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New Species of *Patella* (Gastropoda: Mollusca) from the Miocene and Pliocene of Japan: A Clade Extinct from the Pacific

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Abstract Three new species of patellogastropod limpets are described, two from the early Middle Miocene Mizunami Group of the Mizunami area and one from the early Pliocene Ochiai Formation of the Tanzawa area, central Japan. These species are *Patella mizunamiensis* sp. nov., *Patella itoigawai* sp. nov., and *Patella yajimai* sp. nov. From an analysis of the shell microstructure, these species can be definitely referred to a clade which ranges from two Late Cretaceous species described from Hokkaido, Japan and Sakhalin, Republic of Russia, to the extant species *Patella* (*Olana*) *cochlear* BORN, 1778, from South African bioprovince. The discovery of these three species from the Miocene and Pliocene of Japan is therefore the first record of the occurrence of this clade, representatives of which are known to have had a paleobiogeographic distribution throughout the northwestern Pacific region during Late Cretaceous and Tertiary times, but which became extinct in this paleobiogeographic province at the beginning of the Pliocene. Preliminary investigations of the Miocene species obtained from this region suggests that the assemblage contains certain elements typical of the present-day faunas inhabiting the tropical and sub-tropical regions of the northwestern Pacific.

Introduction

Modern patellogastropod limpets are found to be both diverse and abundant within predominantly high-energy, erosinal, rocky-shore environments. As a consequence of their occupation of such environments, which result in a high degree of post-mortem destruction, the patellogastropod limpets are usually found to comprise only a small component of any fossil assemblage preserved. This has led to them being described in past work as "garnishings" in faunal studies rather than the "main dishes" of formal taxonomic studies. As a result, our knowledge of fossil patellogastropod limpets is very limited.

Difficulty in classification of fossil forms is another reason for our limited knowledge of this fossil group. Suprageneric classification of modern patellogastropod limpets has been based mainly on radular and respiratory characteristics rather than shell (*e.g.*, POWELL, 1973), but such characters are inaccessible for fossil species. Although a number of species have been described from Mesozoic and Cenozoic rocks and attributed to as such genera as *Patella*, *Acmaea* or *Cellana*, these generic assign-

ments are generally untenable because they were based primarily upon comparisons with extant species of similar morphology. A high degree of morphic convergence and parallelism is seen in modern patellogastropod limpet shells, and this hinders a classification based upon shell morphology alone (*e.g.*, LINDBERG, 1988 b). However, MACCLINTOCK (1967) was the first worker to use shell microstructures a determinitive taxobasis for distinguishing particular taxa within the Patellogastropoda. This method is also applicable for fossil species if the shell is preserved enough to determine the original shell structures.

The patellogastropod shell is composed of from four to six layers, depending on the species examined. Each layer is composed of either a microstructure difierent from that of adjacent layers or, where the structure is the same, the two layers' major structural elements are oriented perpendicualr to each other. MACCLINTOCK (1967) recognized four basic structure types (prismatic, foliated, crossed, and complex crossed) and twelve variations in the shell layers of the species he studied. From variations of these structures and the different sequential combinations of layers, he divided the patellogastropod species into 17 shell structure groups and found that the majority, if not all, of these divisions coincide well with previously accepted taxonomic boundaries. The consistency between the classifications based on soft anatomy and shell microstructures has been further emphasized by LINDBERG and MCLEAN (1981) and LINDBERG (1988 b; see also references therein). Of the extant species comprising the major families known to inhabit rocky shore environments, the Patellidae can be diagnosed by the presence of an exterior foliated layer, the Nacellidae by an exterior prismatic layer followed by a foliated layer, and the Lottiidae by the possession of an exterior prismatic layer and crossed-lamellar layer dorsal to the myostracum (LINDBERG, 1988 b).

The purpose of this paper is to describe three new species of *Patella* from the Miocene and Pliocene of Japan by examining the shell structures, and to discuss implications for patellogastropod paleobiogeography and the patellogastropod faunal changes in Japan.

