every essential feature of the shell indicates that it is a congener with deep-water species of *Kelliella*. In fact, the size, disposition of hinge teeth, well-defined lunule, features of Pd I and Pd II and other essential shell characters are surprisingly similar to those of the type species of *Kelliella*, *K. miliaris* (Philippi, 1844) [= *K. abyssicola* Sars, 1870] from the lower sublittoral and bathyal depths of the northern Atlantic and Mediterranean, an Iceland specimen of which was well illustrated by Warén (1989). The umbo of the present species, however, looks somewhat lower and broader than that of *K. miliaris*.

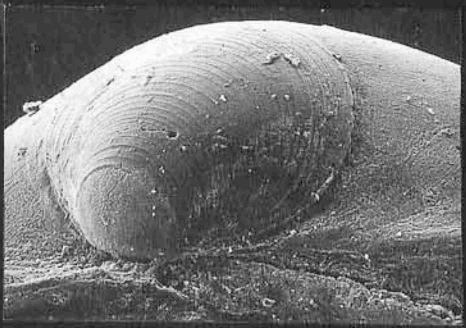
In the shell shape and hinge structure it also resembles *Kelliella galatheae* Knudsen, 1970, from the abyssal bottom of the eastern Pacific and *Kelliella sundaensis* Knudsen, 1970, from the hadal bottom of Sunda Trench. It differs, however, from *K. galatheae* in the smaller umbo and much smaller shell size and from *K. sundaensis* in the more clearly delimited lunule. *Kelliella barbara* Studencka, 1987, from the Middle Miocene of Poland also reveal similar hinge structure, but the umbo is more highly raised above the dorsal margin in that species. *Kelliella elegantula* Bernard, 1989, from British Columbia differs from the present species in the more elongated and lamellar posterior cardinal teeth.

In Japanese waters no extant species of *Kelliella* had been recorded, but the Holocene lower sublittoral-bathyal fossil bed at an islet Moeshima in Kinko Bay near Kagoshima of Kyushu yields numerous specimens of an undoubted species, *Kelliella nakayamai* Habe, 1953. As our SEM observations show, however, the fossil species is characterized by the broader umbo, better differentiated cardinal tooth 2a–2b, shallower groove demarcating the lunule and a more transversely elongated shell than the present species.

Distribution. — Rare in a few sublittoral caves of Ie and Shimoji Islet, Ryukyu Islands.

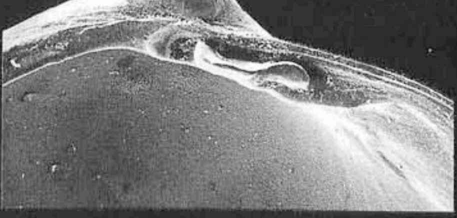
Kelliella japonica sp. nov. マルケシハマグリ (新称)
Figures 321–324: Holotype, RV, RM19543a, 2.20 × 2.05 mm, from "Shodokutsu" [321: exterior, 322: interior, 323: dorsal view of umbonal area (× 250), 324: hinge area (× 75)]. Figures 325–327: LV, RM19543b, 2.05 × 1.95 mm, from "Shodokutsu" [325: exterior, 326: interior, 327: hinge area (× 75)]. Figures 328–330: RV, RM19542a, 1.90 × 1.70 mm, from "Fool's Palace" [328: exterior, 329: interior, 330: umbonal area (×50)].


321

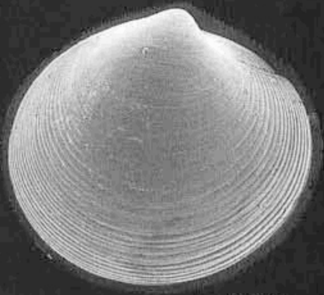

323


322


324


327


325


328


329


326


330

Family **Trapeziidae** Lamy, 1920
Genus ***Coralliophaga*** de Blainville, 1824

Coralliophaga hyalina sp. nov.

Figures 331–338

1992. Vesicomyidae? sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

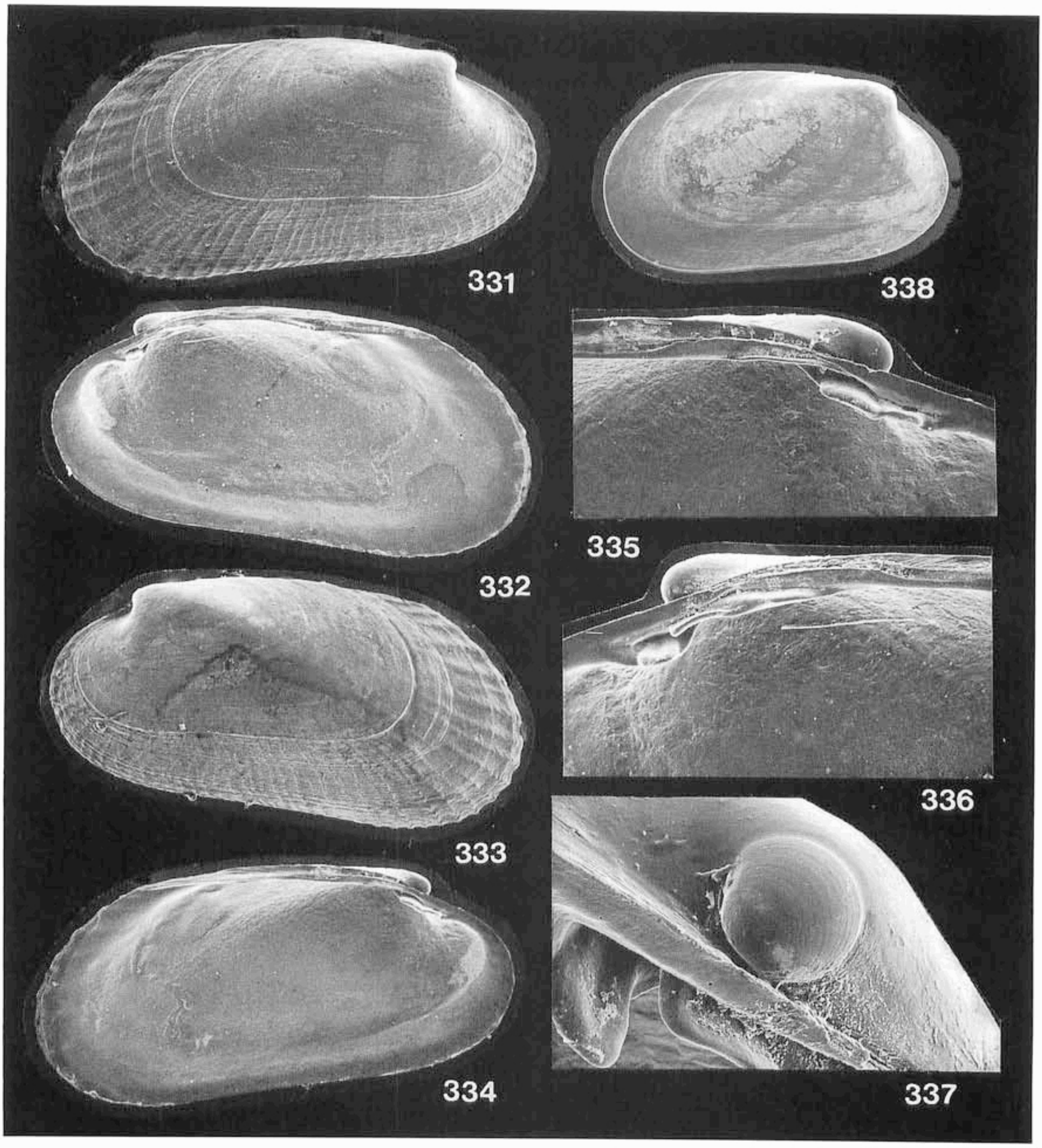
Type and Material. — Holotype, RM19544a, a living specimen, from the bottom sediments of "Devil's Palace" of Shimoji Islet, Miyako Islands. Paratypes: RM19544 (living) from the type locality, RM19545 (dead) from "Fool's Palace", RM19546 (dead) from "Witch's House", RM19611 (dead) from "Coral Hole" of Shimoji Islet. RM19547 (dead) from "Lunch Hole", RM19548 (dead) from "W-arch", RM19549 (living) from "Cross Hole" of Irabu Islet. RM19550 (dead) from "Shodokutsu" of Ie Islet.

Diagnosis. — Very small-sized, hyaline, cocoon-shaped species of *Coralliophaga*, characterized by expanded posterior area, a little concave ventral margin, nearly smooth surface but with numerous variably developed radial threads, and platy cardinal teeth disposed subparallel to valve margin.

Description. — Shell very small for genus, scarcely exceeding 5.5 mm in length, elongate-elliptical, 1.5–1.9 times longer than high, very thin and hyaline, moderately convex, not carinate, with reduced anterior part and expanded posterior part. Umbo small, very prosogyrous, located about one-fifth of shell-length from anterior end. Short antero-dorsal and long postero-dorsal margins gently arcuate with similar curvature, not clearly separated below umbo. Ventral margin slightly concave in middle portion. Lunule and escutcheon not discriminated. Early dissoconch nearly smooth except for weak commarginal lamellae, but later dissoconch marked with variably developed radial threads, which give weak marginal crenulations along posterior margin. Dentition surely of cyprinoid, though difficult to formulate, characterized by two platy cardinal teeth subparallel to dorsal margin in each valve and an elongated ridge-like lateral tooth along postero-dorsal margin in RV. Ligament external, elongated along post-umbonal margin. Pallial line shallowly sinuate below posterior adductor scar. Pd I small, hemispherical, ranging 72–97 μm in maximum diameter; Pd II reddish brown in fresh shell; veliconch (Pd I + Pd II) ranging 138–166 μm in maximum diameter.

Remarks. — The genus *Coralliophaga* is represented by a few coral-nestling species in tropical-subtropical shallow seas in both the Indo-West Pacific and the Atlantic. This genus is generally characterized by somewhat irregular outline and several raised commarginal lamellae in the adult stages. Although the living specimens of the present species were collected from the sediment surface, they remind us of immature individuals of *Coralliophaga* species in their cocoon-shaped outline, translucent shells, subparallel lamellar cardinal teeth and feeble radial threads, though the development of radial threads as well as the form ratio is considerably variable. The cocoon-shaped outline is also considerably similar to that of the type-species of the subgenus Oryctomya Dall, 1898, from the Eocene of Alabama, but the shell is much smaller and the radial threads are not tuberculated in the present species.

The variably developed radial threads and general outline are similar to those of the umbonal part of *Coralliophaga coralliophaga* (Gmelin, 1791), which is known as a



Coralliophaga hyalina sp. nov. ガラスマツカゼガイ (新称)
Figures 331–337: Holotype, living specimen (separated valves), RM19544a, 3.10 × 1.80 mm, from "Devil's Palace" [331: exterior of RV, 332: interior of RV, 333: exterior of LV, 334: interior of LV, 335: hinge area of LV (× 50), 336: hinge area of RV (× 50), 337: umbonal area of RV (× 150)]. Figure 338: living specimen (right view), RM19549a, 4.70 × 3.00 mm, from "Cross Hole".

dominant coral nestler in the western Pacific (Morton, 1980, 1983, 1990). The limited maximum size in several samples and the fact that the commarginal lamellae often becoming denser toward the ventral margin indicate that the present material includes adult individuals. At present, we regard this species as a product of paedomorphic evolution.

Distribution. — Common in several sublittoral caves of Shimoji, Irabu and Ie Islets, Ryukyu Islands. This species also occurs in "Balicasag Cave" off Panglao Islet of Bohol Island, the Philippines, and "Chandelier cave" near Koror, Palau Islands.

Genus ***Glossocardia*** Stoliczka, 1870

Glossocardia was proposed by Stoliczka (1870: 189) on a large ventricose species, *Cypricardia obesa* Reeve, 1843, from India. It has been generally assigned to the family Trapeziidae, as Stoliczka (1870) and Keen (*in* Cox et al., 1969) regarded it as a subgenus of *Trapezium* Megerle von Mühlfeld, 1811. Although it looks somewhat similar to *Trapezium* in the subquadrate and carinated shell, the hinge structure, especially the disposition of well-developed cardinal and posterior lateral teeth reminds us of some genera of the Cretaceous Arcticidae, e.g. *Veniella* Stoliczka, 1870. Little has been known about the ancestry and fossil record of *Glossocardia*, but its archaic morphology and cryptic habitat seem to suggest that this genus is an example of "living fossils".

Glossocardia obesa (Reeve, 1843)

Figures 339–347

1843. *Cypricardia obesa* Reeve, Conchologia Iconica, vol.2, pl.2, fig.10.

1870. *Glossocardia obesa*: Stoliczka, *Palaeont. Indica*, ser.6, vol.3, p.189.

1875. *Cypricardia obesa*: Woodward, A Manual of the Mollusca, p.467, pl.20, fig.4.

1951. *Glossocardia obesa*: Habe, Genera of Japanese Shells, Pelecypoda, no.1, p.118, figs.247, 248.

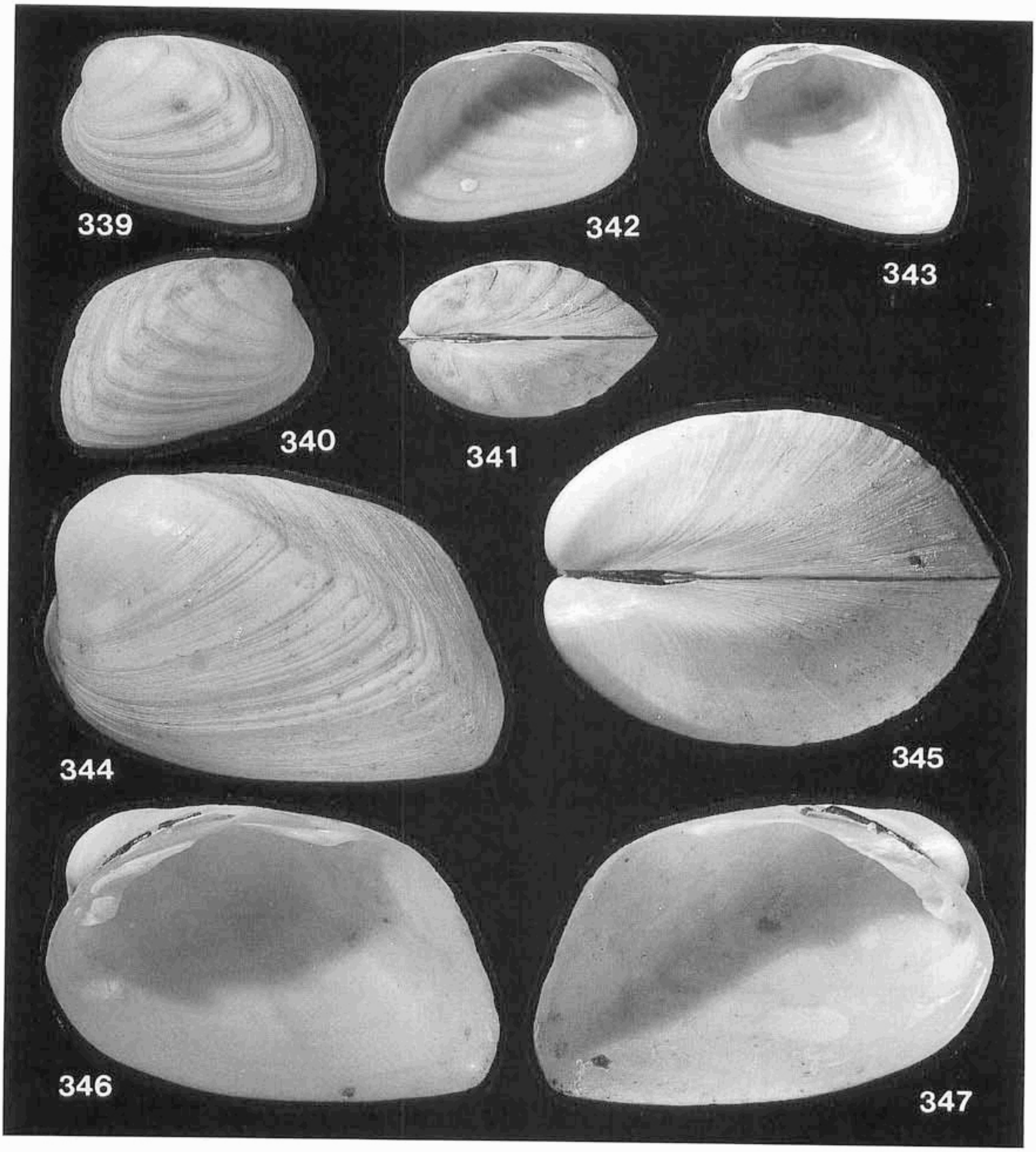
1969. *Trapezium* (*Glossocardia*) *obesum*: Keen in Cox et al., Treatise on Invertebrate Paleontology, Part N, vol.2, p.N655, fig.E132-1a,b.

