

Mode of Occurrence of *Otapiria dubia* (Bivalvia) from the Upper Triassic of West Kyushu, Southwest Japan

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ABSTRACT

Four slabs of Upper Triassic mudstone from the Kurosegawa Belt of Kyushu show crowded occurrence of a Carnian pteriomorph bivalve, *Otapiria dubia* (Ichikawa, 1954). One of them seems to show some shells preserved in the original small clump in which individuals had been attached to each other by their byssus. On the other three slabs disarticulated valves of *O. dubia* are associated with *Halobia* and plant remains. There are no individuals attached to plant fragments or other objects. This mode of occurrence as well as the shell morphology indicate an epibyssate benthic life for *O. dubia*. This paper also provides systematic descriptions of the genus *Otapiria* and *O. dubia* (Ichikawa). The systematic assignment of *Otapiria* to the Monotidae is confirmed by the ligament characteristics and the presence of pseudoctenolia on the upper and lower sides of the byssal notch.

INTRODUCTION

Otapiria Marwick, 1935, is a characteristic and rather cosmopolitan marine bivalve genus ranging from the Lower Triassic (Scythian) to the Upper Jurassic (Tithonian) (Thenius, 1980). It is the most closely related genus to *Monotis*, and may be important for the reconstruction of the paleoecology and phylogeny of Mesozoic thin-shelled pteriomorph bivalves (Ando, 1983, 1984, 1987).

The primary purpose of this paper is to discuss the life habits of *Otapiria dubia* (Ichikawa, 1954) on the basis of mode of fossil occurrence at two localities in Kyushu, southwest Japan. The second purpose is to provide systematic descriptions of this genus and the Japanese species. I pay attention to the morphological features of hinge and anterior ear.

ACKNOWLEDGMENTS

Firstly, I would like to dedicate this paper to Professor Tamio Kotaka on the occasion of his retirement. I express my hearty thanks to Professor Itaru Hayami of the University of Tokyo for his encouraging discussions and critical reading of the manuscript. I gratefully thank Dr Akihiro Murata of the University of Tokyo, who showed me the fossil

locality at Nishinoiwa and provided valuable geological information. Thanks are due to Professor Hiromichi Hirano of Waseda University for his kind advice, and to Mr Akihito Asai for his help in my field survey.

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GEOLOGIC SETTING

As listed in Table 1, *Otapiria dubia* is known from five localities along the Kurosegawa Belt in Kyushu and Shikoku. In this belt *Otapiria dubia*-bearing formations are distributed along some lenticular narrow zones, as well as in other Triassic shelf-facies strata. The fossils treated here were obtained at the following two localities in west Kyushu.

<Loc. 1> Nishinoiwa, eastern part of Izumi Village, Kumamoto Prefecture. There have been few geological investigations except Murata (1981) who first discovered this locality. The route map (Fig. 1) shows the Upper Triassic formation trending E and ESE and dipping steeply to almost vertically to the north along the Shobudani River. It is mainly composed of dark gray, monotonous, stratified, moderately bioturbated, sandy to clayey mudstone, with rare alternating sandstone and mudstone, and bedded or massive sandstone.

The fossil-bearing part of the mudstone is 40 meters thick (Pl. 1, Fig. 20). In the north, the formation seems to be in contact with slump breccias, one bear-

ing chert blocks and serpentinite and the other with a layer of basic volcanic rock, although their boundaries were not observed. In the south, it is separated by several strike faults from similar massive mudstones bearing thick limestone lenses. Whether the Upper Triassic formation is a large block in the slump breccia or *in situ* is not determinable at present, but it should be noted that the formation is undeformed in contrast with the northern chaotic slump breccia.

<Loc. 2> Kurosaki, Tanoura Town, Ashikita-gun, Kumamoto Prefecture. Orita (1962) listed "*Pleuromysidia*" *kanmerai* Tamura [= *Otapiria dubia* (Ichikawa)] from the Carnian Tanoura Formation at Kurosaki and south of Tsurukuchi Pass. The *Otapiria*-bearing beds at Kurosaki are mainly stratified siltstones with some fine-grained sandstone layers (Tamura and Murakami, 1986).

Table 1. Localities of *Otapiria dubia* in Japan

No.	Formation	Localities	References
1		Nishinoiwa, Izumi Village, Ashikita-gun, Kumamoto Prefecture	Murata (1981) and pers. comm.
2	Tanoura Fm.	Kurosaki and south of Tsurukuchi Pass, Tanoura Town, Ashikita-gun, Kumamoto Prefecture	Tamura (1959), Orita (1962) Matsumoto and Kanmera (1964) Tamura and Murakami (1985)
3	Takagochi Fm.	North of Takagochi, Futami-Akamatsu Town, Yatsushiro City, Kumamoto Prefecture	Tamura (1959), Orita (1962) Matsumoto and Kanmera (1964) Tamura and Murakami (1985)
4	Matsukuma Fm.	West of Mameguri, Sakamoto Village, Yatsushiro-gun, Kumamoto Prefecture	Tamura (1959), Orita (1962) Matsumoto and Kanmera (1964)
5	Up. Fm., Low. Kochigatani Subgroup	Nagayasu, Kaminaka Town, Naka-gun, Tokushima Prefecture	Ichikawa (1954)