Material and Occurrence

Patella yajimai *sp. nov.*—The only specimen of this species was collected by Mr. Akira YAJIMA during his field survey of the Tanzawa area in 1971. The locality (National Science Museum, Paleontological Collection Locality 8–61–1; 139°13′37″E, 35°31′46″N) is a large road-cut exposure along the Hayatogawa river at Ochiai, Kiyokawa village, Aiko County, Kanagawa Prefecture. The fossil was collected from a granule- to cobble-sized conglomerate bed of the Ochiai Conglomerate, (=Ochiai Formation) where shallowmarine, gravelly bottom mollusks are commonly found. A calcareous nannofossil analysis by OKADA (1978) indicates that the Ochiai Conglomerate can be stratigraphically assgined to somewhaere between the calcareous nannofossil zones NC10 and NC11 (early Pliocene), although a slight possibility exists of it belonging to zone NC9 (late Miocene).

Patella mizunamiensis *sp. nov.*—The holotype and the specimen illustrated by ITOIGAWA *et al.* (1974, pl. 36, fig. 15) were obtained from the Akeyo Formation, which has been assigned to the planktic foraminferal zone N8 (TSUCHI *et al.*, 1981), giving an early Middle Miocene age. The locality (137°16′08″E, 35°24′33″N) is a large creek-side exposure at Shukubora (locality 18 in ITOIGAWA *et al.*, 1974), Hiyoshimachi, Mizunami City, Gifu Prefecture, where highly diverse, tropical to subtropical mollusks are found throughout the medium-grained sandstone. Depositional environment of the Shukubora facies is thought to be the littoral bottom of an enbayment (ITOIGAWA *et al.*, 1974).

Patella itoigawai *sp. nov.*—The holotype and the specimen illustrated by ITOIGAWA *et al.* (1981, pl. 24, fig. 9) were also obtained from the Akeyo Formation. The locality (137°14′28″E, 35°23′31″N) is a bed of the Hiyoshi river at Akatsukibora (locality 45 in ITOIGAWA *et al.*, 1974), between Hongo and Tsukiyoshi, Mizunami City, Gifu Prefecture.

Systematic Paleontology

Class Gastropoda CUVIER, 1979

Order Patellogastropoda LINDBERG, 1986

Suborder Patellina VON IHERING, 1876

Superfamily Patelloidea RAFINESQUE, 1815

Family Patellidae RAFINESQUE, 1815

Genus ***Patella*** LINNAEUS, 1758

Type species.—*Patella vulgata* LINNAEUS, 1758 [subsequent designation by FLEMING, 1818].

Patella yajimai sp. nov.

Figs. 1–2

Diangosis.—A large, stellate species of *Patella* belonging to group 10 of MACCLINTOCK's (1967) shell structure classification, with seven primary ribs extending slightly from shell margin, and with finer secondary ribs over shell surface.

Description.—Shell large, stellate, with longer apertural diameter of ca. 90 mm and shell thickness of 5 mm in apertural margin. Apex blunt, positioned slightly anterior from shell center; shell profile moderately high, with height/length ratio of ca. 0.4. Aperture stellate, formed by extensions of primary ribs on shell surface, anterior margin more narrowly rounded than posterior one. Shell weakly convex. Shell surface sculptured by seven strong primary ribs and by secondary ribs of variable