1977. *Glossocardia obesa*: Habe, Systematics of Mollusca in Japan, Bivalvia and Scaphopoda, p.234, pl.50, figs.1, 2.

Material. — The material related to the present study consists of a few specimens of various growth stages. One is a large articulated specimen (RM19551a) found near the entrance of "Daidokutsu" of Ie Islet, Okinawa, and other specimens are living and dead juveniles (RM19552) from the sediments of "Cross Hole" of Irabu Islet, Miyako Islands.

Descriptive remarks. — *Glossocardia obesa* was originally described from India by Reeve (1843) and subsequently recorded from Mauritius (Stoliczka, 1871). It has been said to occur also in the tropical West-Pacific region, but its distribution and habitat have not been clarified. Little has been known about its ontogenetic and anatomical features. *G. obesa* may also be an uncommon species in southern Japan, but cooperative divers found fresh empty shells (and, rarely, living individuals) in and around submarine caves open to fore-reef slopes in the Ryukyu Islands.

The specimens from the Ryukyus are similar to the Indian specimens (Reeve, 1843; Woodward, 1875; Fischer, 1880–87) in hinge and other essential characters. The out-



Glossocardia obesa (Reeve) ツキヨミガイ

Figures 339–343: immature CV, RM19552a, 48.7 × 25.5 mm, from "Cross Hole" [339: exterior of LV, 340: exterior of RV, 341: dorsal view of CV, 342: interior of LV, 343: interior of RV]. Figures 344–348: CV, RM19551a, 69.9 × 44.6 mm, from "Daidokutsu" [344: exterior of LV, 345: dorsal view of CV, 346: interior of RV, 347: interior of LV]. (all figures by optical photography) line of the shell is, however, slightly different; the adult articulated specimen (exceeding 65mm in length and 50mm in thickness) from Ryukyu looks more strongly ventricose, more transversely elongated with almost linearly truncated (not sinuate) posterior margin, as illustrated by Habe (1951, 1977a) and herein (Figures 334–338). The difference is attributable to geographic variation within a species, even though subspecific distinction may be possible for the west Pacific populations.

The arcticoid dentition of *G. obesa* can be formulated as: 3a 1 3b PI PII/2a 2b 4b PII. The anterior lateral teeth are undeveloped; 3a very diminutive and rudimentary, 1 large and tubercular (though lamellar and much weaker in juvenile stage), 3b elongated and bifid, 2a and 2b continuous, forming an arch, and posterior lateral teeth completely developed.

The juvenile specimens from "Cross Hole" reveal less ventricose and shorter valves and more centrally located umbo in comparison with the adult specimens. The prodissoconch features are unknown.

Prashad (1932) described another species, *Glossocardia stoliczkana*, from a Siboga station in the Sulu Sea (564 m in depth). The hinge structure resembles that of *G. obesa* (especially its juvenile specimens), but the holotype of the bathyal species differs from the present juvenile specimens of similar size in the more obtusely angulated postero-dorsal corner and more distinct median carina.

The shell of *G. obesa* is almost free from sculpture and appears to be defenseless against predators, unlike many clams in and around coral reefs. These lines of evidence suggest that *G. obesa* represents a relict species inhabiting cryptic environments, even though the fossil record of this genus is scarcely known.

Superfamily **Veneroidea** Rafinesque, 1815
Family **Veneridae** Rafinesque, 1815
Subfamily **Tapetinae** Adams and Adams, 1857

Genus ***Irus*** Schmidt, 1818

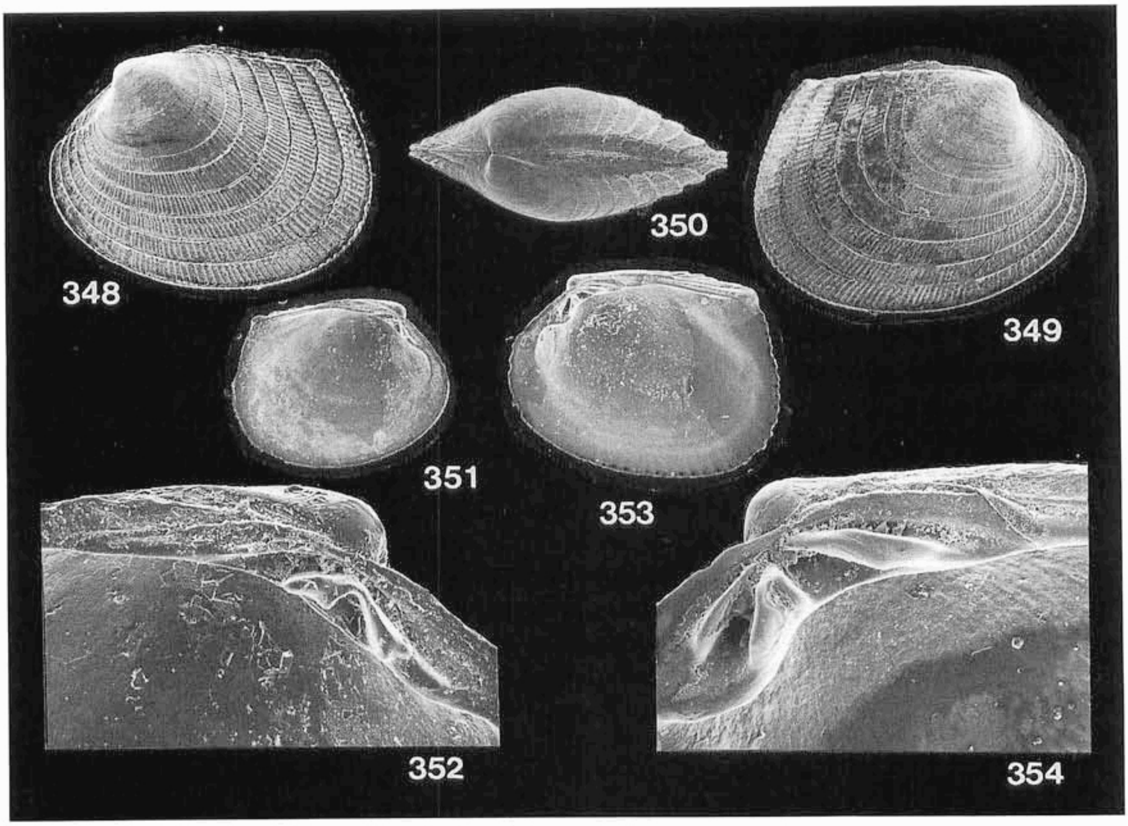
The species of *Irus* are commonly rock-nestling organisms (Morton, 1983; others). They are microcryptic, utilizing small rock (or coral reef) cavities which were bored by other organisms. Two minute species of *Irus*, unlike several described species of this genus, were found alive on the sediment surface in these caves; one is characterized by numerous radial threads between raised commarginal lamellae, and the other is not. These are preliminarily described as stunted cavernicolous species, but it is still uncertain whether the present materials contain adult specimens or merely represent young crawling stages of rock-nestling species.

Subgenus ***Irus*** Schmidt, 1818

Irus (***Irus***) sp. indet.

Figures 348–354

Several specimens were found alive on the bottom sediments of "Lunch Hole" (RM19555) and "Cross Hole" (RM19556) of Irabu Islet, Miyako Islands. Dead specimens were also found from "Devil's Palace" (RM19553), and "Fool's Palace"

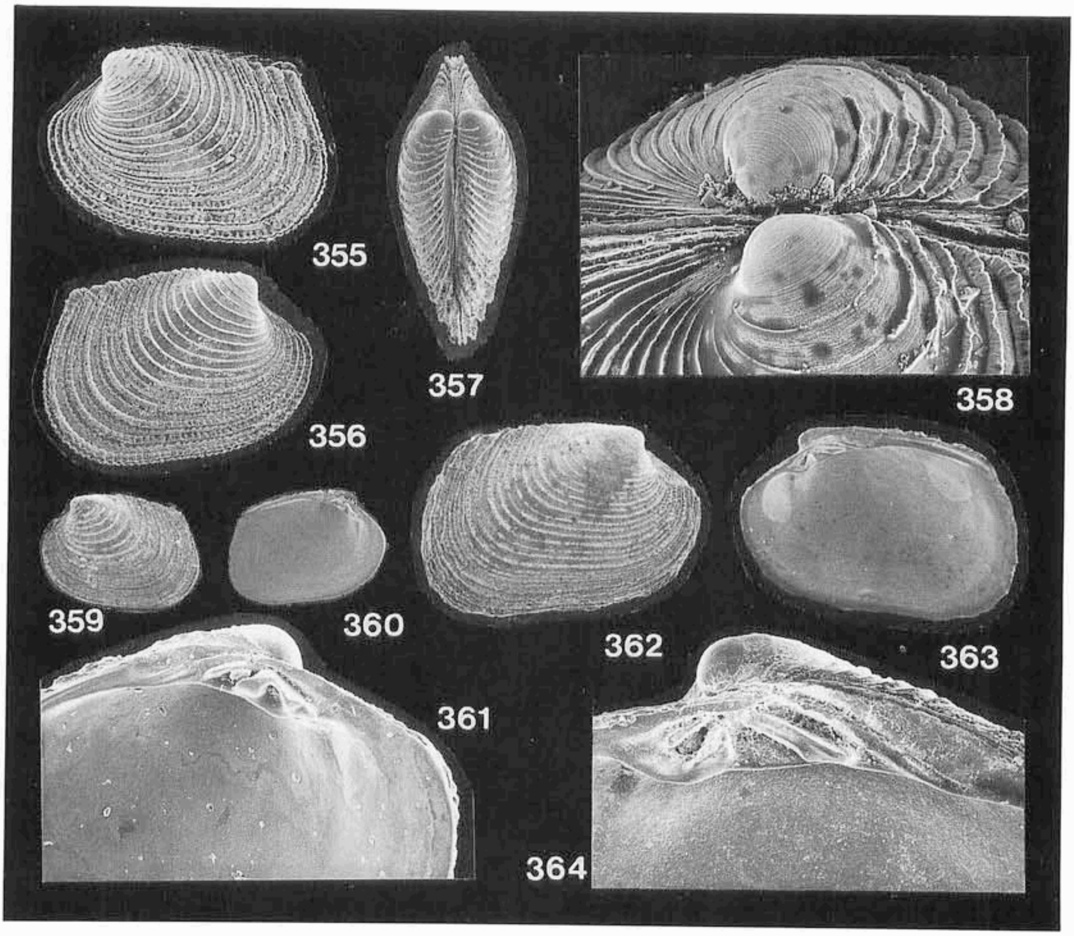


Irus (*Irus*) sp. indet.
Figures 348–350: living specimen, RM19556a, 4.15 × 3.30 mm, from "Cross Hole" [348: left view, 349: right view, 350: dorsal view]. Figures 351–352: LV, RM19553a, 2.65 × 2.25 mm, from "Devil's Palace" [344: interior, 345: hinge area (× 50)]. Figures 353–354: RV, RM19553b, 3.35 × 2.60 mm, from "Devil's Palace" [353: interior, 354: hinge area (× 50)].

(RM19554) of Shimoji Islet.

The shell is subquadrate and regular in shape, very small, about 4 mm in length, white or light brownish, strongly inflated, about 1.3 times longer than high, having widely spaced, narrow but highly raised commarginal lamellae, the intervals of which are marked with numerous radial riblets. Lunule is wide but weakly delimited. Posterior area is obtusely truncated. Hinge typical of veneroid, consisting of three cardinal teeth and a pair of lateral teeth in each valve with long external ligament. Pd I is small, and Pd II is clearly demarcated.

The present species resembles the juvenile stage of *Irus* (*Irus*) *macrophyllus* (Deshayes, 1854) and some other species of this subgenus in the surface ornamentation. No specimen larger than 5 mm, however, has been found in the cave sediments. One possibility is that the present material represents a stunted paedomorphic species adapted to such a cavernicolous environment. Similarly, small specimens of the same species occur in the bottom sediments of "Balicasag Cave" of Bohol, the Philippines.



Irus (*Notirus*) sp. indet.
Figures 355–358: living specimen, RM19558a, 2.35 × 1.75 mm, from "Cross Hole" [355: left view, 356: right view, 357: dorsal view]. Figure 359–361: LV, RM19558b, 2.05 × 1.45 mm, from "Cross Hole" [359: exterior, 360: interior, 361: hinge area (× 40)]. Figures 362–364: RV, RM19558c, 3.50 × 2.50 mm, from "Cross Hole" [362: exterior, 363: interior, 364: hinge area (× 40)].

Subgenus ***Notirus*** Finlay, 1928

Irus (***Notirus***) sp. indet.

Figures 355–364

This species is represented by a living specimen (RM19558) from the bottom sediments of "Cross Hole" of Irabu Islet as well as several empty valves from "Devil's Palace" (RM19557) of Shimoji Islet, Miyako Islands, and from "Shodokutsu" (RM19559) of Ie Islet, Okinawa.

The shell is very small, about 3 mm long, about 1.4 times longer than high, pale pink, regularly subquadrate with truncated posterior margin, not strongly inflated, possessing nearly straight ventral margin, a distinct lunule and highly raised commarginal lamellae. Hinge is veneroid, consisting of three cardinal teeth and a pair of lateral teeth in each valve. Pd I is small, and Pd II is distinct.

The outline of the present species is somewhat similar to the juvenile stage of *Irus ishibashianus* Kuroda and Habe, 1952 [= *Venerupis irus* (Linnaeus) sensu Yokoyama, 1924] which was referred to *Notirus* by Oyama (1973). The commarginal lamellae, however, are more densely spaced, and their interspaces are almost free from radial threads. In the subquadrate outline it somewhat resembles *Venerupis reflexa* Gray, 1843, from New Zealand, the type species of the subgenus *Notirus*, but the shell is much smaller and the ventral margin is not arcuate in the present species.

Order **Myoida** Stoliczka, 1870
Suborder **Myina** Stoliczka, 1870
Superfamily **Hiatelloidea** Gray, 1824
Family **Hiatellidae** Gray, 1824
Genus ***Hiatella*** Bosc, 1801

Hiatella sp. aff. ***H. orientalis*** (Yokoyama)

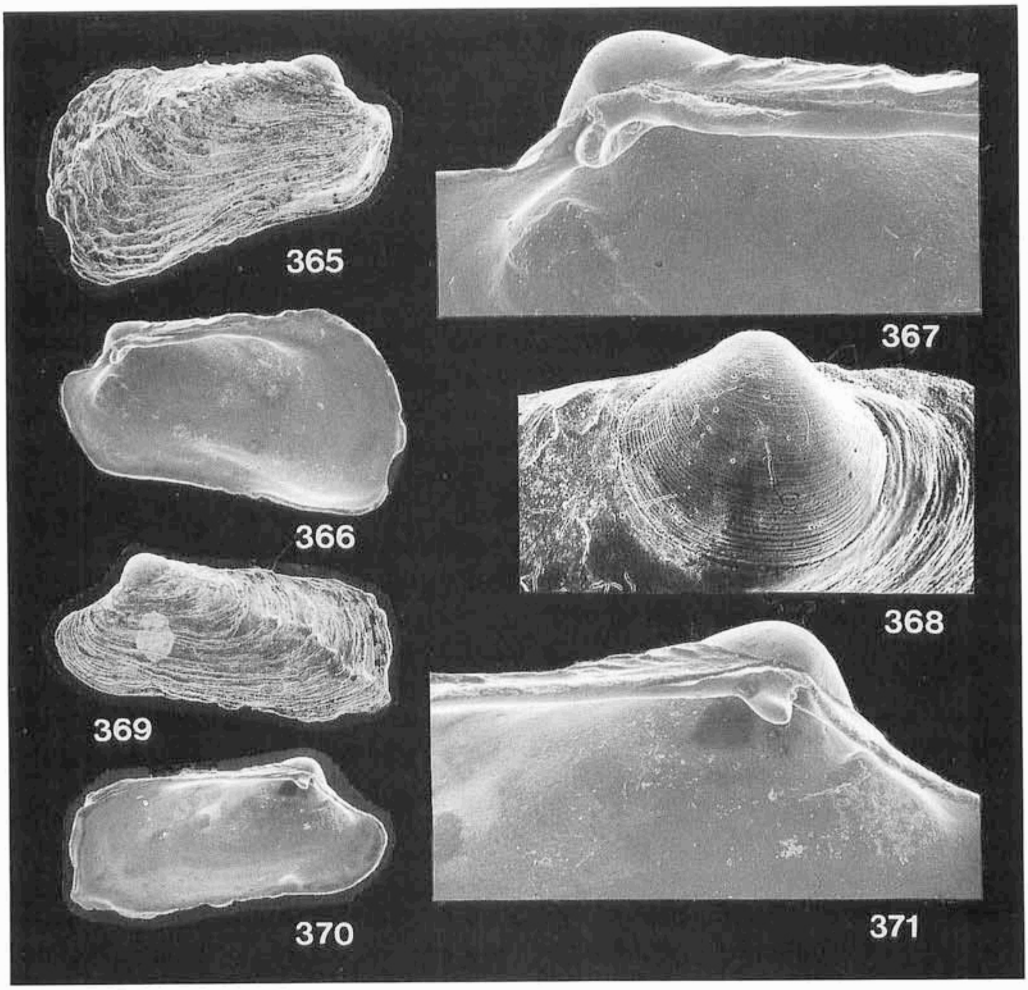
Figures 365–371

1992. *Hiatella* sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

Material. — RM19560 (dead) from "Devil's Palace", RM19561 (dead) from "Fool's Palace", RM19562 (dead) from "Witch's House", RM19563 (dead) from "Toriike" of Shimoji Islet. RM19564 (dead) from "L-arch" of Irabu Islet. RM19565 (dead) from "Shodokutsu" of Ie Islet. No living specimens have been found.