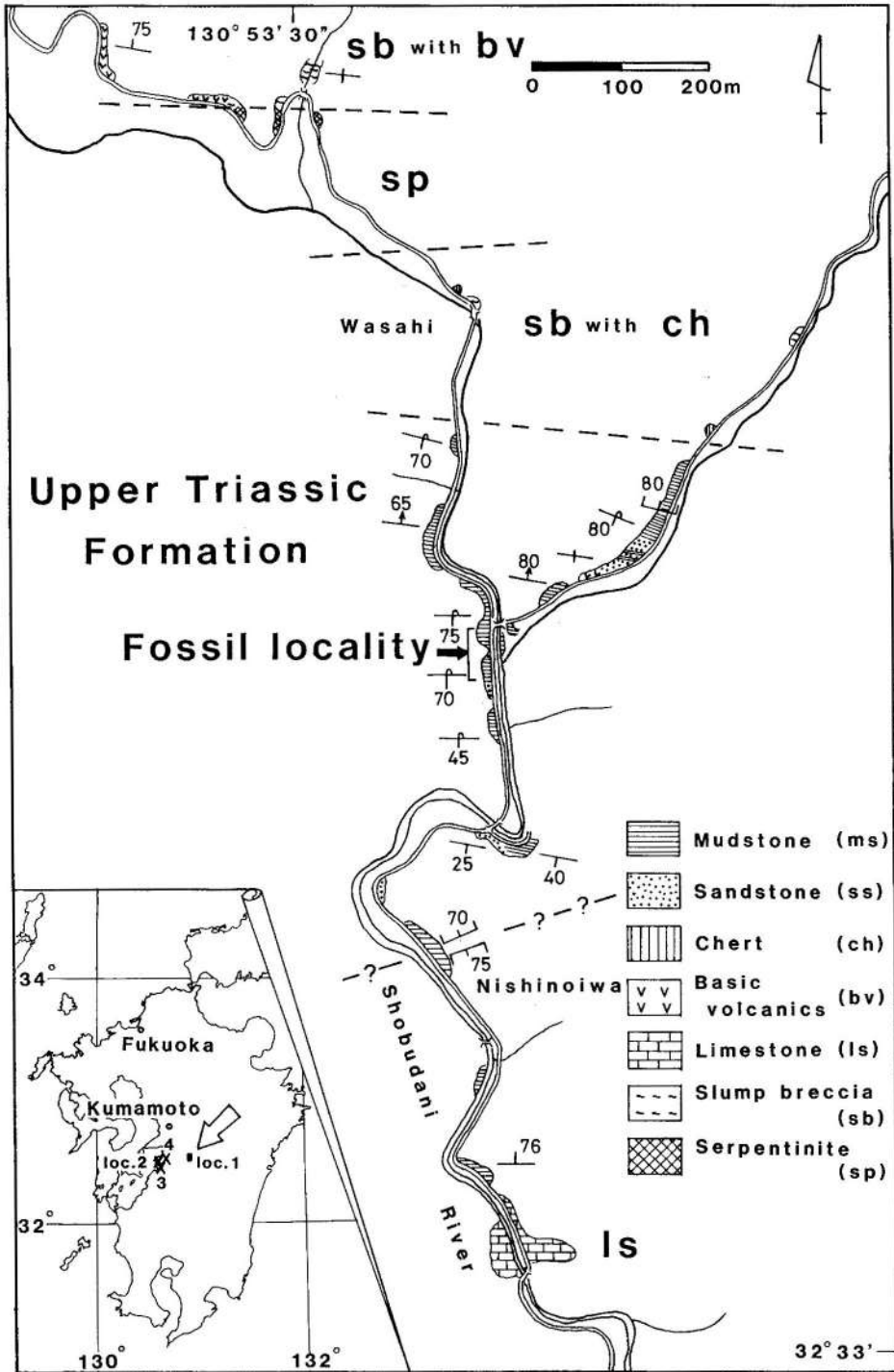


Fig. 1. Geological route map near Locality 1 at Nishinoiwa, east of Izumi Village, Kumamoto Prefecture.

MODE OF OCCURRENCE OF *OTAPIRIA*

A. General mode of occurrence

Otapiria dubia occurs sporadically with *Halobia* throughout the offshore bioturbated mudstone at the two localities described above. Its valves are usually disarticulated, but sometimes many articulated individuals are crowded together. Other associated fossils are epifaunal *Halobia* sp., *Oxytoma mojsisovichi* and *Tosapecten suzukii*, infaunal *Palaeoneilo* sp. (Pl. 1, Fig. 19, 16, 17 and 18, respectively) and crinoid stems. All these bivalves except *Palaeoneilo* sp. are disarticulated or fragmentary. The fossiliferous mudstone is considerably bioturbated, judging from the polished cross sections (Pl. 1, Figs. 21, 22). In Japan, *O. dubia* has not been found from *Monotis* beds.

B. Observation of four *Otapiria*-bearing slabs

Four slabs (A-D) containing abundant shells were obtained from the middle part of the muddy strata at loc. 1 (Fig. 1; Pl. 1, Fig. 20). In general, fossils are

restricted to thin horizons in all slabs.

Slab A (Pl. 2, Figs. 1-4)

Slab A contains more than 100 external molds of *Otapiria dubia* mostly lacking shell material. No other fossils are observed. Table 2 shows the valve composition and size distribution from a rubber cast taken from the surface of the slabs. At least one third of the total individuals are articulated with commissure planes nearly perpendicular to the bedding. Disarticulation of other valves may be only superficial, because it is possible that their counter valves are still buried in the matrix or have been exfoliated. The dominance of left valves in comparison with right appears to be related to the shell orientation which may indicate the original life position. Some individuals look as if they had been attached to each other with their byssus directing downward. It does not appear that separate articulated valves were gathered together by current action during sediment deposition, judging from the lithology and

Table 2. Valve composition of *Otapiria dubia* in a cluster on slab A of dark gray, bioturbated mudstone at loc. 1, Nishinoiwa, Izumi Village, Kumamoto Prefecture.

Valve	Orientation	L>20	20>L>10	L<10	Total
Left valve	Up	2	16	9	27
	Down	2	5	4	11
Right valve	Up		2	4	6
	Down		3		3
L.V. or R.V.	Up		4	4	8
	Down		5	1	6
L.V. + R.V. (articulated valves)	L.V. Up	2	8	7	17
	R.V. Up		2	5	7
	Vertical/nearly vertical	2	9	10	21
Total	8	54	44	106	