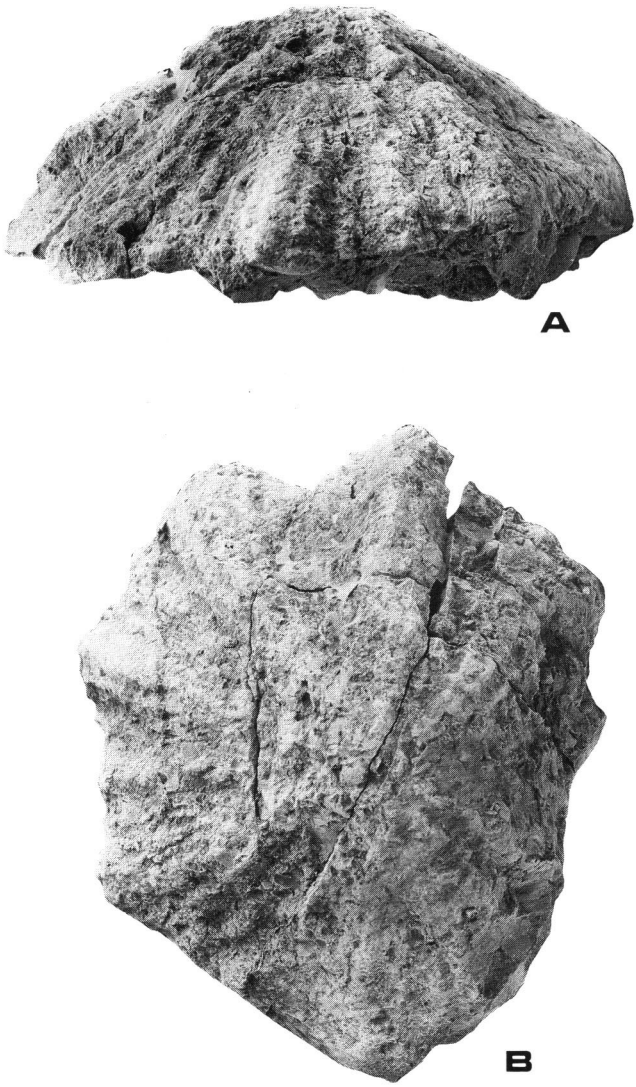

Fig. 1. *Patella yajimai* sp. nov. from the Ochiai Formation in the Tanzawa area. Holotype, NSM PM15492. × ca. 1.

prominence over shell surface. Exterior shell layer (m+2) of thick, radial crossed-foliated, followed by thick, concentric crossed-lamellar laver (m+1), and myostracum (m); inner layer unknown.

Type.—The holotype (NSM PM15492) is deposited in the collection of Section of Invertebrate Paleontology, Department of Geology, National Science Museum, Tokyo.

Holotype dimensions.—Length ca. 90 mm, width 74 mm, height 37 mm.

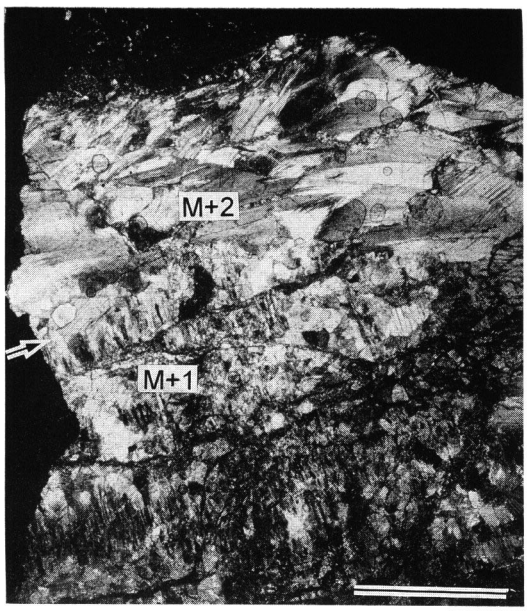

Fig. 2. Polarizing thin section (under crossed nicols) of NSM PM15492 cut radially from the apex to shell margin, showing the outer radial crossed-foliated layer (M+2) followed by the inner concentric crossed-lamellar layer (M+1). The inner shell layer is slightly recrystallized. Arrow indicates the boundary of the two layers. Scale bar equals 0.1 mm.

Type locality.—A road-cut exposure at Ochiai, Kiyokawa Village, Aiko County, Kanagawa Prefecture.

Age.—Early Pliocene.

Etymology.—This species is named after Mr. A. YAJIMA, who collected the holotype.

Remarks.—The holotype is the only available specimen. The specimen was encased in the highly calcareous matrix of the conglomerate, so that the shell is recrystallized to large extent. Polarizing microscope examination of a thin section cut radially from the apex to the shell margin shows, however, that the exterior shell layer (m+2) is of radial crossed-foliated structure and is superimposed directly on a thick, slightly chalky, radial crossed-lamellar shell layer (m+1) (Fig. 2). The combination of such layers dorsal to the myostracum suggests that this species belongs to MACCLINTOCK's shell structure group 10.