Description. — Shell very small for genus, scarcely exceeding 3.0 mm (in Ie sample) and 5.0 mm (in Shimoji sample) in length, considerably irregular but elongated-subtrapezoidal in outline, about twice as long as high, white and opaque in larger but translucent in smaller specimens. Anterior part somewhat reduced; posterior part commonly expanded. Umbo relatively small, located one-fourth to one-fifth of shell length from anterior end. Antero-dorsal margin short, concave in front of beak; postero-dorsal margin long, nearly straight; ventral margin frequently a little concave in middle portion. Surface marked with irregular growth lamellae and two prominent spinose radial ribs in posterior area, which become more or less obscure with growth. RV has an opisthoclinal tubercular cardinal tooth below umbo, while LV is almost edentulous. Ligament opisthodetic, external. Pd I small, ranging 77–103 μm in maximum diameter; Pd II strongly convex, tinged with pink; veliconch (Pd I + Pd II) ranging 303–361 μm in maximum diameter.

Remarks. — The irregularly long subtrapezoidal outline and two significant radial ribs on the posterior area in young shells indicate that the present species belongs to *Hiatella*. As mentioned by Keen (1958), the genus *Hiatella* is a somewhat difficult group to classify at the species level, because of the high irregularity of shell shape. Although the maximum shell-size is somewhat different between the samples of Ie and Shimoji Islets, the present species seems to be much smaller than any described species of *Hiatella* in the Pacific regions.



Hiatella sp. aff. *H. orientalis* (Yokoyama)
Figures 365–368: RV, RM19565a, 2.10 × 1.30 mm, from "Shodokutsu" [365: exterior, 366: interior, 367: hinge area (× 70), 368: umbonal area (× 100)]. Figures 369–371: LV, RM19565b, 1.95 × 0.85 mm, from "Shodokutsu" [369: exterior, 370: interior, 371: hinge area (× 70)].

Some juvenile specimens of *Hiatella orientalis* (Yokoyama, 1920) (see Oyama, 1973, for the synonymy) similarly reveal two spinose radial ribs and a transversely elongated outline. In fact, the cave specimens are hardly distinguishable from juvenile specimens of *H. orientalis*, which were collected, for example, from the beach of a sand bar of Heta Cove, western coast of Izu Peninsula, central Japan, and dredged from the sublittoral substrata of the Funka Bay of southern Hokkaido. The only marked difference is the preservation of Pd I and II, which is much poorer in the compared juvenile specimens. However, no specimen larger than 6 mm in length has been found in the cave sediments of Ie and Shimoji Islets. There is still a possibility that all the present specimens are immature, but it is likely that they are a product of significant stunting occurred in adaptation to such cavernicolous environments.

Distribution. — Common in several sublittoral caves of Ie, Shimoji and Irabu Islets, Ryukyu Islands.

Subclass **Anomalodesmacea** Dall, 1889
Order **Septibranchia** Pelseneer, 1888
Superfamily **Cuspidarioidea** Dall, 1886
Family **Cuspidariidae** Dall, 1886

Genus ***Halonympha*** Dall, 1886

Halonympha was originally proposed as a subgenus of *Cuspidaria* but regarded as a distinct genus by Allen and Morgan (1981) on the basis of different anatomical characters. It is also commonly characterized by the presence of a posterior internal platy buttress (called clavicular rib by some authors) for the insertion of posterior adductor muscle. Species of *Halonympha* have been described exclusively from the bathyal-abyssal substrata of the Atlantic and the west Indian Ocean (Smith, 1885; Dall, 1886; Thiele and Jaeckel, 1931; Nordsieck, 1969; Allen and Morgan, 1981). The cave sediments of Ie Islet contains numerous valves of a small-sized cuspidariid, which possesses a similarly well-developed posterior internal buttress in each valve and a tubercular subumbonal tooth in RV. Although taxonomic evaluation of these characters may be controversial, we regard the cave species as the first record of this genus in the Pacific realm.

Halonympha asiatica sp. nov.

Figures 372–379

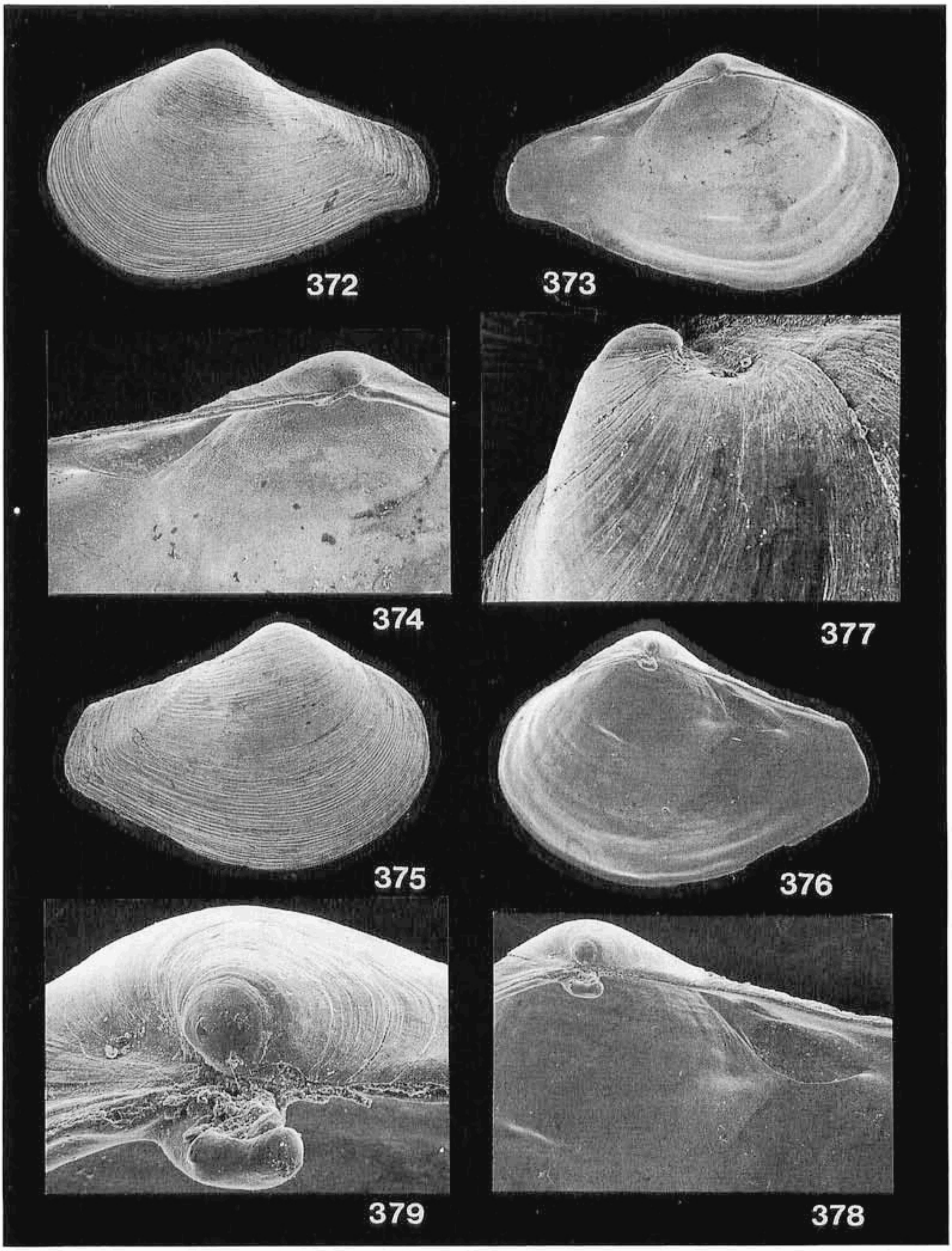
1992. *Halonympha* sp., Kase and Hayami, *Jour. Moll. Studies*, vol.58, p.448, listed.

1993. *Halonympha* sp., Hayami and Kase, *Univ. Mus. Univ. Tokyo, News*, no.27, p.3, fig.9.

Type and material. — Holotype: RM19566a, a left valve, from the bottom sediments of "Shodokutsu" of Ie Islet, Okinawa. Paratypes: RM19566 from the type locality. No living specimen has been found.

Diagnosis. — Small-sized cuspidariid, characterized by slightly inequivalve shell with broader posterior rostrum in RV, blunt posterior carina, fine commarginal lamellae, a tubercular subumbonal tooth in RV, an obliquely triangular chondrophore in LV, and a well-developed internal buttress below middle portion of postero-dorsal margin in each valve.

Description. — Shell small for cuspidariids, rarely exceeding 6.0 mm in length, slightly inequivalve, whitish and opaque, moderately inflated, 1.4–1.5 times longer than high. Umbo slightly prosogyrous, located a little anteriorly from mid-length. Posterior rostrum relatively short, somewhat broader in RV than in LV, suggesting that the dorsal margin of RV overlaps that of LV. Antero-dorsal margin rounded; postero-dorsal margin nearly straight, obliquely truncated by posterior margin. Posterior area bluntly delimited by a carina. Surface smooth except for densely spaced commarginal lamellae. A tubercular subumbonal tooth developed below umbo in RV, while LV is almost edentulous. An obliquely elongated triangular chondrophore observed below post-umbonal margin of LV. Posterior internal buttress (shelf-like proc-



Halonympha asiatica sp. nov. ドウクツシャクシガイ (新称)
Figures 372–374: LV, RM19566b, 5.65 × 3.50 mm, from "Shodokutsu" [372: exterior, 373: interior, 374: hinge area (× 20)]. Figures 375–379: Holotype, RV, RM19566a, 5.35 × 3.65 mm, from "Shodokutsu" [375: exterior, 376: interior, 377: oblique view of umbonal area (× 75), 378: hinge area (× 20), 379: umbonal area and chondrophore (× 75)].

ess for the attachment of posterior adductor muscle) low-triangular, considerably broad, roundly concave, situated below middle course of postero-dorsal margin in each valve. Pd I subovate, considerably large, ranging 161–184 μm in maximum diameter; Pd II not discriminated.

Remarks. — The well-developed posterior internal buttress suggests that this cuspidariid belongs to *Halonympha*, which has been known mainly from bathyal-abyssal waters of the Atlantic. It resembles *Neaera claviculata* Dall, 1881, the type-species of *Halonympha*, but differs from the Caribbean species in the smaller size, broader posterior rostrum and more anteriorly located umbo. It may be closer to *Neaera congenita* Smith, 1885, from the sea off Bermuda, but the posterior internal buttress seems to be broader in the present species. *Neaera depressa* Jeffreys, 1881, from the northern Atlantic, which was anatomically studied and assigned to *Halonympha* by Allen and Morgan (1981), reveals a similar outline but differs from the present species in the presence of a large chondrophore not only in LV but also in RV and a more rectangularly trigonal posterior internal buttress. *Cuspidaria salamensis* Jaeckel and Thiele *in* Thiele and Jaeckel (1931) from the bathyal substrata off Dar es Salaam has a similar posterior buttress, but the posterior rostrated part is much reduced, and the chondrophore of RV is probably undeveloped in the African species.

Although all the specimens are disarticulated, the broader posterior rostrum of RV suggests that the dorsal margin of RV overlaps that of LV, as described by Okutani and Ito (1983) in *Cuspidaria sadoensis* from the bathyal bottom off Sado Island, the Japan Sea. The present species is similar to that cuspidariid in shell-size and shape, but a tubercular tooth of RV and internal buttress are undeveloped in *C. sadoensis*.

Cuspidariidae as well as the Poromyidae are generally regarded as carnivorous bivalves, which feed largely on minute bottom-dwelling crustaceans (Reid and Reid, 1974; Morton, 1981; Allen, 1983). The present cuspidariid is a solitary septibranch bivalve in the cavernicolous fauna. It is unknown whether this species is still alive or already extinct, but numerous empty valves are contained in the bottom sediments of the innermost part of the cave "Shodokutsu". Minute interstitial (?) amphipods are found alive on the sediment surface in these caves, and such diminutive crustaceans possibly provide nutrition for the carnivorous bivalve to feed on.

Distribution. — Empty shells occur abundantly in a sublittoral cave of Ie Islet, Ryukyu Islands. This species has not been found in any cave of Shimoji and Irabu Islets.

General Features of Cave Bivalves

The bivalve fauna discovered in several sublittoral limestone caves of the Ryukyu Islands is unique in many respects. As described in the systematic part, it consists of 48 species belonging to 36 genera in total (Table 1, p. 8–9). Some of them belong to groups unfamiliar to the shallow-water faunas of tropical-subtropical Indo-West Pacific realm. In this section we summarize the common characteristics of this fauna and discuss its taxonomic, ecological and evolutionary significance.

As listed preliminarily (Kase and Hayami, 1992), 35 bivalves were distinguished in the samples collected during 1990–1991 from two submarine caves ("Shodokutsu" and "Daidokutsu") of Ie Islet, Okinawa. The following common characteristics were emphasized in our preliminary study: 1) very small adult shell size (usually less than 5 mm in length), 2) mostly colorless or translucent shells, 3) mostly epifaunal or semi-infaunal suspension feeders, 4) absence of protobranch species except for a nucinellid, 5) many bathyal and abyssal affinities, 6) persistent denticles of provinculum retained until adult stage in many pteriomorph species, suggesting significant paedomorphosis by progenesis, 7) unusually large (sometimes hat-shaped) prodissoconch I in many species, suggesting non-planktotrophic development. Most of these characteristics are also recognized in the subsequently examined bivalves from several similar sublittoral caves of Shimoji and Irabu Islets, Miyako Islands, though the assemblage as well as the relative frequency of common species is somewhat different from that of Ie Islet (Table 2).

The unique assemblage of these bivalves may be related to various physico-chemical and biological factors peculiar to such sheltered environments. Available data about cavernicolous organisms other than molluscs are still limited, but the analyses of the composition, species diversity, stunting, heterochrony, archaism and developmental strategy of these bivalves, which can be based on the collected samples, may be important for consideration of the evolutionary significance of this cryptic fauna.

1. Recognition of cryptic bivalves

It is a fundamental question whether or not these bivalves are really indigenous to such sheltered environments. Some scientists have doubted the endemism of these bivalves which was stressed in our preliminary reports. Because non-cryptic bivalves of such diminutive size have not been sufficiently investigated in Japan and its adjacent regions, we cannot necessarily give an obvious answer to this question. In fact, abraded shells of *Cosa waikikia*, *Cratis kanekoi*, *Cratis ohashii*, *Chlamydella incubata*, *Rochefortina sandwichensis* and *Hiatella* sp. aff. *H. orientalis* have been obtained from dredged or beach sands of Okinawa and some other regions of southern and central Japan (Kaneko, 1984, 1991; our unpublished data). Little, however, has been known about the actual microhabitat of these species outside the caves.