L: Length (mm); Up: Convex side upward; Down: Dconvex side downward

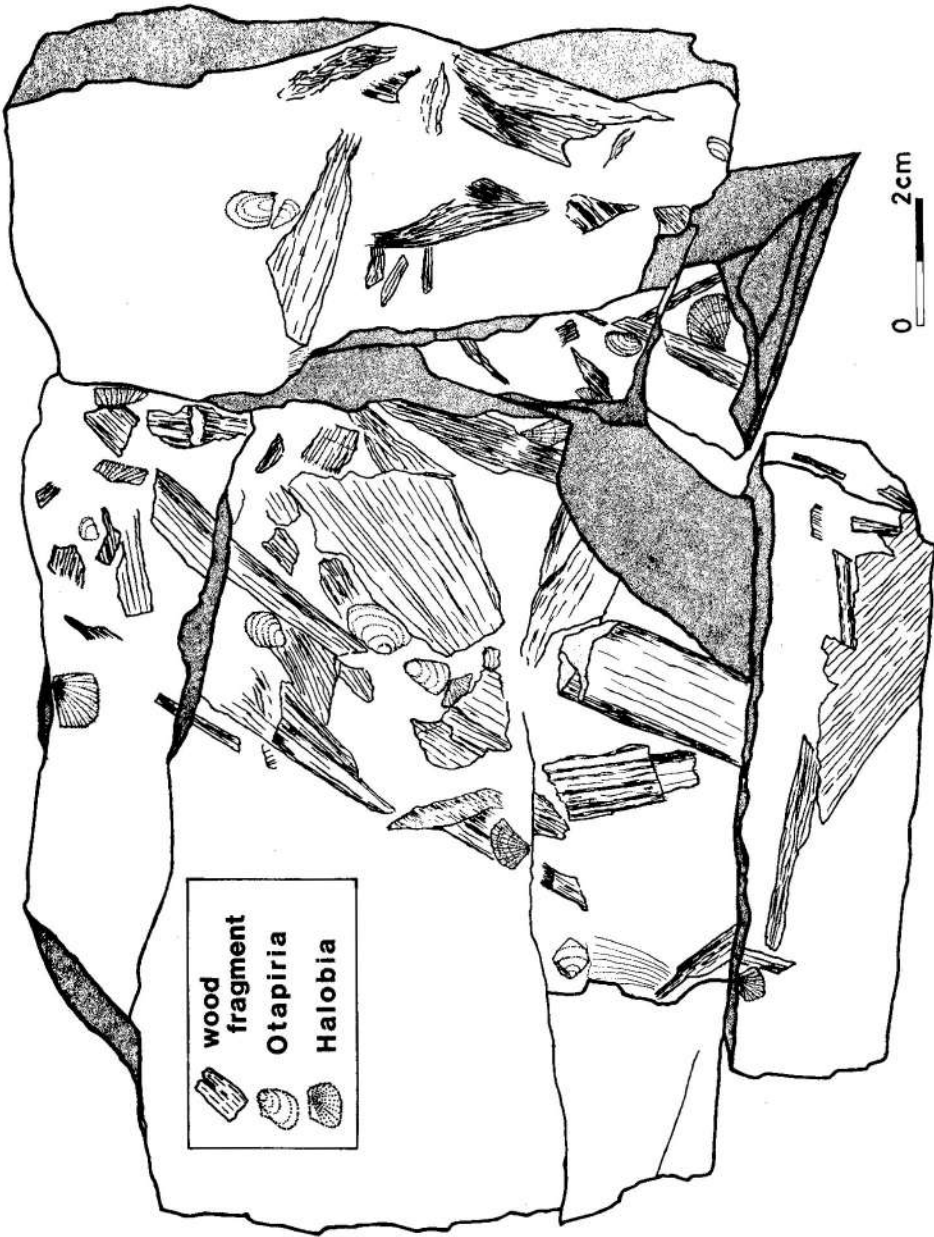


Fig. 2. Surface of slab B bearing disarticulated valves of *Otapiria dubia* (Ichikawa) and *Halobia* sp. and abundant plant fragments (Loc. 1).

relative shell positions in the slab.

Slab B (Fig. 2; Pl. 2, Fig. 5)

This slab contains abundant plant fragments with several disarticulated valves of *Otapiria dubia* and subordinate *Halobia* sp. Although these shells are apparently shown as incomplete in Fig. 2, they appear to have been originally complete. No articulated valves attached to the plant fragments can be found. There is no valve more than 30 mm long. The fossil layer is thinner than 30 mm thick and has no conspicuous lamination. As shown in Fig. 3, the dominant orientation of plant remains suggests the direction of water current and probable transportation of shells from the habitat.

Slab C (Pl. 2, Fig. 6)

This slab contains many fragments of crinoid stems in addition to disarticulated shells of *O. dubia* and *Halobia* sp. and plant remains with a generally consistent long-axis direction. The fossiliferous part constitutes a sandy thin layer less than 40 mm thick in dark gray mudstone. All the fossils in this slab must be allochthonous.

Slab D

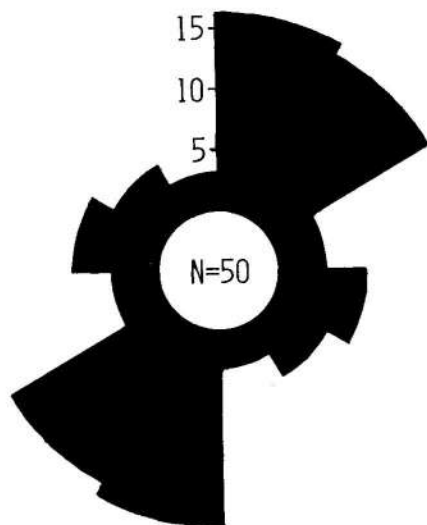


Fig. 3. Rose diagram showing the long-axis direction of plant fragments on slab B shown in Pl. 2, Fig. 5. N means number of plant fragments. The upper edge of the slab on Fig. 2 is consistent with the upward direction of the diagram.

In spite of bad preservation, one can see a few articulated and several disarticulated valves of *O. dubia* associated with plant remains in a layer less than 50 mm thick.

DISCUSSION

The mode of fossil occurrence in the four slabs, provides information for a paleoecological consideration of *Otapiria dubia*. Slab A showing nearly autochthonous occurrence suggests that the species had formed a clump and that many individuals had been attached to each other by a downward directed byssus. The object to which the first individual was attached when settling on the bottom is not preserved.

The coexistence of abundant plant fragments and some *Otapiria* and *Halobia* shells in the slabs B to D is similar to that of *Pseudomytiloides dubius* and *Ostrea* sp. found attached to floating wood in the Lower Jurassic

Posidonienschiefer of West Germany (e.g. Seilacher, 1982, fig. 5c). In Japan a similar occurrence was recently reported for *Pseudomytiloides matsumotoi* (Hayami) from the Lower Jurassic Toyora Group, southwest Japan (Tanabe, 1983). But the bioturbated lithology of the *Otapiria* bed is obviously different from the bituminous black shale of Posidonienschiefer and the Toyora Group indicating anoxic conditions (Seilacher *et al.*, 1985).