YAJIMA (1972) referred this species to *Penepatella optima* (PILSBRY, 1927), the sole species of the Patellidae in Japan. POWELL (1973) regarded *P. optima* as a temperate subspecies of the tropical species *Patella flexuosa* QUOY and GAIMARD (1834), who recorded the largest specimen attains over 90 mm in length, approximating to the size of the holotype of *P. yajimai*. *P. flexuosa* is a high variable species and there seems to be no clearcut distinction in shell form from *P. yajimai*. However, the two species

differ distinctly from each other when assessed in terms of shell microstructure combination: *P. yajimai* has two layers dorsal to the myostracum, whilst three layers are present in *P. flexuosa* (MACCLINTOCK, 1967; personal observation).

Patella yajimai sp. nov. is readily distinguished from *Patella* (*Olana*) *cochlear* BORN, 1778 from South Africa, the single known species of MACCLINTOCK's (1967) shell structure group 10, by its larger shell size, higher shell profile, the presence of seven strong primary ribs and the absence of a spout-like anterior projection, so characteristic of the latter species.

Patella mizunamiensis sp. nov.

Figs. 3 C, D, 4 D, E

Penepatella cf. *stellaeformis* (REEVE). ITOIGAWA *et al.*, 1974, p. 114, pl. 36, fig. 15; ITOIGAWA *et al.*, 1981, p. 128, pl. 24, fig. 13.

Diagnosis.—Medium-sized, stellate, depressed species of *Patella* belonging to MACCLINTOCK's (1967) shell structure group 10, with seven or eight primary ribs and many secondary ribs over shell surface. Apex not curved, situated in anterior two fifths of shell length.

Description.—Shell medium in size, thick, and stellate due to prominence of primary radial ribs. Apex obtuse, not curved, located at two fifths from anterior apertural margin. Profile low, with height about 1/4 of length. Anterior slope weakly

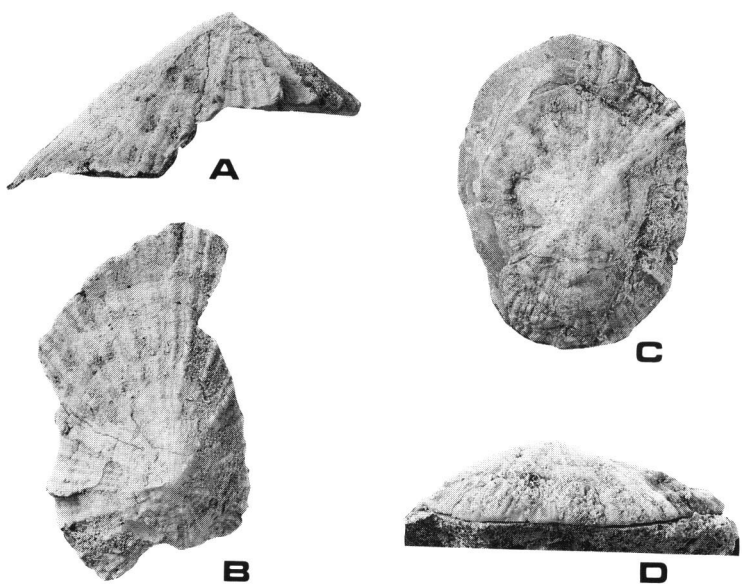

Fig. 3. A, B. *Patella itoigawai* sp. nov. from the Akeyo Formation in the Mizunami area. Holotype, MFM 10096. ×1.7. C, D. *Patella mizunamiensis* sp. nov. from the Akeyo Formation in the Mizunami area. Holotype, MFM 10095. ×1.45.