The following species are actually represented by a large number of living specimens, and it is obvious that, if not strictly endemic, they inhabit cavernicolous environments by preference: *Huxleyia cavernicola*, *Pronucula insignis*, *Bentharca tenuis*, *Bentharca excavata*, *Cosa waikikia*, *Dacrydium zebra*, *Urumella concava*, *Parvamussium crypticum*, *Cyclopecten ryukyuensis*, *Chlamydella incubata*, *Chlamydella tenuistriata*, *Pycnodonte taniguchii*, *Limatula kinjoi*, *Epicodakia pygmaea*, *Carditella iejimensis*, *Carditella shimojiensis*, *Salaputium unicum*, *Rochefortina sandwichensis* and *Coralliophaga hyalina*. As shown in Table 2, these bivalves were found alive on the sediment surface, rock fragments, polychaete tubes and/or cave walls. The following species are also regarded as cryptic because numerous empty shells occur exclusively in the cave sediments: *Bentharca decorata*, *Cosa kinjoi*, *Cosa uchimae*, Limopsoidea gen. and sp. indet., *Divarilima elegans* and *Halonympha asiatica*.

Possibilities for ecophenotypic effect and concentration of immature individuals must also be examined. In many cases, however, asymptotic size distribution indicating the ultimate adult size and other lines of evidence (e.g. parental care of embryos and commarginal lamellae becoming denser near the ventral margin) seem to deny the possibility of invalid dispersal of juveniles. Incubation of several embryos is actually observed in many specimens of *Cosa waikikia*, *Dacrydium zebra*, *Chlamydella incubata* and *Chlamydella tenuissima*, which were collected in late June of 1992 and mid April of 1993.

Only a few living individuals of *Solemya* (*Petrasma*) sp., *Septifer* sp., *Crenella* sp., *Lima* sp., *Limaria* sp. and *Irus* 2 spp. were found in the caves. *Acar* sp. aff. *A. plicata*, *Bathyarca* sp., *Brachidontes* sp., *Cardita* sp. and *Hiatella* sp. aff. *H. orientalis* are represented by a small number of empty shells from the cave sediments. Because the adult shell size is still difficult to estimate from the cave specimens, it is uncertain whether these species are actually reproducing in such cavernicolous environments. They may also be undescribed stunted species, but we hesitate to propose new specific names for this reason.

2. Biased composition of taxonomic groups

The Arcoidea, Limopsoidea, Mytiloidea, Pectinoidea, Limoidea and Carditoidea are the most dominant bivalve superfamilies in these caves, not only in species diversity but also in number of individuals. These superfamilies are also common in exposed environments of the same region, but their familial, subfamilial and generic compositions are unique. The cave Arcoidea are mostly composed of species belonging to *Bentharca*, and the Limopsoidea belong to *Cosa* and *Cratis* of the Philobryidae. All the cave Pectinoidea belong to the Propeamussiidae (*Parvamussium*, *Cyclopecten* and *Chlamydella*) instead of to the Pectinidae, Plicatulidae and Spondylidae.

The abundant occurrence of the species belonging to *Huxleyia*, *Dacrydium*, *Divarilima*, *Carditella* and *Halonympha* is also remarkable, because these genera scarcely occur in the upper sublittoral faunas of this region. In contrast, the absence or rarity of the species belonging to the Pterioidea, Anomioidea, Ostreoidea, Chamoidea, Cardioidea, Mactroidea, Tellinoidea, and Veneroidea (except some cavity-dwelling genera) is also noticed, because these superfamilies generally exhibit large species diversity in and around the coral reefs of this region. *Pycnodonte taniguchii* is a solitary cementing bivalve, but its habitat is restricted to the gloomy walls and ceilings near cave entrances and beneath overhangs (Hayami and Kase, 1992). *Malleus*

Table 2. Geographic distribution and microhabitat of cavernicolous bivalves

Species	Distribution				Microhabitat			
	Oki	Miy	Boh	Pal	Soft	Hard	Tube	Wall
1. Solemya (Petrasma) sp.		+				+		
2. Huxleyia cavernicola sp. nov. ｶｸﾚｷﾋﾞｶﾞﾗｶﾞｲ(新称)	+	+	+		+			
3. Pronucula insignis sp. nov. ｹｼｸﾙﾐｶﾞｲ(新称)	+	+			+			
4. Acar sp. aff. A. plicata (Dillwyn)	+	+	+	+				
5. Bentharca tenuis sp. nov. ｳｽｸﾏｻｶﾔﾄﾞﾘ(新称)	+	+	+		+		+	+
6. Bentharca decorata sp. nov. ｶｻﾞﾘｸﾏｻｶﾔﾄﾞﾘ(新称)	+	+						
7. Bentharca irregularis sp. nov. ﾎｿｸﾏｻｶﾔﾄﾞﾘ(新称)	+	+						
8. Bentharca excavata sp. nov. ﾍﾞﾆｸﾏｻｶﾔﾄﾞﾘ(新称)	+	+			+			+
9. Bathyarca sp. ｼﾗｽﾅｶﾞｲﾓﾄﾞｷ(新称)		+						
10. Cosa waikikia (Dall, Bartsch and Rehder)	+	+			+	+	+	+
11. Cosa kinjoi sp. nov. ｷﾝｼﾞｮｳｼﾗｽﾅｶﾞｲﾓﾄﾞｷ(新称)	+	+	+	+				+
12. Cosa uchimae sp. nov. ｳﾁﾏｼﾗｽﾅｶﾞｲﾓﾄﾞｷ(新称)	+							
13. Cosa sp.		+	+					
14. Cratis kanekoi sp. nov. ｶﾈｺｼﾗｽﾅｶﾞｲﾓﾄﾞｷ(新称)		+						
15. Cratis ohashii sp. nov. ｵｵﾊｼｼﾗｽﾅｶﾞｲﾓﾄﾞｷ(新称)	+	+						
16. Limopsoidea? gen. et sp. indet.	+	+	+	+				
17. Brachidontes sp.	+	+						
18. Septifer sp.		+	+	+	+			+
19. Crenella sp.	+	+						+
20. Dacrydium zebra sp. nov. ﾄﾞｳｸﾂﾋﾊﾞﾘｶﾞｲ(新称)	+	+	+		+	+	+	+
21. Urumella concava gen. et sp. nov. ｳﾙﾏﾋﾊﾞﾘｶﾞｲ(新称)		+	+					
22. Malleus (Malvufundus) sp.		+			+			+
23. Parvamussium crypticum sp. nov. ｶｸﾚﾂｷﾋｶﾞｲ(新称)	+							+
24. Parvamussium decoratum sp. nov. ﾐｼﾞﾝﾂｷﾋｶﾞｲ(新称)		+				+		
25. Cyclopecten ryukyuensis sp. nov. ｹｼﾊﾘﾅﾃﾞｼｺ(新称)	+	+	+		+			+

Species	Distribution				Microhabitat			
	Oki	Miy	Boh	Pal	Soft	Hard	Tube	Wall
26. Chlamydella incubata sp. nov. コモチハリナデシコ(新称)	+	+			+	+	+	+
27. Chlamydella tenuissima sp. nov. ウスハリナデシコ(新称)	+	+			+		+	+
28. Pycnodonte taniguchii Hayami and Kase オオベッコウガキ	+	+						+
29. Lima sp.	+	+			+			
30. Divarilima elegans sp. nov. ヒメタキハネガイ(新称)	+							
31. Ctenoides minimus sp. nov. ケシハネガイ(新称)	+	+	+			+		
32. Isolimea limopsis (Nomura and Zinbo) シラスナユキミノガイ		+						
33. Limatula kinjoi sp. nov. キンジョウユキバネガイ(新称)	+	+			+	+		
34. Limaria sp.	+	+	+		+			
35. Epicodakia pygmaea sp. nov. コビトウミアサガイ(新称)	+	+			+			
36. Cardita uruma sp. nov. イガトマヤガイ(新称)	+	+			+			+
37. Cardita sp.	+							
38. Carditella iejimensis sp. nov. イエジマケシザルガイ(新称)	+				+			
39. Carditella shimojiensis sp. nov. シモジケシザルガイ(新称)		+			+			
40. Salaputium unicum sp. nov. チビモシオガイ(新称)	+	+			+			
41. Rochefortina sandwichensis (Smith) ハコベノハナガイ	+	+	+		+			
42. Kelliella japonica sp. nov. マルケシハマグリ(新称)	+	+						
43. Coralliophaga hyalina sp. nov. ガラスマツカゼガイ(新称)	+	+	+	+	+			
44. Glossocardia obesa (Reeve) ツキヨミガイ	+	+			+			
45. Irus (Irus) sp.		+	+		+			
46. Irus (Notirus) sp.	+	+			+			
47. Hiatella sp. aff. H. orientalis (Yokoyama)	+	+						
48. Halonympa asiatica sp. nov. ドウクツシャクシガイ(新称)	+							

Distribution. Oki: Caves of Okinawa Islands, Miy: Caves of Miyako Islands, Boh: Balicasag Cave of Bohol Island, Pal: Chandelier Cave of Palau Islands.

Microhabitat. Soft: Soft bottom surface, Hard: Hard bottom surface, Tube: Polychaete tubes, Wall: Wall and ceiling surface.

(*Malvufundus*) sp. characteristically inhabits some narrow cavities of cave walls, though its stunted and peculiar morphology may only be due to some ecophenotypic effect in a widely distributed species. Another large-sized bivalve, *Glossocardia obesa*, may also be a cryptic species, because the empty shells (and also living individuals according to divers) have been found primarily from the bottom of such a sheltered environment.

Most of the cave bivalves must be epifaunal or semi-infaunal suspension feeders, though a few possible deposit feeders (*Solemya*, *Huxleyia* and *Pronucula*) and a carnivorous species of the Cuspidariidae have been discovered in association. Symbioses with sulfate-reducing bacteria have been recognized or inferred in some small-sized species of the Solemyidae and Nucinellidae as well as in many bivalves around deep-water hydrothermal vents (Reid, 1990, etc.). This trophic habit is, however, unlikely for these cave bivalves because the cave sediments are free from sulfur dioxide and never indicate an anaerobic condition.

3. Stunting of the cave bivalves

All of the cave bivalves, except for *Malleus* (*Malvufundus*) sp., *Pycnodonte taniguchii* and *Glossocardia obesa*, are very small in adult shell size (generally less than 5 mm in length and height). This is also the case with the associated gastropods and brachiopods. *Neritopsis radula* and certain soft sponges are the only conspicuous large-sized benthic organisms in the lightless innermost part of these caves. Remarkable stunting, regardless of taxonomic groups, appears to have occurred in the cave fauna.

The diminutive shell-size of the present cave bivalves may be the result of two different processes. One is the superficial stunting caused by the arrival of species which belong to originally small-sized taxonomic groups; for example, the cave species of *Cosa*, *Cratis*, *Dacrydium*, *Rochefortina* and *Kelliella* are not much smaller than ordinary non-cryptic species of the same genera. The other is the true stunting which may have occurred in adaptation to the cryptic environment; for example, the cave species of *Huxleyia*, *Pronucula*, *Bentharca*, *Parvamussium*, *Cyclopecten*, *Chlamydella*, *Divarilima*, *Ctenoides*, *Limatula*, *Cardita*, *Carditella*, *Coralliophaga* and *Halonympha* are much smaller than the most closely related non-cryptic species.

Several paleontologists reviewed previous studies of "dwarf" or "micromorph" faunas of fossil and extant marine benthic invertebrates and discussed causal factors of stunting (Tasch, 1953; Ager, 1963; Hallam, 1965; Mancini, 1978; etc.). They regarded abnormal salinity, metallic cations (Fe, Cu), oxygen deficiency, high turbidity, strong water agitation, high population density, abnormal pH, temperature variations and deficient food supply as possible causes. One famous example is the stunting of bivalves (e.g. *Mytilus edulis* and *Cardium edule*) in the Baltic Sea, where the shell size and the salinity show a significant correlation with each other (Sorgenfrei, 1958). Such a correlation, however, does not necessarily mean direct causal relation.

In the present caves, the salinity seems to be normal, notwithstanding that the caves must have been formed by underground water during some low sea-level stages of the Pleistocene. At present, the level of underground water in these islets is almost equal to or a little above the sea level, as evidenced by a number of active limestone caves open to the coastal cliffs.

Two tubular sediment cores (approximately 16 and 20 cm in length) were successfully taken by a cooperative diver at the innermost part of the cave "Shodokutsu" of Ie Islet. The sediments are parallel-laminated and scarcely bioturbated. The cores were sliced every 2 cm in height, and the sediments and organic remains in each subsample were examined. The physical environment of this site seems to have been maintained for a long time (probably several thousand years) under a tranquil but never oxygen-depleted condition. The water temperature in the caves is almost the same as, or only slightly lower than, that of the outside, at least in the seasons from spring to autumn. In the Ryukyu Islands the temperature of oceanic waters is maintained between 21° and 28° throughout a year. There is also no evidence that any of these cave bivalves is parasitic.

Of the above-mentioned possible factors, nutritional deficiency is likely to place a strong constraint on the growth rate and ultimate body size of the present cave bivalves, though some other factors (e.g. selective predation on larger-sized species) may also be related to the stunting. Thiel (1975) and many others regarded the diminutive size of most deep-water benthos as related to limited nutrient supply. Vermeij (1990) presented the interesting hypothesis that a general decline in nutrients for suspension feeders from the western rim of the tropical Pacific to the oceanic islands results in smaller adult size as well as lower species diversity. As pointed out by Snyder and Bretsky (1971) and Gould (1977: 325), stunting may be a positive response to a particular condition (oligotrophic environment in this case). Examinations of trophic nature, larval development and heterochrony may be important to test this hypothesis, because oligotrophic condition seems to have strong influence on the life cycle and adaptive strategy of organisms.

Another question to be examined is the possibility that these diminutive bivalves might be interstitial animals. Sediment surface samples from a cave of Ie Islet often contain numerous living individuals of *Carditella iejimensis*, and *Huxleyia cavernicola*, *Cosa waikikia*, *Dacrydium zebra*, *Chlamydella incubata*, *Carditella shimojiensis* and *Rochefortina sandwichensis* are found in samples from some caves of Shimoji Islet. These bivalves are mostly regarded as epibyssate or semi-infaunal species. The shells of these living bivalves attain 1 to 3 mm in length and height in the adult stages, and seem to be larger than the sediment particles. Commonly known interstitial meiobenthos are generally smaller than 500 μm in breadth. So far as we observed in the core samples taken at the innermost part of "Shodokutsu", no bivalve individual seems to live below the sediment surface. In these bivalves, therefore, it is unlikely that the selection for smaller shell-size is related to interstitial life. Moreover, numerous living individuals of *Cosa waikikia*, *Dacrydium zebra* and *Chlamydella incubata* were found attached by the byssus to the terminal part of polychaete tubes (Figure 212) exposed above the sediment surface as well as to sediment grains, rock fragments and cave walls.

4. Species diversity and biomass

The species diversity of bivalves in each cave appears to be quite great. For example, different species within a genus often occur together in the bottom sediments at one and the same locality. A sediment sample at one locality often contains numerous empty shells of more than 30 bivalves. However, the great diversity may sometimes be superficial, because it is not necessarily based on actually living specimens. In spite of our repeated examinations of samples carefully collected from the cave wall and sediment surfaces, living individuals are relatively few in comparison with empty shells.

In a cave of Ie Islet ("Shodokutsu"), for example, *Bentharca*, *Cosa*, *Dacrydium*, *Parvamussium*, *Cardita* and *Carditella* was found alive, but each genus is represented by one species. In spite of thorough sampling in this cave, other bivalve species are represented by numerous but dead specimens. More than 90 % of living individuals from the bottom sediments belong to *Carditella iejimensis*. Therefore, the composition of bivalves in this cave should be regarded as an integration of all the species that ever lived there over many years. Because the inner part of this cave has remained in a low-energetic physical condition, even delicate molluscan shells can be preserved for a long time without destruction. In spite of the apparent great diversity and large quantity of organic remains, the biomass per unit space is very small.

Species diversity of bivalves is also generally low in the totally dark caves of Shimoji Islet. In most caves of Shimoji and Irabu Islets, *Cosa waikikia*, *Dacrydium zebra* or *Chlamydella incubata* constitute the dominant species; more than 90% of living individuals belong to the three species. It is interesting, as will be discussed later, that all three dominant bivalves are brooding species.

In a gloomy cave of Irabu Islet (called "Cross Hole"), however, more than 20 bivalves were found alive at one and the same sampling point, where other living organisms and polychaete tubes were also abundant. Other sediment samples in the same cave did not necessarily contain so many living organisms. This fact indicates that the distribution of organisms in each cave is patchy rather than uniform or random. The spectral change of organisms from the entrance to the innermost part of each cave is indeed the most interesting subject of study, but systematic sampling for this purpose is difficult because of the patchy distribution of organisms and the restricted distribution of fine-grained sediments on the cave floor.