The *Otapiria* beds appear to have been deposited in a stagnant but more or less oxygenated environment where some benthic animals had lived and moved on and in the substrate. There are no wood

fragments to which the shells certainly had been attached. Both shells and wood have been rearranged by bottom current after sinking and before burial.

Gruber (1984) inferred an epiphytic algal attached mode of life for *Otapiria marshalli alpina* on the basis of shell morphology, paraautochthonous occurrence and lithofacies. He pointed out three morphological features suggesting a benthic habit, i.e. 1) inequilateral and inequivalve form, suggesting that the sagittal plane had been oblique to horizontal to the sea bottom, 2) difference in sculptural strength between the two valves, suggesting slightly different environmental conditions, and 3) the remarkable variability of shell outline, suggesting ecophenotypic variation adapted to differential environmental conditions. Gruber thought that the objects to which *Otapiria* had attached had been sessile seaweeds, because encrusted foraminifers which appear to have lived attached to seaweeds, predominate in the European *Otapiria* bed. Such a mode of life is presumed for certain species of *Monotis* (Ando, 1987), but difficult to assume for *O. dubia*, because the clumped occurrence observed in slab A strongly suggests an originally bottom dwelling colony. An epiphytic mode of life would hardly accommodate such the clump.

O. dubia is not found associated with

Monotis. As compared with *Monotis* beds, the mother rock is more fine-grained and does not form continuous and conspicuous fossil layers with significant thickness. Taking the mode of occurrence of *Otapiria* and the lithology of the *Otapiria* bed into account, it may have lived in more offshore stagnant environments than *Monotis*. *Otapiria* may have been a little different from *Monotis* in life habits (Ando, 1987, pp. 51-53).

Considering the presence of pseudoctenolia in the anterior part of the right valve in *O. marshalli alpina* (Gruber, 1984), other species of *Otapiria* also may have pseudoctenolia. *O. dubia*, however, could not be found to have them. Nevertheless, it is concluded that a byssally attached epibenthic life is generally most likely for *Otapiria*. While *O. marshalli alpina* is presumed to have been attached to seaweeds, *O. dubia* may have been attached to each other, with the right valve down, forming clumps on the soft substrate.

The world-wide or disjunct geographic distribution of the Mesozoic thin-shelled pteriomorph genera has been sometimes explained by the long period of their planktonic larval stage (Thenius, 1980; Gruber, 1984). The hypothesis is feasible but untestable due to the difficulty of obtaining any positive evidence.

SYSTEMATIC DESCRIPTION

Superfamily Buchiacea Cox, 1952

Family Monotidae Fischer, 1887

Genus *Otapiria* Marwick, 1935

Synonym: *Pleuromysidia* Ichikawa, 1954

Type-species: *Pseudomonotis marshalli* Trechmann, 1923

Diagnosis: Small- to moderate-sized, very thin-shelled, weakly to moderately inflated, inequivalve with less inflated right valve; outline obliquely oval with

considerable variation; umbo prosogyrous; posterior wing small, obscurely separated from disc, and obtusely truncated; anterior ear minute and projecting forward and obliquely inward; byssal notch very narrow but not so deep; ligament external, short, and or alivincular type with a shallow small pit; shell surface ornamented with irregularly weak concentric rugae, and with numerous fine radial plicae, stronger on left valve, weakly or scarcely plicated on

right valve.

Comparison: The genus is more oval, prosogyrous and posteroventrally elongate in outline than typical *Monotis*. The radial plication is much finer and weaker. A more strongly inflated but weakly plicated right valve with a smaller byssal ear is the most distinctive difference from *Monotis*. The ligament pit is a little smaller but more deeply excavated.

Taxonomic remarks: The suprafamilial classification in this paper follows Waller's (1978) scheme instead of Hertlein *et al.* (1969). In addition to the family Buchiidae, he included the Monotidae and such other families as Oxytomidae and Pseudomonotidae in the Buchiaceae. Many of the Mesozoic genera assigned by Hertlein *et al.* (1969) to the Aviculopectinidae were also included in the superfamily.

The assignment of *Otapiria* to the Monotidae was already discussed in Ando (1987, p. 80) and Damborenea (1987, p. 154). Hertlein *et al.* (1969) excluded *Otapiria* from the Monotidae with reference to the presence of a triangular ligament pit in *Otapiria*. But the ligament areas of *Otapiria* and *Monotis* are similar enough to assign them to the same family, because *Monotis* also has a more obtuse, long shallow ligament pit.

Pleuromysidia was proposed and questionably included in the Monotidae by Ichikawa (1954). Zakharov (1962) recognized the genus as a junior synonym of *Otapiria*. He detected the wide and continuous intraspecific variation of the Lower Jurassic *O. limaeformis* from the Okhotsk Sea coast in shell outline, represented by three forms, *longa*, *ovalis* and *alta*. Vozin and Tikhomirova (1964), however, reported a Carnian to Norian species as *Pleuromysidia dubia*. Some authors did not accept the synonymy of *Pleuromysidia* with *Otapiria* (Imlay, 1967; Covacevich and Es-

cobar, 1979; Gruber, 1984), but there is no significant morphologic difference between the two.

Recently, Kurushin (in Dagys and Kurushin, 1985) proposed the new subgenus *Praeotapiria* from the upper Olenekian *Dieneroceras demokidovi* Zone in the lower reaches of the Lena River. He described a new species, *Otapiria* (*Praeotapiria*) *bakevelliiformis* thought to be the oldest species of *Otapiria*. I think, however, that the subgeneric division is unnecessary because the morphologic difference is subtle, judging from his diagnosis.

Most recently, Damborenea (1987) described the systematic position of *Otapiria* in detail and proposed a new species for newly found specimens from the Lower Jurassic in southwestern Argentina. In the Jurassic bivalve monograph, she tentatively attempted a quadripartite supraspecific grouping of *Otapiria* species, but the morphologic differences between four species groups are thought to be subtle. She also pointed out that "*Lupherella* could be considered as a subgenus of *Otapiria*, perhaps originated by paedomorphosis of organisms from the groups (a) (including *O. marshalli* and other five species) or (c) (including *O. pseudooriginalis* and other two ones)" (Damborenea, 1987, p. 156).