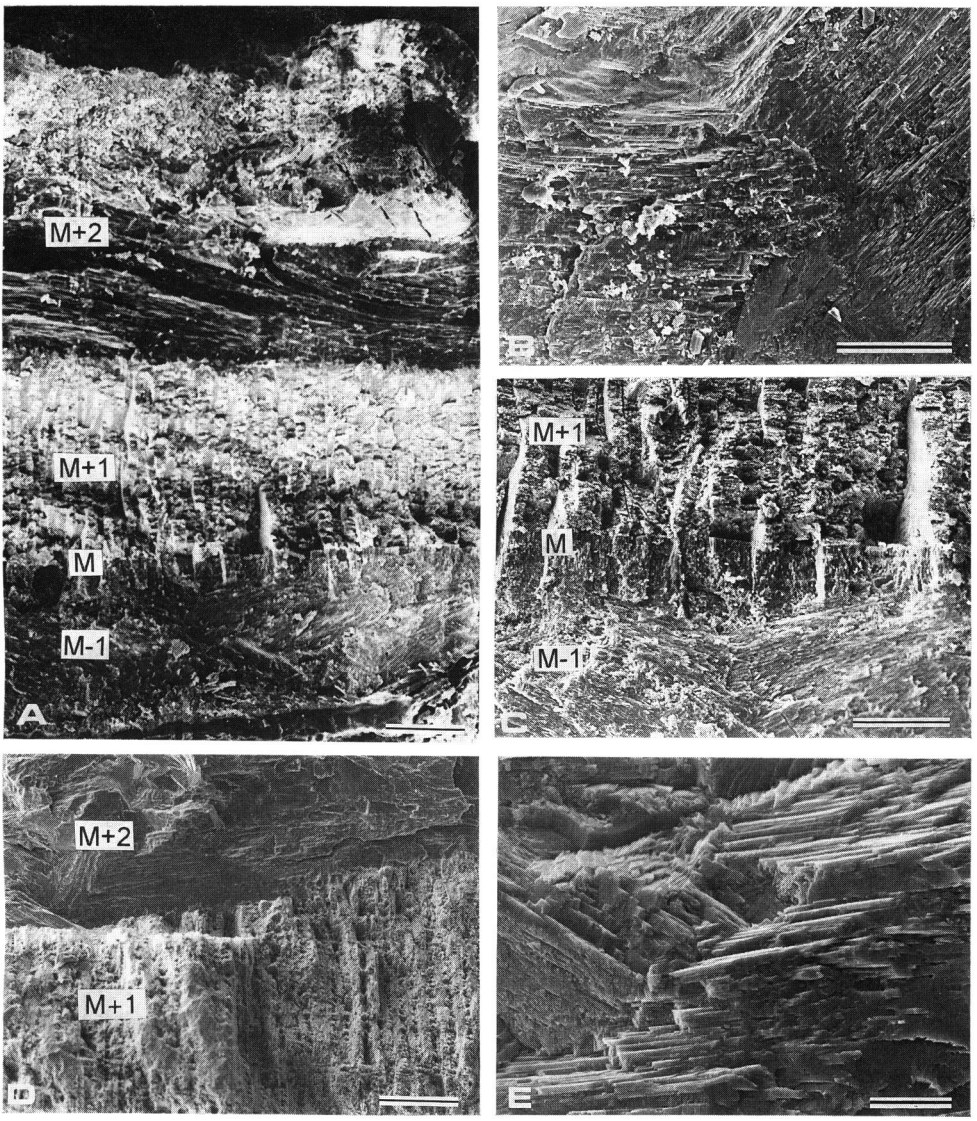

Fig. 4. SEM micrographs of the shell walls in *Patella itoigawai* sp. nov. and *Patella mizunamiensis* sp. nov. Scale bars represent 100 μm for A and D, 50 μm for B and C, and 10 μm for E. A–C, *Patella itoigawai* sp. nov.; A, cross section cut almost radially from the apex to shell margin showing the outermost radial crossed-foliated layer (M+2), followed by the outer concentric crossed-lamellar layer (M+1), the myostracum (M), and the inner radial crossed-lamellar layer (M−1); B, enlargement of the outermost radial crossed-foliated layer; C, enlargement of the outer concentric crossed-lamellar layer (M+1), the myostracum (M), and the inner radial crossed-lamellar layer (M+1). D, E, *Patella mizunamiensis* sp. nov.; D, cross section cut almost radially from the apex to shell margin showing the outermost radial crossed-foliated layer (M+2) followed by the outer concentric crossed-lamellar layer (M+1); E, enlargement of the outermost radial crossed-foliated layer.