5. Affinities with deep-water faunas

One of the most interesting features of the present cave bivalves is the presence of many lower sublittoral, bathyal and abyssal affinities (Table 3). No cave bivalve is strictly identical with deep-water species, but this does not rule out the possibility of direct gene flows between these caves and deep-sea bottoms. Most significant deep-water affinities are the species of *Huxleyia*, *Bentharca*, *Cratis*, *Dacrydium*, *Parvamussium*, *Chlamydella*, *Divarilima*, *Carditella*, *Kelliella* and *Halonympha*.

Because the sampling sites of the present material lie between sea level and about − 40 m, the discovery of these genera certainly breaks the shallowest records of their bathymetric distribution. At the same time it is suggested that neither high hydrostatic pressure nor low water temperature is a decisive factor for the restricted distribution of these genera. Although certain species of *Huxleyia*, *Dacrydium* and *Parvamussium* often inhabit sublittoral substrata in high latitudinal seas (Bernard, 1983, etc.), these genera so far recorded in low-middle latitudinal seas are restricted to bathyal to abyssal depths. Moreover, *Bentharca*, *Dacrydium*, *Kelliella* and *Halonympha* are important constituent genera in abyssal faunas (Clarke, 1962; Knudsen, 1967, 1970; Oliver and Allen, 1980; Allen and Morgan, 1981; Poutiers, 1989; etc.). Why do so many species of deep-water-type genera inhabit these sublittoral caves?

Table 3. Bathymetric distribution of cavernicolous bivalve genera

Genus	Sublittoral 0-50m	Sublittoral 50-200m	Bathyal 200-1000m	Abyssal 1000-6000m	Hadal 6000m-
Solemya	+	+ +	+ +	+	
Huxleyia		+ +	+ +		
Pronucula		+			
Acar	+ +	+			
Bentharca	(+)	+	+ +	+ +	
Bathyarca		+	+ +	+ +	
Cosa	+	+ +			
Cratis		+			
Brachidontes	+ +				
Septifer	+ +	(+)			
Crenella	+	+ +	+		
Dacrydium	(+)	(+)	+	+ +	
Malleus	+				
Parvamussium	(+)	+	+ +	+ +	
Cyclopecten	(+)	+	+ +	+	
Chlamydella		+	+ +		
Pycnodonte	+				
Lima	+ +	+	+		
Divarilima		+ +			
Ctenoides	+	+ +			
Isolimea		+			
Limatula	+	+ +	+ +	+	
Limaria	+ +	+			
Epicodakia	+ +				
Cardita	+ +	+	(+)		
Carditella	+	+ +	+ +		
Salaputium		+			
Rochefortina	+				
Kelliella			(+)	+ +	+
Coralliophaga	+ +				
Glossocardia	+ +	+	(+)		
Irus	+ +				
Hiatella	+ +	+	(+)		
Halonympha			+	+ +	

Occurrence in restricted seas (e.g. shallow-water records only in high latitudinal region) is indicated with parentheses. Data compiled from Dall (1889), Knudsen (1970), Habe (1977), Bernard (1983) and many other sources.

Some investigators have asked why cryptic organisms resemble deep-sea ones (Iliffe, Hart and Manning, 1983; Vermeij, 1987; Kobluk, 1988). Their interpretations are somewhat different, and their discussions were not necessarily based on substantial molluscan data. Iliffe, Hart and Manning (1983) seem to have attributed the occurrence of deep-sea type decapod species in some inland marine caves of Bermuda in part to the small seasonal change of water temperature. This reasoning, however, is hardly applicable for the present cave bivalves, because the water temperature in the caves is not much different from that of the exposed environment. Kobluk (1988) attached importance to the low level of illumination, which gives an analogous constraint to cryptic and deep-sea organisms. On the other hand, Vermeij (1987) emphasized the low level of predation pressure in both cryptic and deep-sea environments.

The resemblance between the cave and deep-water bivalve faunas can be recognized not only in their taxonomic aspect but also in their shell-size and developmental strategy. As will be summarized by Allen (1983), the biomass and shell-size of molluscs decrease significantly with depth; abyssal infaunal molluscs are rarely larger than 5 mm. As will be discussed later, the general adaptive strategy of the cave bivalves, as judged from the features of Pd I, is comparable with that of deep-sea and cold-water bivalve faunas.

On the other hand, some compositional differences exist between the cave and deep-water bivalve faunas. Deposit feeders and carnivores are decidedly less common in the cave bivalves. The Nuculanoidea, for example, constitute dominant groups in deep-water faunas (Knudsen, 1970; Allen, 1983), but no nuculanacean shell has been found in the sediments of these caves. The Nuculoidea and Poromyoidea are represented by only one species each. No representatives of the Thyasiridae and Pandoroidea have been found.

Some cave species belong to such shallow-water genera as *Malleus*, *Coralliophaga*, *Irus* and *Hiatella*. Significant stunting also seems to have occurred in these species, but their planktotrophic developmental strategy (indicated by the presence of Pd II) is retained. It is noticed that these genera mainly consist of coral-nestling and cavity-dwelling species (Morton, 1980, 1983, 1990, etc.), and their occurrence in dark caves may not be very strange.

6. Paedomorphosis by progenesis

As described in the systematic part, paedomorphic features are often observed in these cavernicolous bivalves. In many pteriomorph species, numerous subvertical denticles along the dorsal margin persist until the latest growth stage. We regard them as a paedomorphic retention of provinculum. The relatively small number of adult hinge teeth in the cave species of *Huxleyia*, *Pronucula*, *Acar*, *Bentharca* and *Bathyarca* may also be a paedomorphic feature, because they are additional with growth. More than half of these cavernicolous bivalves are regarded as paedomorphic (Table 4).

Two different processes are assumed for the paedomorphosis. One is the adaptation of intrinsically paedomorphic groups to the cryptic environment. *Cosa*, *Cratis* and *Dacrydium* species are regarded as good examples of this case, because all the species of these genera reveal similarly diminutive shell-size and paedomorphic features. As suggested by Boss (1969), *Kelliella* is probably also a paedomorphic veneroid genus. The other is the case in which rapid paedomorphic evolution possibly occurred in adaptation to the cryptic environment. Most cavernicolous species of the Arcidae, Mytilidae, Propeamussiidae and Limidae retain numerous denticles of provinculum throughout the ontogeny, but at the same time the shell-size is much reduced in comparison with closely related non-cryptic species.

In some cave arcids, e.g. *Bentharca excavata*, primary alivincular amphidetic ligament is active throughout the growth, and an incipient secondary duplivincular ligament appears only occasionally on the posterior cardinal area in adult individuals (Figures 60, 61). Because this feature corresponds to the ligament structure of juvenile arcid shells of similar size, the phenomenon should be regarded as paedomorphosis by progenesis.

The Philobryidae were commonly regarded as a neotenous group derived from the Limopsidae (Tevesz, 1977; Morton, 1978). Many species of the Philobryidae have persistent denticles of provinculum, and prionodont teeth are absent or only incipiently developed even in adult individuals. If the phylogenetic relation is accepted, the paedomorphic evolution is better regarded as due to progenesis instead of neoteny, because significant size reduction has occurred. The shell-size of the Philobryidae is generally one digit smaller than that of the Limopsidae. Considering the much-reduced shell-size in many species of other families, paedomorphosis by progenesis is a widespread phenomenon in the present bivalve fauna.

Little is known about the growth rates and life cycles of these cavernicolous bivalves. It is, however, likely that their growth is generally slow, because nutrition is generally deficient in the caves. Several studies have indicated that slow growth in bivalves is associated with strong shell convexity (Seed, 1968; Vermeij, 1990). We intuitively feel that the cave bivalves, especially the species of the Nucinellidae, Arcidae, Phylobryidae, Mytilidae, Propeamussiidae, Limidae, Carditidae and Trapeziidae, generally reveal strong shell convexity in comparison with those of ordinary environments.

7. Dominance of non-planktotrophic development

The mode of larval development of molluscs, in general, has been classified into three types: planktotrophic, lecithotrophic, and direct development (Thorson, 1946, 1950). The following relation between the developmental strategy and the egg size in bivalves has been approved (Ockelmann, 1965; Jablonski and Lutz, 1980, 1983; Mackie, 1984):

1) Planktotrophic development is characterized by a large number of small eggs that hatch into pelagic larvae feeding on phytoplanktons.

2) Lecithotrophic development is characterized by relatively large-sized eggs with yolk and a very short (or no) pelagic stage of non-feeding larvae.

3) Direct development is generally characterized by very large eggs and no pelagic stage (often accompanied by parental incubation of embryos).

4) The developmental type could also be estimated by the size of prodissoconch I. Planktotrophic, lecithotrophic and direct developments are commonly characterized by the maximum diameter of Pd I, ranging 70–150 µm, 135–230 µm and 230–500 (+) µm, respectively. The presence of prodissoconch II indicates a long pelagic stage (and planktotrophic development).

It is interesting that the ratio of developmental types changes geographically.

Table 4. Prodissoconch features, developmental strategy, heterochrony and inferred origin of cavernicolous bivalves from Ryukyu Islands

Species	PdI	PdII	DS	HC	Cryptic?	Origin
1. Solemya (Petrasma) sp.	?	307	P		doubtful	?
2. Huxleyia cavernicola sp. nov.	262	-	L	P(s)	certainly	D
3. Pronucula insignis sp. nov.	196	-	D	P(g)	certainly	D
4. Acar sp. aff. A. plicata (Dillwyn)	184	-	L		doubtful	?
5. Bentharca tenuis sp. nov.	311	-	L	P(s)	certainly	D
6. Bentharca decorata sp. nov.	292*	-	D	P(s)	certainly	D
7. Bentharca irregularis sp. nov.	132	208	P		doubtful	?
8. Bentharca excavata sp. nov.	180	-	L	P(s)	certainly	D
9. Bathyarca sp.	135	-	L?		doubtful	D
10. Cosa waikikia (Dall, Bartsch and Rehder)	274*	-	D*	P(g)	probably	D?
11. Cosa kinjoi sp. nov.	250	-	D	P(g)	certainly	D?
12. Cosa uchimae sp. nov.	213*	-	D	P(g)	certainly	D?
13. Cosa sp.	295*		D	P(g)	probably	D?
14. Cratis kanekoi sp. nov.	320*	-	D	P(g)	doubtful	D?
15. Cratis ohashii sp. nov.	559*	-	D	P(g)	doubtful	D
16. Limopsoidea? gen. et sp. indet.	277	-	L		certainly	?
17. Brachidontes sp.	132	254	P		doubtful	SE
18. Septifer sp.	100	410	P		doubtful	SE
19. Crenella sp.	268	-	L	P(s)	probably	D?
20. Dacrydium zebra sp. nov.	193	-	D*	P(g)	certainly	D
21. Urumella concava gen. et sp. nov.	160	-	L	P(g)	certainly	?
22. Malleus (Malvufundus) sp.	69	379	P		probably	SE?
23. Parvamussium crypticum sp. nov.	189	-	L	P(s)	certainly	D
24. Parvamussium decoratum sp. nov.	167	-	L	P(s)	doubtful	D
25. Cyclopecten ryukyuensis sp. nov.	170	-	L	P(s)	certainly	D
26. Chlamydella incubata sp. nov.	265*	-	D*	P(g)	probably	D

Species	PdI	PdⅡ	DS	HC	Cryptic?	Origin
27. Chlamydella tenuissima sp. nov.	274*	-	D*	P(g)	probably	D
28. Pycnodonte taniguchii Hayami and Kase	?	?	?		certainly	SR
29. Lima sp.	226	-	L	P(s)	doubtful	D?
30. Divarilima elegans sp. nov.	210	-	L	P(s)	certainly	D
31. Ctenoides minimus sp. nov.	186	-	L	P(s)	probably	D?
32. Isolimea limopsis (Nomura and Zinbo)	169	-	L		doubtful	D?
33. Limatula kinjoi sp. nov.	247*	-	D	P(s)	certainly	D
34. Limaria sp.	99	269	P		doubtful	SE?
35. Epicodakia pygmaea sp. nov.	153	199	P		probably	SE
36. Cardita uruma sp. nov.	120	260	P		probably	?
37. Cardita sp.	168	-	L		doubtful	?
38. Carditella iejimensis sp. nov.	143	-	L		certainly	D
39. Carditella shimojiensis sp. nov.	138	-	L		certainly	D
40. Salaputium unicum sp. nov.	198	-	L		certainly	D
41. Rochefortina sandwichensis (Smith)	78	244	P		doubtful	SE
42. Kelliella japonica sp. nov.	90	178	P	P(g)	probably	D
43. Coralliophaga hyalina sp. nov.	85	148	P	P(s)	probably	SE
44. Glossocardia obesa (Reeve)	?	?	?		probably	SR?
45. Irus (Irus) sp.	70	219	P		probably	SE
46. Irus (Notirus) sp.	102	212	P		probably	SE
47. Hiatella sp. aff. H. orientalis (Yokoyama)	90	332	P	P(s)	doubtful	SE
48. Halonympa asiatica sp. nov.	173	-	L		certainly	D

Pd I: Mean of maximum diameter of prodissoconch I (μm) [*: hat-shaped], Pd Ⅱ: Mean of maximum diameter of veliconch (prodissoconchs I + Ⅱ)(μm), DS: Developmental strategy [P: planktotrophic, L: lecithotrophic, D: direct development, *: parental incubation ascertained], HC: Heterochrony [P(s): paedomorphic species, P(g): paedomorphic as a genus]. Cryptic?: Is the species really indigenous to cryptic environments? Origin: Supposed origin of the species [D: originated from deep-water species, SE: originated from shallow-water species by extension of habitat, SR: relict species of Tethyan shallow-sea fauna].

Table 5. Frequency of developmental types in bivalves of various environments

Environment		N	P	L	D	Source
Shallow-water(NE Atlantic)	36°-45°N	125	95(76%)	19(15%)	11(9%)	Ockelmann, 1965
	61°-64°N	132	79(60%)	28(21%)	25(19%)	Ockelmann, 1965
	ca. 77°N	53	8(15%)	21(40%)	24(45%)	Ockelmann, 1965
Deep-water (John Murray Expedition)		26	2 (8%)	15(58%)	9(34%)	Knudsen, 1967
Deep-water (Galathea Expedition)		23	2 (9%)	18(78%)	3(13%)	Knudsen, 1970
Cavernicolous (Ryukyu Islands)		46	14(30%)	20(43%)	12(26%)	herein

N: number of species, P: Planktotrophic, L: Lecithotrophic, D: Direct development

Ockelmann (1965) examined the relative frequency of many shallow-water bivalve faunas along the European Atlantic coast from Gibraltar to Spitzbergen. The ratio of planktotrophic species significantly decreases toward the north; it is about 76 % (N = 125) near Gibraltar but only about 15 % (N = 53) in Spitzbergen (Table 5). A similar tendency has been known also in gastropods of this region (Thorson, 1965). This is generally called "Thorson's Rule".

Bivalves of non-planktotrophic development are more frequent in deep-waters than in shallow waters (Ockelmann, 1965; Allen, 1983; Mackie, 1984). Knudsen (1967, 1970) suggested that the deep-water molluscs collected by the John Murray Expedition consist of 8 % planktotrophic, 58 % lecithotrophic and 34 % directly developing species, and that those collected by the Galathea Expedition are composed of 9 % planktotrophic, 78 % lecithotrophic and 13 % directly developing species (Table 5). Although the egg size of bivalves seems to decrease from bathyal to abyssal-hadal (Mackie, 1984), the difference of developmental strategy between shallow- and deep-water bivalves is quite obvious, at least in low and middle latitudinal regions.

In the present cave bivalves the prodissoconch is generally well preserved without abrasion (or erosion), probably because of the low-energetic physical condition and the oversaturation of $CaCO_3$ in the sea water. The size and shape of Pd I are generally variable among the species within one and the same genus but considerably stable in each cavernicolous species. The coefficient of variation (100 × standard deviation/mean) for the maximum diameter of Pd I rarely exceeds 10. As emphasized in our preliminary study (Kase and Hayami, 1992), the size of Pd I is unusually large in many cave species, and Pd II are observed in relatively few species. Among 46 cavernicolous bivalves, the presence of Pd II is recognized in only 14 species. If the above-mentioned criteria are applied to this case, the present bivalves consist of 14 planktotrophic (30 %), 20 lecithotrophic (43 %), and 12 directly developing (26 %) species (Tables 4 and 5). If several doubtfully cryptic species are excluded, the ratio of non-planktotrophic species becomes still higher.