Table 3 lists all known species of *Otapiria*, some of which are very little discriminated from each other. Certain morphologic features appear to be variable but this may be largely due to secondary deformation. From Japan, only *O. dubia* [= *O. kanmerai*] has been described.

Remarks on pseudoctenolia: Gruber (1984) described the detailed morphology of the ligament area and anterior ear of *Otapiria marshalli alpina* from the western Austrian Alps, on the basis of nearly autochthonous specimens. His plate provides significant evidence for consideration of the systematic relation

Table 3. Known species of *Otapiria*

Species of <i>Otapiria</i>	Distribution	Age	References
<i>O. (Praeotapiria) bakevellaeformis</i> Kurushin	N. Central Siberia	Late Early Triassic (Olenekian)	Dagys and Kurushin (1985)
<i>O. ussuriensis</i> (Voronetz)	N.E. Siberia Primorsky	Late Triassic (Carnian-Norian, or Lower Norian)	Vozin and Tikhomirova (1964) Kiparisova <i>et al.</i> (1966) Kiparisova (1972) Okuneva (1976, 1986)
<i>O. dubia</i> (Ichikawa)	Japan N.E. Siberia Primorsky	Late Triassic (Carnian or Lower Norian)	Ichikawa (1954) Kiparisova <i>et al.</i> (1966) Kiparisova (1972) Okuneva (1976, 1986)
<i>O. kanmerai</i> (Tamura) [= <i>O. dubia</i>]	Japan	Late Triassic (Carnian)	Tamura (1959)
<i>O. annulata</i> Polubotko, 1976	N.E. Siberia Primorsky	Late Triassic (Low.-Mid. Norian)	Okuneva (1986)
<i>O. depensis</i> Brudnitzkaja & Okuneva, 1985	N.E. Siberia Primorsky	Late Triassic (Lower Norian)	Okuneva (1986)
<i>O. reticularis</i> Truchelev, 1984	N.E. Siberia	Late Triassic (Low.-Mid. Norian)	Okuneva (1986)
<i>O. tugurensis</i> Okuneva	N.E. Siberia Primorsky	Late Triassic (Lowest Norian)	Okuneva (1986)
<i>O. zeensis</i> Okuneva	N.E. Siberia Primorsky	Late Triassic (Lower Norian)	Okuneva (1986)
<i>O. nodosus</i> Truchelev, 1984	N.E. Siberia	Late Triassic (Lower Norian)	Okuneva (1986)
<i>O. netkanensis</i> Truchelev, 1984	N.E. Siberia	Late Triassic (Low.-Mid. Norian)	Okuneva (1986)
<i>O. korkodonensis</i> Polubotko, 1976	N.E. Siberia	Late Triassic (Middle Norian)	Okuneva (1986)
<i>O. marshalli alpina</i> Zapfe	Austrian Alps	Late Triassic (Lorian- Rhaetian)	Zapfe (1973) Gruber (1984)
<i>O. sp.</i>	S.E. Czechoslovakia	Late Triassic (Norian-Rhaetian)	Kochanova (1977)
<i>O. (?) cf. O. ussuriensis</i>	Central Chile	Latest Triassic (Rhaetian)	Cecioni and Westermann (1968)
<i>O. dissimilis</i> (Cox)	New Zealand	Latest Triassic (Rhaetian, Otapirian in N.Z. scale)	Marwick (1953)
<i>O. marshalli</i> (Trechmann)	New Zealand New Caledonia	Early Jurassic (Hettangian & Sinemurian, Aratauran in N.Z. scale)	Trechmann (1923) Marwick (1935, 1953) Avias (1953)
<i>O. limaeformis</i> Zakharov	N.E. Siberia	Early Jurassic (Hettangian & Sinemurian)	Zakharov (1962) Efimova <i>et al.</i> (1968)
<i>O. limaeformis</i> <i>affecta</i> Polubotko	N.E. Siberia	Early Jurassic (late Sinemurian)	Efimova <i>et al.</i> (1968)
<i>O. pseudooriginalis</i> (Zakharov)	N.E. Siberia	Early Jurassic (Hettangian)	Zakharov (1962) Efimova <i>et al.</i> (1968)

Table 3. continued

Species of <i>Otapiria</i>	Distribution	Age	References
<i>O. ? originalis</i> (Kiparisova)	N.E. Siberia	Early Jurassic (Hettangian)	Efimova <i>et al.</i> (1968)
<i>O. ex. gr. marshalli</i> (Trechmann)	N.E. Siberia	Early Jurassic (Sinemurian)	Efimova <i>et al.</i> (1968)
<i>O. omolonica</i> Polubotko	N.E. Siberia	Early Jurassic (Hettangian & Sinemurian)	Efimova <i>et al.</i> (1968)
<i>O. inaequicostata</i> Geyer	Colombia	Early Jurassic (Sinerurian)	Geyer (1973)
<i>O. pacifica</i> Covacevich and Escobar	Central Chile	Early Jurassic (Sinerurian)	Covacevich and Escobar (1979) Escobar (1980)
<i>O. neuquensis</i> Damborenea	Argentina	Early Jurassic (latest Sinemurian- early Pliensbachian)	Damborenea (1987)
<i>O. ? frequellii</i> Damborenea	Argentina	Early Jurassic (precisely unknown)	Damborenea (1987)
<i>O. tailleuri</i> Imlay	N. Alaska	Late Earlyearly Middle Jurassic (Bajocian)	Imlay (1967)
<i>O. masoni</i> Marwick	New Zealand	Late Jurassic (Tithonian, Puaroran in N.Z. scale)	Marwick (1953)

between *Monotis* and *Otapiria*. Three of his figures are redrawn in Fig. 4 to show the detailed features. Figure 4a indicates a transversely striated and shallow ligament pit which is more or less similar to that of *Monotis*. Inner and outer views of the anterior ear are shown in Figs. 4b and c. The upper and lower margins of the byssal notch each have three spines less than 100 microns wide. Along both sides of the byssal fasciole there are also several weak nodes as traces of other spines. These two rows of nodes and spines were recognized as a ctenolium by Gruber, but they are equivalent to the active and inactive pseudoctenolia recognized by Waller (1984) as transformed external sculpture not homologous to the ctenolium in the Pectinidae. They are similar to pseudoctenolia of *Monotis* in size, but the lower series differs from that of *Monotis* (Ando, 1987, pp. 56-58). They

resemble the disk-type pseudoctenolia observed in *Oxytoma inequivalvis* (Waller, 1984, fig. 3c, p. 211), although much smaller. In spite of their small size, the pseudoctenolia of *Otapiria marshalli alpina* seem to function as a ctenolium in separating byssal threads and preventing the body from twisting. The anterior three spines must be the active part for byssal attachment. Other species of *Otapiria* are thought also to have such pseudoctenolia. If so, the presence of pseudoctenolia may be a common character in the Monotidae. But pseudoctenolia could not be observed in the specimens of *O. dubia* treated here, probably due to bad preservation.