Although the developmental types of western Pacific shallow-water bivalves have scarcely been analyzed, non-planktotrophic development is more frequent in the cave bivalves than in non-cryptic bivalves of the same region. In other words, the developmental strategy of these cavernicolous bivalves is generally comparable with that of boreal or deep-water species.

The shape of Pd I may also be meaningful. The cave species of the Philobryidae, except for *Cosa kinjoi*, show large and hat-shaped Pd I with a central boss and a wide marginal brim, as usual for this family. Similarly, hat-shaped Pd I is known also in *Bentharca decorata* (Figures 44, 45), *Chlamydella incubata* (Figures 204, 210) and *Limatula kinjoi* (Figures 256, 259). The saucer-shaped summit of Pd I of *Pronucula insignis* (Figures 20, 23) is also an abnormal feature in the Nuculacea. We presume that such a hat- or saucer-shaped Pd I suggests parental care of larvae. In fact, we found several pre-released larvae within the living valves of *Cosa waikikia*, *Dacrydium zebra*, *Chlamydella incubata* and *C. tenuissima*. These facts lead us to suspect that parental care of larvae may occur in wider taxonomic groups than was ever thought (e.g. Arcidae, Propeamussiidae and Limidae), and that the size and shape of Pd I (and probably also developmental strategy) are considerably plastic even in one and the same genus (e.g. *Bentharca*, *Chlamydella* and *Limatula*).

8. Dominance of *K*-selection

The diameter of Pd I in the cave bivalves is generally very large and often exceeds 10 % of adult shell size. This fact strongly suggests relatively small clutch size and low fecundity. Mainly on these grounds it was preliminarily inferred that *K*-strategy predominates in the cave bivalves (Kase and Hayami, 1992).

Some authors postulated that *K*-strategy also prevails in deep-water bivalves, chiefly because of their low fecundity and relatively stable physical condition (Calow, 1983; Mackie, 1984). Primary production by photosynthesis does not occur in lightless environments such as the deep-sea bottom and submarine caves. Suspension feeders in the caves are forced to share a small amount of nutrition which has been brought from exposed environments by a weak current. Although the carrying capacity must be very small in the caves, equilibrium populations, if anything, may be maintained like deep-water benthos. The resemblance of generic composition and reproductive strategy between the cavernicolous and deep-water bivalve faunas may be consistent with this assumption.

Another important common factor between submarine caves and deep-sea bottoms may be the relative rarity of predators. According to the divers' underwater observations as well as collected remains, teleosts, asteroids, shell-breaking crustaceans and durophagous gastropods (e.g. naticids and muricids) are much less common in these caves than outside. Bored and injured-and-repaired shell remains are less commonly met with. These lines of evidence strongly suggest a low level of predation pressure in these submarine caves. In such an environment it is generally supposed that the biomass of suspension feeders approaches the carrying capacity.

The constant deficiency of nutrition as well as the presumably saturated condition may force the cavernicolous bivalves to most efficiently utilize the limited food source of phytoplankton. *K*-strategy characterized by small clutch size and non-planktotrophic development probably becomes more advantageous than wasteful *r*-strategy characterized by large clutch size and planktotrophy.

As generalized by Pianka (1970, 1978), however, *K*-selection may be commonly accompanied by slower growth, larger body size and longer longevity of individuals.

In a comprehensive discussion of the relation between phylogeny and ontogeny, Gould (1977) has attempted to test his hypothesis that progenesis and neoteny are commonly related to *r*-selection and *K*-selection, respectively. Little has been known about the growth rate and longevity of cave bivalves, but their stunting and progenetic (instead of neotenous) features are evident. Judging from the diminutive shell-size, the life cycle of these bivalves may be relatively short, even if their growth is slow. Is the *r*-*K* model inapplicable to the strategy of cave bivalves? Or is our assumption of *K*-strategy for the cave bivalves inadequate?

Jablonski and Lutz (1980) already pointed out that the relation between the body size (or mode of heterochrony) and *r*-*K* spectrum in marine molluscs is not necessarily compatible with Pianka's (1970) generalization and Gould's (1977) prediction. We believe that nutrition deficiency (or small carrying capacity) is a decisive causal factor in the adaptive strategy of cave bivalves. The remarkable stunting and progenesis may be the only adoptable strategy against such a constantly oligotrophic condition. Large body size and retardation of sexual maturation would make it impossible to maintain the minimum population size necessary to survive. The amount of nutrition required by a large-sized individual would suffice for 1,000 individuals of a one-digit-smaller species, even if their longevity were the same. Progenesis as well as *K*-strategy must reduce the waste of nutrition. Among the cave bivalves, *Malleus* (*Malvufundus*) sp., *Pycnodonte taniguchii* and *Glossocardia obesa* are exceptionally large in body size, but they never inhabit the totally dark inner part of these caves.

9. Fossil records of the cavernicolous bivalves

Though the present cave bivalves generally exhibit archaic aspects, little has been known about their fossil records at the species level. This is probably because fossil bivalves of such diminutive size have been overlooked or are only rarely described.

Are these bivalves archaic at the level of supraspecific taxa? It is not necessary to say that the geologic range of each higher taxon largely depends on the ranking in classification as well as on the incompleteness of fossil records. In Table 6 the first appearances of the cavernicolous bivalve genera and families are shown on the basis of Cox et al. (1969) and some subsequent emendations; the first appearances are 1 (?) in the Devonian, 3 in the Triassic, 4 in the Jurassic, 2 in the Cretaceous, 16 in the Tertiary, 2 in the Quaternary, and 5 not represented by fossils. These figures may give the impression that the constituent genera of the cave bivalves are not particularly archaic.

Most of the constituent families, however, first appeared in Paleozoic or Mesozoic times; that is, 1 in the Ordovician, 1 in the Silurian, 2 in the Devonian, 1 in the Carboniferous, 2 in the Permian, 3 in the Triassic, 4 in the Jurassic, 2 in the Cretaceous, and only 2 in the Tertiary. Thus, most cave bivalves belong to long-ranging families. This is consistent with the composition of coexistent gastropods which almost lacks neogastropods except for a few species of the Columbellidae and Turridae (Kase and Hayami, 1992).

Knudsen (1970) surveyed the geologic ranges of abyssal bivalve genera and families. Although his discussion was based on somewhat older data, taxonomic archaism is also obscure in abyssal bivalves. The archaism of cavernicolous (probably also deep-sea) bivalves, we believe, is more clearly shown in their life mode than in their taxonomic composition. The present bivalves are mostly composed of epibyssate or semi-

Table 6. Geologic range of families and genera of cavernicolous bivalves

Taxon	First appearance	Source
Solemyiidae	Ordovician (Llandeilian)	Skelton and Benton in Benton (1993 ed)
Solemya	Devonian?	Cox in Cox et al. (1969)
Nucinellidae	Jurassic (Hettangian)	Keen in Cox et al. (1969)
Huxleyia	Tertiary (Pliocene)	herein
Nuculidae	Devonian (Eifel/Givetian)	Skelton and Benton in Benton (1993 ed)
Pronucula	Tertiary (Oligocene)	Keen in Cox et al. (1969)
Arcidae	Jurassic (Aalenian)	Skelton and Benton in Benton (1993 ed)
Acar	Tertiary (Paleocene)	Newell in Cox et al. (1969)
Bentharca	Tertiary (Pliocene)	herein
Bathyarca	Tertiary (Eocene)	Newell in Cox et al. (1969)
Philobryidae	Jurassic (Kimmeridgian)	Skelton and Benton in Benton (1993 ed)
Cosa	Tertiary (Eocene)	Keen in Cox et al. (1969)
Cratis	Tertiary (Miocene)	Keen in Cox et al. (1969)
Mytilidae	Devonian (Frasnian)	Skelton and Benton in Benton (1993 ed)
Brachidontes	Jurassic	Soot-Ryen in Cox et al. (1969)
Septifer	Triassic	Soot-Ryen in Cox et al. (1969)
Crenella	Cretaceous	Soot-Ryen in Cox et al. (1969)
Dacrydium	Tertiary (Pliocene)	Soot-Ryen in Cox et al. (1969)
Malleidae	Jurassic (Bathonian)	Hertlein and Cox in Cox et al. (1969)
Malleus	no fossil record	
Propeamussiidae	Carboniferous (Early)	Waller (1978)
Parvamussium	Triassic (Carnian)	herein
Cyclopecten	Tertiary (Miocene)	Hertlein in Cox et al. (1969)
Chlamydella	no fossil record	
Gryphaeidae	Triassic (Norian)	Stenzel (1971)
Pycnodonte	Cretaceous (Aptian)	Hayami and Kase (1992)
Limidae	Carboniferous (Viséan)	Skelton and Benton in Benton (1993 ed)
Lima	Jurassic (Late)	Cox and Hertlein in Cox et al. (1969)
Divarilima	no fossil record	
Ctenoides	Jurassic (Tithonian)	Cox and Hertlein in Cox et al. (1969)
Isolimea	Quaternary (Pleistocene)	herein
Limatula	Triassic	Cox and Hertlein in Cox et al. (1969)
Limaria	Tertiary (Eocene)	Cox and Hertlein in Cox et al. (1969)
Lucinidae	Silurian (Wenlockian)	Chavan in Cox et al. (1969)
Epicodakia	Quaternary (Pleistocene)	Chavan in Cox et al. (1969)
Carditidae	Permian (Tatarian)	Skelton and Benton in Benton (1993 ed)
Cardita	Tertiary (Paleocene)	Chavan in Cox et al. (1969)
Carditella	Tertiary (Pliocene)	Chavan in Cox et al. (1969)
Crasatellidae	Permian (? Rotliegend)	Skelton and Benton in Benton (1993 ed)
Salaputium	Tertiary (Neogene)	Chavan in Cox et al. (1969)
Mesodesmatidae	Tertiary (Eocene)	Keen in Cox et al. (1969)
Rochefortina	no fossil record	
Kelliellidae	Tertiary (Eocene)	Skelton and Benton in Benton (1993 ed)
Kelliella	Tertiary (Miocene)	Studencka (1987)
Trapeziidae	Cretaceous (? Aptian)	Keen in Cox et al. (1969)
Coralliophaga	Tertiary (Eocene)	Keen in Cox et al. (1969)
Glossocardia	no fossil record	
Veneridae	Cretaceous (Aptian)	Skelton and Benton in Benton (1993 ed)
Irus	Tertiary (Oligocene)	Keen in Cox et al. (1969)
Hiatellidae	Permian	Keen in Cox et al. (1969)
Hiatella	Jurassic (Late)	Keen in Cox et al. (1969)
Cuspidariidae	Triassic (Ladinian)	Skelton and Benton in Benton (1993 ed)
Halonympha	no fossil record	

infaunal species, while few deep-burrowers and cemented species have been found. In other words, the archaic and defenseless mode of life before "Mesozoic marine revolution" (Vermeij, 1977) appears to be retained in cave bivalves.

10. Origin and adaptation of cavernicolous bivalves

The origin and adaptation of the extraneous cavernicolous bivalves may be an interesting problem. The occurrence of several species belonging to shallow-water genera (e.g. *Brachidontes*, *Septifer*, *Malleus*, *Epicodakia*, *Coralliophaga*, *Irus* and *Hiatella*) may be explained as an extended habitat of ancestral species (or populations). In addition, an exceptionally large bivalve, *Pycnodonte* (*Pycnodonte*) *taniguchii*, is regarded as a relic of Tethyan fauna along with *Neritopsis radula*. It is bradytelic and probably has survived for a long geologic period since the Miocene by adapting to cryptic environments (Hayami and Kase, 1992).

As summarized before, there are many species belonging to deep-water genera (e. g. *Huxleyia*, *Pronucula*, *Bentharca*, *Bathyarca*, *Cratis*, *Dacrydium*, *Parvamussium*, *Chlamydella*, *Divarilima*, *Limatula*, *Carditella*, *Kelliella* and *Halonympha*). Although none of them seems to be identical with deep-water species, their deep-sea origin is very likely.

Most species of these deep-water type genera indicate lecithotrophic or direct larval development, and their migration for long distances must be difficult in comparison with planktotrophic species. The populations of these species must at present be almost isolated between caves. Nevertheless, they are often distributed widely not only in various caves of the Ryukyu Islands but also in similarly sheltered environments of Bohol Island of the Philippines and Palau Islands (Table 2).

The assemblages of bivalves are somewhat different between Ie Islet (Okinawa) and Shimoji-Irabu Islet (Miyako Islands). Okinawa and Miyako are separated by a deep sea called "Kerama Gap" which is wider than 300 km and deeper than 1,000 m (Map 1). The endemism of several species (e.g. *Cosa uchimae*, *Parvamussium crypticum*, *Divarilima elegans*, *Carditella iejimensis* and *Halonympha asiatica* restricted to Ie Islet, and *Urumella convava* and *Carditella shimojiensis* restricted to Shimoji-Irabu Islet) may be explained by this barrier. It is noted that these endemic species are non-planktotrophic.

The geographic distribution of *Cosa waikikia*, *Chlamydella incubata* and *Chlamydella tenuissima*, however, is incredibly extensive, if their parental care of juveniles is considered. The first species is distributed in Hawaii, Samoa (?) and many isolated islands of the western Pacific; the second and third species, in many distant areas of southern Japan. It is still a mystery how these bivalves can have extended their distribution. Though there is no positive evidence, we now hypothesize that these species could tolerate long pseudoplanktic lives. Because the individuals of these species easily attach themselves by byssus to various objects, fishes, large crustaceans and some floating materials probably transport them for long distances.

Another unsolved problem is related to the occurrence of three deep-water genera, *Dacrydium*, *Kelliella* and *Halonympha*, in the caves. The cave species of these genera are morphologically more closely related to northern Atlantic species than to any described species in the Indo-Pacific region. *Dacrydium zebra*, another brooding species, is very close to *Dacrydium viviparum* from the deep water of the northern Atlantic. *Kelliella japonica* is undoubtedly a close ally to *Kelliella miliaris*, also from the northern Atlantic. *Halonympha* has been known almost exclusively from the deep water of the Atlantic. As pointed out by many authors (e.g. Knudsen, 1970), however, it must be noted that bivalves of abyssal depths do not show clear provinciality; many species have cosmopolitan distribution. If we consider the incomplete and biased research on deep-water organisms, it is possible that such "Atlantic" species will be found in the Indo-Pacific in the future.

When and how did the bivalves of deep-water origin reach these sublittoral caves? The following discussion is no more than a speculation. Although the present submarine caves must have been drowned during a post-Glacial sea-level rise, the adaptation of these deep-water ancestors to such caves is not necessarily a Holocene event. It is more likely that since the Pleistocene (or earlier) these cavernicolous bivalves have been wandering similarly sheltered environments in shallow waters. As was discussed by Bouchet and Warén (1979), coastal upwelling may be able to transport the larvae (even non-planktotrophic) of deep-water bivalves within a few days. It is known that larvae of marine animals are generally more tolerant of changeable temperature and hydrostatic pressure than are the adults. If they accidentally settle in a sheltered environment, they may be able to exploit a new habitat. Rapid changes of body size and developmental strategy may occur in adaptation.

Conclusion

Although several authors paid attention to the evolutionary significance of pantropical cryptic organisms (especially sclerosponge-brachiopod fauna) in and around coral reefs, little had been known about the features of molluscs in such sheltered environments. The newly discovered cavernicolous fauna from the Ryukyu Islands contains numerous characteristic diminutive bivalves as well as gastropods and other taxonomic groups. Further taxonomic, ecologic and environmental studies by specialists are, of course, needed to understand the unique community and ecosystem, but the composition and characteristics of the bivalves seem to suggest the possibility that submarine cave biota offers substantial data to test various theories and ideas of evolutionary ecology, historical biology and marine biogeography.

As described in this paper, 13 sublittoral limestone caves of Ie, Shimoji and Irabu Islets of the Ryukyu Islands yield 48 characteristic bivalves, which are mostly new and at least in part indigenous to such cryptic environments. The common and predominant features of these cavernicolous bivalves are:

1) small adult size and frequent stunting,
2) dominance of epibyssate and semi-infaunal suspension feeders,
3) absence or rarity of cemented species and deep burrowers,
4) presence of many deep-water type genera (e.g. *Huxleyia*, *Pronucula*, *Bentharca*, *Cratis*, *Dacrydium*, *Parvamussium*, *Chlamydella*, *Divarilima*, *Carditella*, *Kelliella* and *Halonympha*),
5) dominance of paedomorphosis by progenesis, though little is as yet known about the actual growth rate,
6) dominance of non-planktotrophic (lecithotrophic and direct) development which is comparable with that of deep-water and high-latitudinal bivalves,
7) small clutch size and low fecundity suggested by the large-sized Pd I in many species and parental incubation of embryos in several species.

The marked species diversity of cavernicolous bivalves, in spite of narrow space, is certainly due to their diminutive body size. The acknowledged relation between area and number of species (MacArthur and Wilson, 1967) would be invalidated, if mean body size were significantly different between regions. The abundant occurrence of many deep-water type genera from upper sublittoral caves in this subtropical region indicates that neither high hydrostatic pressure nor low water temperature is a decisive factor for the restricted distribution of these genera.

These remarkable features are probably related to one another and mainly caused by the steadily oligotrophic condition for suspension feeders, because no primary production of nutrition (phytoplanktons) by photosynthesis occurs in dark caves. Low predation pressure may be also a factor analogous to the deep-sea bottom. *K*-selection, if anything, seems to prevail in the cavernicolous bivalves like deep-water species, although the tendency of stunting and progenesis is not compatible with current theories of evolutionary ecology, probably because the deficiency of nutrition is a decisive factor in the survival strategy.

Prodissoconchs are generally well preserved in these cave bivalves. Remarkable plasticity in prodissoconch size and shape within a genus is strongly indicated by the cave species of the Arcidae, Philobryidae, Propeamussiidae and Limidae. Submarine caves seem to offer refuges to relatively defenseless organisms of archaic life mode. Rapid evolutionary changes of adult size and developmental strategy may have occurred, as the ancestral populations adapted to such a sheltered environment.

The origin and speciation of these cavernicolous bivalves are still an unsolved problem because fossil and extant bivalves of such diminutive size have been insufficiently described in this region. It is still not known why some brooding bivalves (e.g. *Cosa waikikia* and *Chlamydella incubata*) actually show such a wide geographic distribution. We expect, however, that further comparative studies of cryptic biota from different regions would solve these problems, because there are numerous similar submarine caves around coral reefs of tropical-subtropical regions. Discovery of various "living fossil" organisms is anticipated as well in future research.

Acknowledgments

This study has been supported by many cooperative skilled divers and other kind persons in Okinawa and Miyako Islands. We sincerely thanks Messrs. Shuichi Ohashi, Shigemitsu Kinjo, Nagaaki Yosa, Hiroyuki Gibo, Hiroyuki Kinjo and Kiyoshi Kijima and Miss Miyoko Uchima of Okinawa, Messrs. Mitsutoshi Taniguchi and Ayato Tamura of Miyako, and Mr. Shinichi Shimizu of Tokyo for their self-sacrificing contribution in collecting samples. Some comparative samples outside the Ryukyu Islands were supplied by Messrs. Peter Reber, Toshio Kanazawa and Hisamichi Nabeshima. Mr. Sueo Kaneko kindly gave us full information about his unpublished data on the Philobryidae and Propeamussiidae. Concerning the taxonomic identification, one of us (Hayami) received various important suggestions and comments from Professor John Allen (Scotland), Drs. Thomas Waller, Eugene Coan, Paul Scott and Robert Prezant (U. S. A.) and Dr. Jean Poutiers (France) at the time of the 1991 International Marine Bivalve Symposium at Berkeley. Our cordial thanks are due to Dr. R. K. Dell (New Zealand) and Dr. Philippe Bouchet (France) for their instructive information in relation to the present study, to the staff members of the Australian Museum for their kind loan of some type specimens, to Drs. Tadashige Habe and Akihiko Matsukuma and Mr. Eiji Tsuchida for their kind assistance in observing comparative specimens and literature, to Dr. Yasunari Shigeta and Mr. Takao Ubukata for their assistance in scanning electron microscopy, and also to many faculty members and students of the Paleobiological Laboratory of the University of Tokyo for their fruitful discussions. Among others, Professor Kazushige Tanabe kindly reviewed the final manuscript and gave us important comments and suggestions. This study was financially supported by grants from the Ministry of Education, Science and Culture, Japan (Nos. 01460062, 02402017, 02640616, 04454032), the Fujiwara Natural History Foundation, and Research Institute of Marine Invertebrates.

References

Adams, A. 1856. Descriptions of thirty-four new species of bivalve mollusca (*Leda*, *Nucula* and *Pythina*) from the Cuming collections. *Proc. Zool. Soc. London*, **1855**: 47–53.

Adams, A. 1860. On some new genera and species of Mollusca from Japan. *Ann. Mag. Nat. Hist.*, [3] **5**: 299–303.

Adams, A. 1862. On some new species of Mollusca from Japan. *Ann. Mag. Nat. Hist.*, [3] **9**: 295–298.

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

Allen, J. A. 1983. The ecology of deep-sea molluscs. 29–75. *In* Russell-Hunter, W. D. (ed.) *The Mollusca, Vol.6. Ecology*. Academic Press.

Allen, J. A. and Morgan, R. E. 1981. The functional morphology of Atlantic deep water species of the families Cuspidariidae and Poromyidae (Bivalvia): an analysis of the evolution of the septibranch condition. *Phil. Trans. Roy. Soc. London*, [B] **294**: 413–546.

Allen, J. A. and Sanders, H. L. 1969. *Nucinella serrei* Lamy (Bivalvia: Protobranchia), a monomyarian solemyid and possible living actinodont. *Malacologia*, **7**: 381–396.

Barnard, K. H. 1964. Contributions to the knowledge of South African marine Mollusca. Part 5. Lamellibranchiata. *Ann. South Afr. Mus.*, **47**: 361–593.

Benton, M. J. 1993 ed. *Fossil Record 2*. 688p. Chapman & Hall, London.

Bernard, F. R. 1978. New bivalve molluscs, subclass Pteriomorphia, from the northeastern Pacific. *Venus*, **37**: 61–75.

Bernard, F. R. 1983. Catalogue of the living Bivalvia of the Eastern Pacific Ocean: Bering Strait to Cape Horn. *Canad. Spec. Pub. Fish. Aquat. Sci.*, **61**: 1–102.

Bernard, F. R. 1989. *Kelliella elegantula* sp. nov., first record of the genus from British Columbia, Canada (Bivalvia: Kelliellidae). *Veliger*, **32**: 185–187.

Bernard, M. F. 1896. Diagnoses de coquilles nouvelles de lamellibranches (genres *Hochstetteria* et *Condylocardia*). *Bull. Mus. Nat. Hist. Natur. (Paris)*, **2**: 193–197.

Boss, K. J. 1969. Systematics of the Vesicomyidae (Mollusca: Bivalvia). *Malacologia*, **9**: 254–255.

Bouchet, P. and Warén, 1979. Planktotrophic larval development in deep-water gastropods. *Sarsia*, **64**: 37–40.

Calow, P. 1983. Life-cycle patterns and evolution. *In* Russell-Hunter, W. D. (ed.): *The Mollusca, Vol.6. Ecology*. Academic Press.

Carter, J. G. 1990 ed. *Skeletal Biomineralization: Patterns, Process and Evolutionary Trends*. 2 vols. 832 + 101p., 200pls. Van Nostrand, New York.

Chinzei, K. 1959. Molluscan fauna of the Pliocene Sannohe Group of northeast Honshu, Japan. 1. The fauna of the Kubo Formation. *J. Fac. Sci. Univ. Tokyo*, [2] **12**: 103–132.

Clarke, A. H. 1962. Annotated list and bibliography of the abyssal marine molluscs of the world. *Bull. Natn. Mus. Canada*, **181**: 1–114.

Cotton, B. C. and Godfrey, F. K. 1938. *The Molluscs of South Australia. Part 1. The Pelecypoda*. 314p. Frank Trigg, Adelaide.

Cox, L. R. 1943. The English Upper Lias and Inferior Oolite species of *Lima*. *Proc. Malac. Soc. London*, **25**: 151–187.

Cox, L. R. et al. 1969. *Treatise on Invertebrate Paleontology*. Part N. Mollusca 6 (2 vols.), 1–952. Geol. Soc. America and Univ. Kansas.

Dall, W. H. 1872. Description of sixty new forms of mollusks from the west coast of North America and the north Pacific Ocean, with notes on others already described. *Amer. J. Conch.*, **7**: 93–160.

Dall, W. H. 1881. Preliminary report on the Mollusca (Blake deep sea expedition in the Gulf of Mexico). *Bull. Mus. Comp. Zool. Harvard Univ.*, **9**: 33–144.

Dall, W. H. 1886. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877–79, by the U. S. coast survey steamer Blake XXIV. Report on the Mollusca. Part 1. Brachiopoda and Pelecypoda. *Bull. Mus. Comp. Zool. Harvard Univ.*, **12**: 171–318.

Dall, W. H. 1889 (reprint edition, 1903). A preliminary catalogue of the shell-bearing marine mollusks and brachiopods of the southeastern coast of the United States, with illustrations of many of the species. *Bull. U. S. Nat. Mus.*, **37**: 1–232.

Dall, W. H. 1898. Contributions to the Tertiary fauna of Florida, with special reference to the Silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River, including in many cases a complete revision of the generic groups treated of and their American Tertiary species. *Trans. Wagner Free Inst. Sci. Phila.*, **3**: 571–947.

Dall, W. H. 1902. Illustrations and descriptions of new, unfigured or imperfectly known shells chiefly American, in the U. S. National Museum. *Proc. U. S. Nat. Mus.*, **24**: 499–566.

Dall, W. H. 1916. Diagnoses of new species of marine bivalve mollusks from northwest coast of America in the collection of the United States National Museum. *Proc. U. S. Nat. Mus.*, **52**: 393–417.

Dall, W. H., Bartsch, P. and Rehder, H. A. 1938. A manual of the Recent and fossil marine pelecypod mollusks of the Hawaiian Islands. *Bernice P. Bishop Mus., Bull.* **153**: 1–233.

Dautzenberg, P. and Bavay, A. 1912. *Les Lamellibranches de l'Expedition du Siboga.* Partie systematique. 1. Pectinidés. 127–167, pls.27, 28. E. J. Brill, Leiden.

Dell, R. K. 1956. The archibenthal Mollusca of New Zealand. *Bull. Dominion Mus.*, **18**: 1–215.

Dell, R. K. 1990. Antarctic Mollusca with special reference to the fauna of the Ross Sea. *Roy. Soc. New Zealand, Bull.*, **27**, 1–311.

Dijkstra, H. H. 1991. A contribution to the knowledge of the pectinacean Mollusca (Bivalvia: Propeamussiidae, Entoliidae, Pectinidae) from the Indonesian Archipelago. *Zool. Verhandl.*, **271**: 1–57.

Dillwyn, L. W. 1817. *A Descriptive Catalogue of Recent Shells.* Vol.2. 1092p. (not seen)

Finlay, H. J. 1927. A further commentary on New Zealand molluscan systematics. *Trans. N. Z. Inst.*, **57**: 320–485.

Fischer, P. 1880–1887. *Manuel de Conchyliologie et Paléontologie conchyliologique.* 1–114 [1880], 115–304 [1881], 305–416 [1882], 417–608 [1883], 609–688 [1884], 689–896 [1885], 897–1008 [1886], 1009–1369 [1887], F. Savy, Paris.

Fleming, C. A. 1978. The bivalve mollusc genus *Limatula*: a list of described species and a review of living and fossil species in the Southwest Pacific. *Jour. Roy. Soc. New Zealand*, **8**: 17–91.

Gould, A. A. 1861. Description of new shells collected by the North Pacific Exploring Expedition. *Proc. Boston Soc. Nat. Hist.*, **8**: 14–40.

Gould, S. J. 1977. *Ontogeny and Phylogeny.* 501p. Harvard Univ. Press.

Habe, T. 1951–53. *Genera of Japanese Shells.* Pelecypoda. no.1, 1–96 [1951], no.2, 97–186 [1951], no.3, 187–278 [1952], no.4, 281–326 [1953]. (in Japanese)

Habe, T. 1953. Descriptions of twelve new Japanese shells. *Venus*, **17**: 130–144.

Habe, T. 1958. Report on the Mollusca chiefly collected by the S. S. Soyo-maru of the imperial fisheries experimental station on the continental shelf bordering Japan during the years 1922–1930. Part 3. Lamellibranchiata (1). *Publ. Seto Mar. Biol. Lab., Kyoto Univ.*, **3**: 241–279.

Habe, T. 1961a. Descriptions of fifteen new species of Japanese shells. *Venus*, **21**: 416–431.

Habe, T. 1961b. *Coloured Illustrations of the Shells of Japan*, II. 183p., 66pls. Hoikusha, Osaka. (in Japanese)

Habe, T. 1977a. *Systematics of Mollusca in Japan.* Bivalvia and Scaphopoda. 372p. Hokuryukan, Tokyo. (in Japanese)

Habe, T. 1977b. Notes on *Antarctolima* (n. gen.) *hodgsoni* (Smith, 1907). *Venus*, **36**: 105–107.

Hallam, A. 1965. Environmental causes of stunting in living and fossil marine benthonic invertebrates. *Palaeontology*, **8**: 132–155.

Hartman, W. D. and Goreau, T. F. 1970. Jamaican coralline sponges: their morphology, ecology and fossil relatives. 205–243. *In* Fry, W. G. (ed.) *The Biology of the Porifera.* Symposium of the Zoological Society of London, vol.25.

Hayami, I. 1988a. Functional and taxonomic implications of internal ribs of *Propeamussium. Trans. Proc. Palaeont. Soc. Japan*, [n. s.] **150**: 476–490.

Hayami, I. 1988b. Taxonomic characters of propeamussiids from Japan. *Venus*, **47**: 71–82. (in Japanese with English abstract)

Hayami, I. and Kase, T. 1991. Cryptic propeamussiids and other bivalves from a submarine cave of Okinawa, south Japan. Amer. Malacol. Union and West. Soc. Malacologists, Joint Annual Meeting, Program and Abstracts, p.34.

Hayami, I. and Kase, T. 1992. A new cryptic species of *Pycnodonte* from Ryukyu Islands: a living fossil oyster. *Trans. Proc. Palaeont. Soc. Japan*, [n. s.] **165**: 1070–1089.

Hayami, I. and Kase, T. 1993. Bivalves of submarine caves. *Univ. Mus. Univ. Tokyo, News*, **27**: 1–3. (in Japanese)

Hedley, C. 1901. Some new or unfigured Australian shells. *Mem. Austr. Mus.*, **4**: 22–27.

Hedley, C. 1902. Scientific results of the trawling expedition of H.M.C.S. "Thetis". *Mem. Austr. Mus.*, **4**: 287–324.

Hedley, C. 1915. Studies on Australian Mollusca. Part 12. *Proc. Linn. Soc. New South Wales*, **34**: 695–755.

Higo, S. and Goto, Y. 1993. *A Systematic List of Molluscan Shells from the Japanese Is. and the Adjacent Area.* 693 + 13 + 148p. Eru Shell Publ. Co., Yao. (in Japanese)

Iliffe, T. M., Hart, C. W. Jr. and Manning, R. B. 1983. Biogeography and the caves of Bermuda. *Nature*, **302**: 141–142.

Iredale, T. 1929. Mollusca from the continental shelf of eastern Australia. No.2. *Rec. Austral. Mus.*, **17**: 157–189.

Iredale, T. 1939. Mollusca (I). *Great Barrier Reef Expedition 1928–29. Sci. Rep.*, **5**: 209–425.

Jablonski, D. and Lutz, R. A. 1980. Molluscan larval shell morphology: ecological and paleontological applications. *In* Rhoads, D.C. and Lutz, R.A. (ed.) *Skeletal Growth of Aquatic Organisms.* 323–377. Plenum Press, New York.

Jablonski, D. and Lutz, R.A. 1983. Larval ecology of marine benthic invertebrates: paleobiologic implications. *Biol. Rev.*, **58**: 21–89.

Jackson, J.B.C., Goreau, T.F. and Hartman, W.D. 1971. Recent brachiopod-coralline sponge communities and their paleoecological significance. *Science*, **173**: 623–625.

Jackson, J.B.C. and Winston, J.E. 1982. Ecology of cryptic coral reef communities. 1. Distribution and abundance of major groups of encrusting organisms. *J. Exper. Mar. Biol. Ecol.*, **57**: 135–147.