As pointed out by Waller (1984), the presence of a true ctenolium and pseudoctenolium is one of the keys in taxonomic analysis and phyletic reconstruction in the Pectinacea as well as for ecological research. He believed that

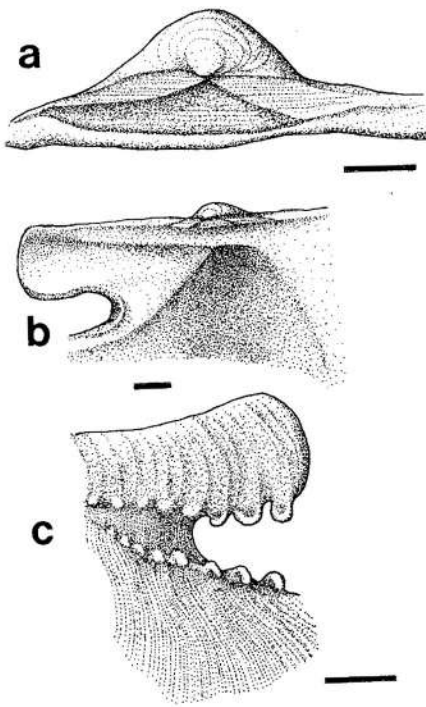


Fig. 4. Sketches of the ligamental area and anterior ear of *Otapiria marshalli alpina* Zapfe redrawn from in Gruber (1984, pl. 1). a: inner view of ligamental area of left valve (fig. A of Gruber); b: inner view of ligamental area and anterior ear in right valve (fig. E of Gruber); c: outer view of pseudoctenolia on both sides of the byssal notch in the anterior part of the right valve (fig. G of Gruber). Scale bars are 20 microns.

"the evolution of the disk-type pseudoctenolium is iterative, as evidenced by the fact that it is found at different times in two superfamilies, the Pectinacea and the Buchiacea" (Waller, 1984, p. 216). Now this type of pseudoctenolium was confirmed to exist only in *Aucellina* and *Oxytoma* (Hertlein *et al.*, 1969; Waller, 1984), *Monotis* (Marwick, 1935; Ando, 1987) and *Otapiria marshalli alpina* (Gruber, 1984).

Stratigraphic occurrence: Upper Lower Triassic (Olenekian) to Upper Jurassic (Tithonian). The genus is most com-

mon from Carnian to Early Jurassic (Table 3).

Geographic distribution: Rather cosmopolitan, although not as much as *Monotis* (Table 3). Japan, Northeast Siberia, Primorsky region, North Alaska, Central Chile, Argentine, New Zealand, New Caledonia, Austrian Alps and west Carpathians.

Otapiria dubia (Ichikawa)

Fig. 5; Pl. 1, figs. 1-15

- 1954 *Pleuromysidia dubia* Ichikawa, p. 52, pl. 1, figs. 13, 14, pl. 2, figs. 1-5.
 1959 *Pleuromysidia dubia*, Tamura, p. 222, pl. 2, figs. 25, 26.
 1959 "*Pleuromysidia*" *kanmerai* Tamura, p. 222, pl. 2, fig. 9, 27.
 1964 *Pleuromysidia dubia*, Vozin and Tikhomirova, p. 18, pl. 7, figs. 4-6.
 1966 *Otapiria dubia*, Kiparisova *et al.*, p. 110, pl. 13, figs. 1, 2.
 1972 *Otapiria dubia*, Kiparisova, p. 43, pl. 4, figs. 12, 13.
 1976 *Otapiria dubia*, Okuneva, p. 126, pl. 1, fig. 8, pl. 2, figs. 6-11.

Holotype: An internal mold of right valve from Fujinohira, Kaminaka Town, Tokushima Prefecture, was originally designated by Ichikawa (1954, pl. 1, fig. 14, UMUT MM5475, preserved in University Museum, University of Tokyo).

Material: 11 right and 13 left valves extracted from dark gray mudstone at loc. 1; in addition, 4 slabs with many articulated and disarticulated valves as described above. 9 right and 11 left disarticulated valves from dark gray mudstone at loc. 2.

Diagnosis: Small- to medium-sized, obliquely oval, a little longer than high, with moderately inflated left valve and less inflated right valve; disc of left valve ornamented with numerous fine radial plicae, more than 100 in number in adult stage, weaker on posterior wing; radial plicae commonly absent on right valve but sometimes present as weak threads fewer than half the number in left valve; concentric wrinkles irregular,

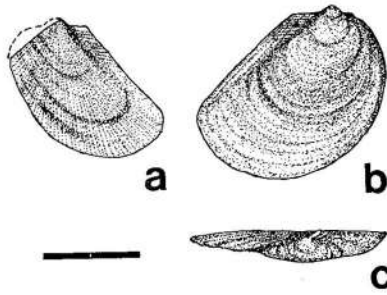


Fig. 5. Schematic outline of *Otapiria dubia* (Ichikawa). a: left valve; b: right valve (UMUT MM18727, Pl. 1, Fig. 1); c: dorsal view of the same specimen. Scale bar is 20 mm.

fewer than 20.

Description: Shell size does not exceed 40 millimeters in length. Left valve more inflated than right. Shell outline subrounded in younger stages smaller than 5 millimeters in length, but becoming posteroventrally elongate with growth. Anterior to ventral margin moderately arched, but postero-dorsal margin nearly straight or slightly convex, passing into short hinge line with an obtuse truncation angle (120° – 140°). Prosogyrous umbo projected upward a little over hinge line in left valve. Shell surface covered with regularly and closely spaced, very fine radial plicae with narrower interspaces. The number of plicae increases with insertion until middle growth stage. Hinge edentulous with a transversely striated shallow ligament pit. Posterior wing is not well developed, and weakly demarcated from disc. Anterior ear of right valve projected forward and inward is very minute and with a narrow byssal notch.