Kaneko, S. 1984. "Minute shells". Explanation of the 11th special exhibition, Osaka City Mus. Nat. Hist., 22–24. (in Japanese)

Kaneko, S. 1991. "Five species of the Philobryidae (Bivalvia: Limopsacea) from Japan (preliminary report)." *Venus*, **50**: 158. (in Japanese)

Kase, T. and Hayami, I. 1992. Unique submarine cave mollusc fauna: composition, origin and adaptation. *Jour. Moll. Studies*, **58**: 446–449.

Kay, E. A. 1979. Hawaiian Marine Shells. Reef and shore fauna of Hawaii, Section 4: Mollusca. *Bernice P. Bishop Mus. Spec. Publ.*, **64**, 1–653.

Keen, A. Myra, 1958. *Sea Shells of Tropical West America*. 623p., 10pls. Stanford Univ. Press.

Knudsen, J. 1967. The deep sea Bivalvia. *Sci. Rep. John Murray Exped.*, **11**: 235–343.

Knudsen, J. 1970. The systematics and biology of abyssal and hadal Bivalvia. *Galathea Report*, **11**: 7–241.

Kobluk, D. R. 1988. Cryptic faunas in reefs: ecology and geologic importance. *Palaios*, **3**: 379–390.

Kuroda, T. 1930. An illustrated catalogue of the Japanese shells, Part 5. *Venus*, **2**: app. 17–24.

Kuroda, T. and Habe, T. 1952. *Check List and Bibliography of the Recent Marine Mollusca of Japan*. 210p. Published by Leo. E. Stach, M. Sc., Box 121, Tokyo Central Post Office, Japan.

LaBarbera, M. 1974. Larval and post-larval development of five species of Miocene bivalves (Mollusca). *J. Paleontol.*, **48**: 256–277.

Lamprell, K. and Whitehead, T. 1992. *Bivalves of Australia*. Vol.1. 182p. Crawford House Press, Bathurst.

Laseron, C. F. 1953. Minute bivalves from New South Wales. *Rec. Austr. Mus.*, **23**: 33–53.

Le Pennec, M. 1980. The larval and post-larval hinge of some families of bivalve molluscs. *J. Mar. Biol. Assoc. U. K.*, **60**: 601–617.

MacArthur, R. H. and Wilson, E. O. 1967. *Island Biogeography*. Monograph in population biology, 1. 203p. Princeton Univ. Press.

MacIntyre, I. G., Rutzler, K., Norris, J. N. and Fauchald, K. 1982. A submarine cave near Columbus Cay, Belize: a bizarre cryptic habitat. 127–141. *In* Rutzler, K. and MacIntyre, I. G. (ed.) *The Atlantic Reef Ecosystem at Carrie Bow Cay, Belize*, I. Structure and Communities. Smithsonian Contribution to Marine Sciences, no.12.

Mackie, G. L. 1984. Bivalves. 351–418. *In* Tompa, A. S., Verdonk, N. H. and van den Biggelaar, J. A. M. (ed.) *The Mollusca*. Vol.7. Reproduction. Academic Press.

Mancini, E. A. 1978. Origin of micromorph faunas in the geologic record. *J. Paleontol.*, **52**: 311–322.

Masahito and Habe, T. 1972. A new species of the family Limidae from Japan. *Venus*, **31**: 1–3.

Matsui, S. 1991. Larval ecology of limopsid bivalves: evidence of paedomorphosis and developmental adjustment. 1991 Ann. Meeting Palaeont. Soc. Japan, Abstract, p.40. (in Japanese)

Matsukuma, A., Okutani, T. and Tsuchi, R. 1982. Three new species of the Nucinellidae (Bivalvia: Protobranchia) from Pacific coast of Japan. *Venus*, **40**: 177–186.

McKinney, M. L. and McNamara, K. J. 1991. *Heterochrony. The Evolution of Ontogeny*. 437p. Plenum Press, New York.

Melvill, J. C. and Standen, R. 1907. The marine Mollusca of the Scottish National Antarctic Expedition. *Trans. R. Soc. Edinburgh*, **46**: 119–157.

Morton, B. S. 1978. The biology and functional morphology of *Philobryia munita* (Bivalvia: Philobryidae). *J. Zoology*, **185**: 173–196.

Morton, B. 1980. Some aspects of the biology and functional morphology of *Coralliophaga* (*Coralliophaga*) *coralliophaga* (Gmelin, 1791)(Bivalvia: Arcticacea): a coral associated nestler in Hong Kong. 311–330. *In* Morton, B. (ed.): *Proceedings of the 1st International Workshop on the Malacofauna of Hong Kong and Southern China*. Hongkong Univ. Press.

Morton, B. 1981. Prey capture in the carnivorous septibranch *Poromya granulata* (Bivalvia:

Anomalodesmata: Poromyacea). *Sarsia*, **66**: 241–256.

Morton, B. 1983. Coral associated bivalves of the Indo-Pacific. 139–224. *In* Wilbur, K. M. and Russell-Hunter, W. D. (ed.) The Mollusca. Vol.6, Ecology. Academic Press, New York.

Morton, B. 1990. Corals and their bivalve borers — the evolution of a symbiosis. 11–46. *In* Morton, B. (ed.) *The Bivalvia*. Hong Kong Univ. Press.

Nicol, D. 1966. Description, ecology, and geographic distribution of some Antarctic pelecypods. *Bull. Am. Paleont.*, **51**: 1–102.

Noda, H. 1980. Molluscan fossils from the Ryukyu Islands, southwestern Japan. Part 1. Gastropoda and Pelecypoda from the Shinzato Formation in the southeastern part of Okinawa-jima. *Sci. Rep. Inst. Geosci. Univ. Tsukuba*, [B] **1**: 1–95.

Nomura, S. 1936. A new species of the genus *Septifer* from Japan (*S. keeni*). *Venus*, **6**: 205–208.

Nomura, S. and Hatai, K. 1940. The marine fauna of Kyuroku-sima and its vicinity, northeast Honsyu, Japan. *Saito Ho-on Kai Mus., Res. Bull.*, **19**: 57–115.

Nomura, S. and Zinbo, N. 1934. Marine shells from the "Ryukyu Limestone" of Kikai-sima, Ryukyu Group. *Sci. Rep. Tohoku Imp. Univ.*, [2] **16**: 109–164.

Nordsieck, F. 1969. *Die europäischen Meeresmuscheln (Bivalvia) vom Eismeer bis Kapverden, Mittelmeer und Schwarzes Meer*. 256p. Gustav Fischer Verlag, Stuttgart.

Ockelmann, W.K. 1965. Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe. 25–35. *In* Cox, L.R. and Peake, J.F. (ed.) *Proceedings of the 1st European Malacological Congress, London, 1962*. Conchological Society of Great Britain and Ireland and the Malacological Society of London, London.

Ockelmann, W. K. 1983. Descriptions of mytilid species and definition of the Dacrydiinae n. subfam. (Mytilacea-Bivalvia). *Ophelia*, **22**: 81–123.

Okutani, T. 1962. Report on the archibenthal and abyssal lamellibranchiate Mollusca mainly collected from Sagami Bay and adjacent waters by the R.V. Soyo-maru during the years 1955–1960. *Bull. Tokai Reg. Fish. Res. Lab.*, **32**: 1–40.

Okutani, T. 1968. Bathyal and abyssal Mollusca trawled from Sagami Bay and the south off Boso Peninsula by the R/V Soyo-Maru, 1965–1967. *Bull. Tokai Reg. Fish. Res. Lab.*, **56**: 7–56.

Okutani, T. 1975. Deep-sea bivalves and scaphopods collected from deeper than 2,000 m in the northwestern Pacific by the R/V Soyo-Maru and the R/V Kaiyo-Maru during the years 1969–1974. *Bull. Tokai Reg. Fish. Res. Lab.*, **82**: 57–87.

Okutani, T. and Ito, K. 1983. A new cuspidariid bivalve from the Sado Strait, Japan Sea (Bivalvia: Cuspidariidae). *Venus*, **42**: 167–169.

Oliver, G. and Allen, J.A. 1980. The functional and adaptive morphology of the deep-sea species of the Arcacea (Mollusca: Bivalvia) from the Atlantic. *Philos. Trans. Roy. Soc. London*, [B] **291**: 45–76.

Oyama, K. 1943. Familia Limidae. *In* Taki, I., Otuka, Y. and Suzuki, K. (ed.) *Conchologia Asiatica*, vol.1, 1–74. Kajitani-shoin, Tokyo. (in Japanese)

Oyama, K. 1973. Revision of Matajiro Yokoyama's type Mollusca from the Tertiary and Quaternary of the Kanto area. *Palaeont. Soc. Japan, Spec. Pap.*, **17**: 1–148.

Philippi, R.A. 1844. *Enumeratio molluscorum siciliae cum viventium tum in tellure tertiaria fossilium*. 303p. Halle. (not seen)

Pianka, E.R. 1970. On *r* and *K* selection. *Amer. Natur.*, **104**: 592–597.

Pianka, E.R. 1983. *Evolutionary Ecology*. 3rd ed. 337p. Harper and Row, New York.

Poutiers, J.-M. 1989. Note sur le genre *Dacrydium* Torell, 1859 dans l'ocean indien (mollusques bivalves: Mytilidae), avec description de deux especes nouvelles. *J. Conch.* **33**, 209–217.

Powell, A.W.B. 1933. New pelecypod Mollusca from northern New Zealand. *Proc. Malac. Soc. London*, **20**: 199–206.

Powell, A.W.B. 1937. New species of marine Mollusca from New Zealand. *Discovery Rep.*, **15**: 153–222.

Powell, A.W.B. 1955. Mollusca of the Southern Islands of New Zealand. *Cape Exped. Ser., Bull.*, **15**: 1–151.

Powell, A.W.B. 1958. *Shells of New Zealand.* 3rd and enlarged edition. 203p. Whitcombe and Tombs Ltd., Christchurch.

Prashad, B. 1932. The Lamellibranchia of the Siboga Expedition. Systematics Part 2. *Siboga Exped.* C **53**: 1–353.

Prezant, R.S. 1990. Shell and hinge ontogeny of the Antarctic bivalve *Lissarca notorcadensis. J. Mar. Biol. Ass. U.K.*, **70**: 841–855.

Reeve, L.A. 1843. *Conchologia Iconica*, Vol.2, pl.2. London.

Reid, R.G.B. 1990. Evolutionary implications of sulphide-oxidizing symbioses in bivalves. 127–140. *In* Morton, B. (ed.) *The Bivalvia.* Hong Kong Univ. Press.

Reid, R.G.B. and Reid, A.M. 1974. The carnivorous habit of members of the septibranch genus *Cuspidaria* (Mollusca: Bivalvia) . *Sarsia*, **56**: 47–56.

Rombouts, A. 1991. *Guidebook to Pecten Shells. Recent Pectinidae and Propeamussiidae of the World.* 157p. Oegstgeest, Universal Book Services.

Sakurai, K. and Habe, T. 1973. Family Mesodesmatidae of Japan and adjacent area with the description of a new species. *Venus*, **32**: 4–8.

Sars, M. 1870. *Bidrag til Kundskaben om Norges arktise Fauna.* 1. Mollusca reglonis arcticae Norvegiae. 466p. Oslo.

Scacchi, A. 1834: Notizie intorno alle conchiglie ed a zoofiti fossili. *Annali Civili*, **6**: 75–84. (not seen)

Schein, E. 1989. Pectinidae (Mollusca, Bivalvia) bathyaux et abyssaux des campagnes BIOGAS (Golfe de Gascogne). Systématique et biogéographie. *Ann. l'Inst. Océanogr. Paris*, **65**: 59–125.

Seed, R. 1968. Factors influencing shell shape in the mussel *Mytilus edulis. J. Mar. Biol. Assoc. U.K.*, **48**: 561–584.

Smith, E.A. 1885. Report on the Lamellibranchia collected by H.M.S. Challenger during the years 1873–76. *Rep. Sci. Res. 'Challenger'*, **13**: 1–341.

Snyder, J. and Bretsky, P.W. 1971. Life habit of diminutive bivalve molluscs in the Maquoketa Formation (Upper Ordovician). *Amer. J. Sci.*, **271**: 227–251.

Soot-Ryen, T. 1960. Pelecypods from Tristan da Cunha. *Results Norw. Sci. Exped. Tristan da Cunha*, **49**: 1–47.

Sorgenfrei, T. 1958. *Molluscan Assemblages from the Marine Middle Miocene of South Jutland and their Environments.* 2 vols. 503p. Reitzel, Copenhagen.

Stoliczka, F. 1870. Cretaceous fauna of southern India. Vol.3. The Pelecypoda. *Palaeontologia Indica*, [6] **3**: 1–537.

Studencka, B. 1987. The occurrence of the genus *Kelliella* (Bivalvia, Kelliellidae) in shallow-water, Middle Miocene deposits of Poland. *Acta Palaeont. Polonica*, **32**: 73–81.

Sugimura, A. 1977. Ice, continents and oceans. Kagaku (Science), **47**: 749–755. (in Japanese)

Suter, H. 1913. *Manual of New Zealand Mollusca.* 1120p. Goverment Printer, Wellington.

Tanabe, K. 1990. Early life history of two middle Pleistocene species of *Limopsis* (Arcoida: Bivalvia). *Trans. Proc. Palaeont. Soc. Japan*, [n. s.] **160**: 631–641.

Tasch, P. 1953. Causes and paleoecological significance of dwarfed fossil marine invertebrates. *J. Paleontol.*, **27**: 356–444.

Tenison-Woods, J.E. 1878. On some new marine Mollusca. *Trans. Roy. Soc. Victoria*, **14**: 55–65.

Tevesz, M.J.S. 1977. Taxonomy and ecology of the Philobryidae and Limopsidae (Mollusca: Pelecypoda). *Postilla, Peabody Mus. Yale Univ.*, **171**: 1–64.

Thiel, H. 1975. The size structure of the deep-sea benthos. *Int. Rev. Ges. Hydrobiol.*, **60**: 575–606.

Thiele, J. 1935. *Handbuch der systematischen Weichtierkunde*. Bd. 2. 779–1154. Gustav Fischer, Jena.

Thiele, J. and Jaeckel, S. 1931. Muscheln der deutschen Tiefsee Expedition. Wiss. Ergebn. Deut. Tiefsee-Exped. »*Valdivia*«, **21**: 159–268.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. *Medd. Dan. Fisk. Havunders.*, **4**: 1–523.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, **25**: 1–45.

Vermeij, G.J. 1987. *Evolution and Escalation, an Ecological History of Life*. 527p. Princeton Univ. Press.

Vermeij, G.J. 1990. Tropical Pacific pelecypods and productivity: a hypothesis. *Bull. Mar. Sci.*, **47**: 62–67.

Verrill, A.E. 1897. A study of the family Pectinidae, with a revision of the genera and subgenera. *Trans. Connecticut Acad. Sci.*, **10**: 41–96.

Waller, T.R. 1972. The functional significance of some shell microstructure in the Pectinacea (Mollusca: Bivalvia). *24th Intern. Geol. Congr. Montreal*, sec.7, 48–56.

Waller, T.R. 1978. Morphology, morphoclines and a new classification of the Pteriomorphia (Mollusca: Bivalvia). *Phil. Trans. Roy. Soc. London*, Biol. Sci., **284**: 345–365.

Waller, T.R. 1984. The ctenolium of scallop shells: functional morphology and evolution of a key family-level character in the Pectinacea (Mollusca: Bivalvia). *Malacologia*, **25**: 203–219.

Waller, T.R. 1990. The evolution of ligament systems in the Bivalvia. 49–71. *In* Morton, B. ed. *The Bivalvia*. Hong Kong Univ. Press.

Warén, A. 1989. New and little known Mollusca from Iceland. *Sarsia*, **74**: 1–28.

Woodward, S.P. 1875. *A Manual of the Mollusca*. 3rd ed. 543 + 81p. Lockwood & Co., London.

Yokoyama, M. 1910. On species of *Limopsis* found in the Neogene of Koshiba. *J. Geol. Soc. Tokyo*, **17**: 1–5.

Yokoyama, M. 1920. Fossils from the Miura Peninsula and its immediate north. *J. Coll. Sci. Imp. Univ. Tokyo*, **39**: 1–198.

Yokoyama, M. 1922. Fossils from the Upper Musashino of Kazusa and Shimosa. *J. Coll. Sci. Imp. Univ. Tokyo*, **44**: 1–200.

Yokoyama, M. 1924. Mollusca from the coral-bed of Awa. *J. Coll. Sci. Imp. Univ. Tokyo*, **45**: 1–62.

Yoshida, H. 1937. On the pelagic larvae and youngs of *Brachidontes senhausi* (Reeve). *Venus*, **7**: 121–128. (in Japanese)