Measurements (in mm):

reg. no.	R/L	L	H	T	A	B
MM18727	R	35.9	33.2	4.6	10.6	7.9
MM18728	R	28.9	24.8	3.5	8.6	4.3
MM18729	R	9.8	9.0	1.3	3.7	2.8
MM18730	R	20.7	19.1	2.5	4.2	4.5
MM18731	R	22.6	22.6	c3	4.9	—

MM18732	R	16.0	19.1	2.5	4.2	4.2
MM18733	R	23.9	18.6	3.7	6.9	5.0
MM18734	R	>18	c17	1.9	4.8	5.0
MM18735	R	14.8	13.3	1.8	5.6	3.4
MM18736	L	c30	23.4	7.2	9.4	4.4
MM18737	L	21.8	26.2	3.9	7.8	6.2

R/L: Right valve or Left valve; L: length; H: Height; T: Thickness; A: Anterior length; B: length of posterior wing; c: circa

Observation: Because of muddy lithology of the *Otapiria* beds, specimens are often secondarily deformed by compaction. So the original convexity is difficult to measure. But slab A contains undeformed articulated valves. They do not necessarily show such a wide intrapopulation variation in shell form and sculpture as reported in *Otapiria limaeformis* from the Okhotsk Sea coast by Zakharov (1962).

Comparison: This species seems to be closely related to *O. ussuriensis* from the Carnian of northeast Siberia and the Primorsky region, judging from their similar stratigraphic position and general morphologic similarity. I find no marked difference between the two except that *O. dubia* has a smaller size, finer plication and more weakly ornamented right valve.

Another closely similar species is *O. limaeformis* Zakharov, 1962 from the Lower Jurassic in northeast Siberia, which shows almost no distinct morphologic differences from *O. dubia* except its smaller size.

Otapiria pacifica from central Chile recently proposed by Covacevich and Escobar (1979), is closely similar to *O. limaeformis*, judging from the morphology and stratigraphic position.

Otapiria dissimilis (Cox) from the Uppermost Triassic (Otapirian) in New Zealand (Marwick, 1953) is easily distinguished from this species in having fewer coarser radial plicae on the left valve. The type species of this genus, *Otapiria marshalli* Marwick, 1935 from the lower

Jurassic (Aratauran) in New Zealand and its closely similar species, *Otapiria tailleuri* Imlay, 1967 from the upper Lower to lower Middle Jurassic in North Alaska, are different from *O. dubia* in having regularly plicated right valves. The youngest species, *Otapiria masoni* Marwick, 1953 from the Tithonian (Puarooan) of New Zealand has conspicuous concentric rugae on the right valve.

Otapiria kanmerai, which was described by Tamura (1959) from Carnian strata together with *O. dubia* near Locs. 1 and 2, seems to have been based on deformed specimens of *O. dubia*.

Occurrence: Five localities as far as I know, are listed in Table 1. Judging from its occurrence with *Halobia* sp., the *Otapiria* bed may be Carnian or Early Norian in age. But the precise age is not still confirmed, due to the lack of zonal index fossils such as ammonites, conodonts and radiolarians. I failed to

extract radiolarians at or near loc. 1. It is probably because *Otapiria* beds are rather shallow shelf sediments.

Kiparisova *et al.* (1966) stated that *O. ussuriensis* occurs in fine-grained Carnian sandstone with *O. dubia*, *Monotis* ex. gr. *scutiformis* (Teller), *Halobia* spp. and *Sirenites hayesi* Smith at some localities in northeast Siberia (e.g. loc. 17 in their fig. 3 along a tributary of the middle course of the Kolyma River). On the other hand, Kiparisova (1972) recognized *O. ussuriensis* Zone below the *M. scutiformis* Zone within the "Carnian" (Nowadays, *M. scutiformis* Zone is correlated with the Middle Norian) near Vladivostok in southmost Sikhote Alin. According to her, *O. ussuriensis* occurs in beds several tens of meters below the *M. scutiformis* bed. The stratigraphic and systematic relations between *O. ussuriensis* and *O. dubia* should be further studied.

CONCLUSION

The mode of fossil occurrence described here is a very important example for paleoecological inference, but still furnishes negative evidence. *Otapiria dubia* appears to have lived in a way considerably different from *Monotis*. I have interpreted the life habit of *Monotis* as byssally attached to algae or gorgonacean anthozoa (Ando, 1987). On the other hand, *O. dubia* seems to have formed clusters in which many individuals were attached to each other on the soft substrate.

The presence of pseudoctenolia in *Otapiria marshalli alpina* is worthy of notice, because this character as well as such a diminutive right anterior auricle is shared with many genera of the Buchiacea. Though pseudoctenolia are not yet ascertained in other species of *Otapiria*, this genus is safely referable to the Monotidae. I have already suggested that they are a primitive character com-

mon to some buchiacean and pectinacean families (Ando, 1987). The occurrence of pseudoctenolia in other *Otapiria* species and within the Buchiacea should be further studied in detail.

The stratigraphic relationship between *Otapiria* and *Monotis* may be important for consideration of the phylogeny of the Monotidae. *Otapiria*, unlike *Monotis*, survived a long geologic period, showing relatively conservative morphology. It may have constituted the main stock of the Monotidae, from which *Monotis* was derived in the Norian. In particular it is possible that the oldest and most multiplied species of *Monotis*, *M. scutiformis*, was evolved from such a Carnian species of *Otapiria* as *O. dubia* or *O. ussuriensis*.

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Plate 1

All figures are in natural size unless otherwise stated.

All valves are internal molds except Figs. 3, 4,

15-19 of latex casts from external molds.

UMUT: University Museum, the University of Tokyo.

Figs. 1-15. *Otapiria dubia* (Ichikawa)

Figs. 1-5. Right valves, loc. 2, Kurosaki, Tanoura Town, Kumamoto Prefecture, Tanoura Formation, Carnian, Upper Triassic.

1. UMUT MM18727; 2. UMUT MM18728, with a left valve below;

3, 4. UMUT MM18729, 4. $\times 2.1$; 5. UMUT MM18730.

Figs. 6-12. Right valves, loc. 1, Nishinoiwa, east of Izumi Village, Kumamoto Prefecture, Carnian, Upper Triassic.

6. UMUT MM18731; 7. UMUT MM18732; 8. UMUT MM18733; 9, 10. UMUT MM18734

10. $\times 1.6$; 11, 12 UMUT MM18735, 12. $\times 2$.

Figs. 13-15. Left valves, loc. 1

13, 14. UMUT MM18736, 14. $\times 1.6$; 15. UMMT MM18737.

Fig. 16. *Oxytoma mojsisovicsi* Teller, left valve (UMUT MM18738), loc. 1

Fig. 17. *Tosapekten suzukii* (Kobayashi), left valve (UMUT MM18739), loc. 1

Fig. 18. *Palaeoneilo* sp., right valve (UMMT MM18740), loc. 1

Fig. 19. *Halobia* sp., right valve (UMMT MM18741), loc. 1.

Fig. 20. Outcrop at loc. 1. A-D: horizons of slabs A-D with abundant articulated or disarticulated valves of *Otapiria dubia*. Scale is a hammer in the left. The right side is the upward direction of steeply reverse bedding.

Fig. 21, 22. Vertical polished cross sections of dark gray mudstone showing conspicuous bioturbation, loc. 1, $\times 1$.

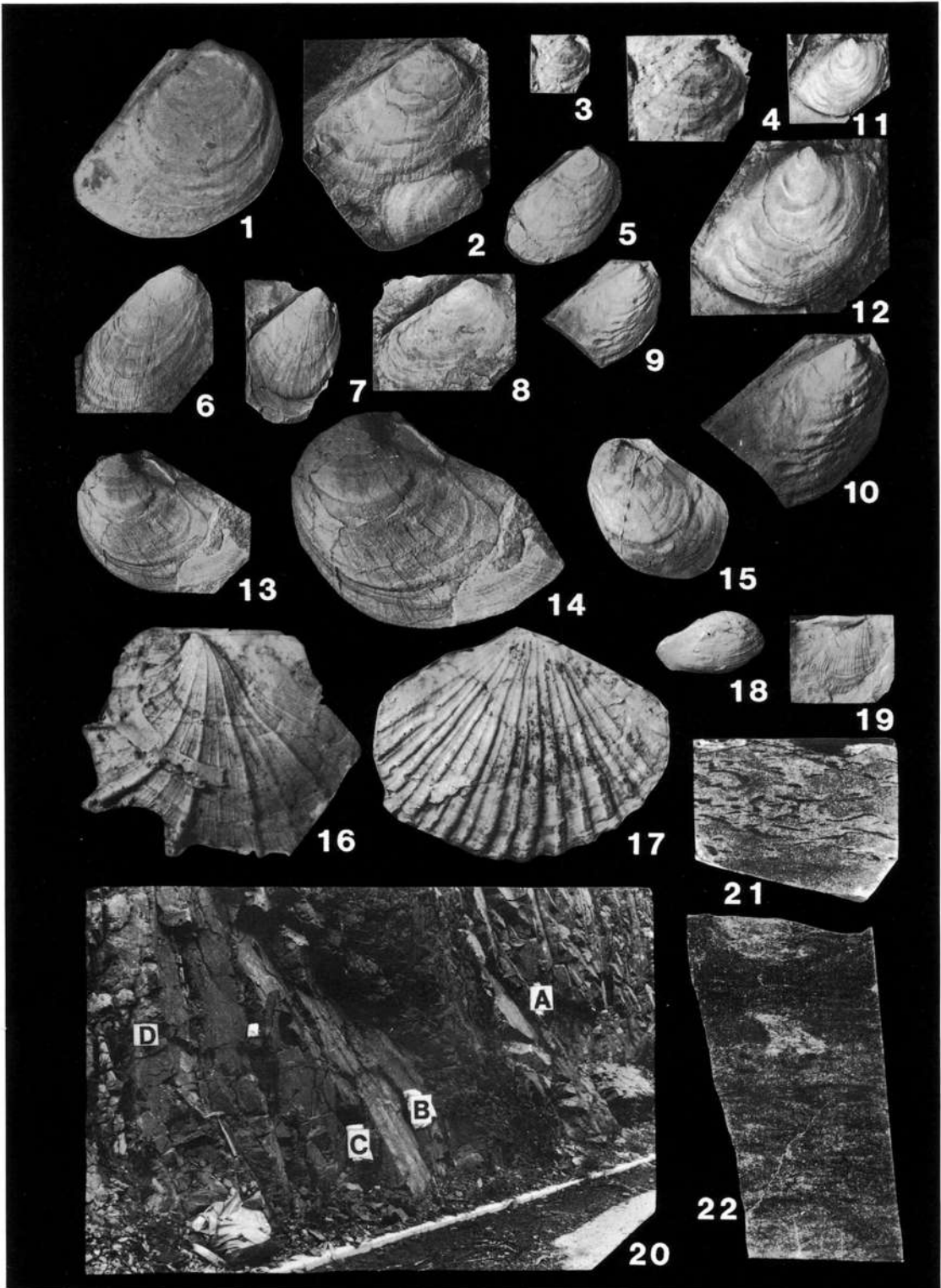


Plate 2

- Figs. 1-6. Mode of fossil occurrence of *Otapiria dubia* (Ichikawa) in slabs A-C at loc. 1 (Pl. 1, Fig. 20), Nishinoiwa, east of Izumi Village, Kumamoto Prefecture. Scale bar is 4 cm.
- Figs. 1-4. Slab A (UMMT MM18742). Autochthonous occurrence of a cluster with abundant articulated undeformed individuals.
1. Outcrop. Lens cap is 5 cm in diameter. The other side is the upward direction of bedding
 2. External cast collected. This side is the lower surface of the stratum. ; 3, 4. Latex cast from the external mold of Fig. 2. This side is the upper surface of the stratum. 4. Enlargement of the left part of Fig. 3.
- Fig. 5. Slab B (UMUT MM18743). Abundant plant fragments concentrated on the lower surface of a mudstone bed with some disarticulated valves of *Otapiria dubia* and *Halobia* sp. This side is the lower surface of the mudstone.
- Fig. 6. Slab C (UMUT MM18744). Abundant plant fragments, crinoid stems and disarticulated valves of *Otapiria dubia*. This side is the lower surface of the mudstone bed.