convex, and posterior and lateral slopes almost straight. Aperture polygonal, anterior margin more narrowly rounded than posterior one, with width about 3/4 of length. Sculpture of seven or eight, slightly strong primary ribs that extend slightly from shel. margin, and also of many secondary ribs over the shell surface. Exterior shell layer (m+2) of radial crossed-foliated structure, followed by thick concentric crossed-lamellar layer (m+1), myostracum (m), and inner layer(s) unknown.

Type.—The holotype (MFM 10095) is deposited in the collection of Mizunami Fossil Museum, Mizunami, Gifu Prefecture.

Holotype dimensions.—Length 29.1 mm, width 21.6 mm, height 7.7 mm.

Type locality.—Creek side exposure at Shukubora, Hiyoshimachi, Mizunami City, Gifu Prefecture.

Age.—Early Middle Miocene.

Etymology.—This species is named for the Mizunami City in which the type locality is located.

Remarks.—The holotype is an imprefect specimen lacking the posterior and right-lateral shell margins, and post-mortem wear of the shell seems to have resulted in the apertural outline more rounded than the original form. Another, more intact specimen from the type locality illustrated by ITOIGAWA *et al.* (1974, 1981) has a more angular aperture than the holotype.

ITOIGAWA *et al.* (1974, 1981) regarded this species as being close to *Penepatella stellaeformis* (REEVE, 1842) (=*Patella flexuosa* QUOY & GAIMARD, 1834). As pointed out by ITOIGAWA *et al.* (1981) the Mizunami taxon seems to differ from *P. flexuosa* in possessing a more antero-posteriorly elongate and anteriorly narrower aperture, and a smaller number of radial ribs. Because of their shell microstructure, however, the two species are distinct because the Mizunami taxon belongs to MACCLINTOCK's (1967) shell structure group 10 (Fig. 4 D, E), while *P. flexuosa* belongs to his group 9.

P. mizunamiensis sp. nov. is distinct from *P.* (*O.*) *cochlear* BORN, 1778 in its small shell size, stellate aperture, the presence of primary radial ribs, and the lack of anterior apertural projection. It also differs from *P. yajimai* sp. nov. by its much smaller shell size, lower shell profile and more antero-posteriorly elongate aperture.

Patella itoigawai sp. nov.

Figs. 3 A, B, 4 A–C

"*Acmaea*" sp. ITOIGAWA *et al.*, 1981, p. 128, pl. 24, fig. 9.

Diagnosis.—Moderately small species of *Patella* belonging to group 10 of MACCLINTOCK's (1967) shell structure classification, with higher shell profile and numerous scaly radial ribs.

Description.—Shell medium in size, moderately thick, pear-shaped in apical view. Apex pointed, not curved, located at two fifths length from anterior margin. Profile moderately high, with height about 2/5 of length. Anterior and posterior slopes weakly convex, lateral slopes almost straight. Aperture oval, anterior margin narrowly

rounded and posterior margin broadly arched, with width 4/5 of length. Surface sculptured by numerous, scaly radial ribs of variable prominence, of which about 15 are prominent. Apertural margin digitate in registration with radial ribs. Shell consists of four layers including myostracum; exterior layer (m+2) radial crossed-foliated, followed by thick concentric crossed-lamellar layer (m+1), myostracum (m), and radial crossed-lamellar layer (m−1).

Type.—The holotype (MFM 10096) is deposited in the collection of Mizunami Fossil Museum, Mizunami.

Dimensions of holotype.—Preserved shell length 28.5 mm, preserved shell width, 17.7 mm.

Type locality.—Akatsukibora, Hiyoshimachi, Mizunami City, Gifu Prefecture.

Age.—Early Middle Miocene.

Etymology.—This species is name after Prof. Junji ITOIGAWA who contributed greatly to the geology and paleontology of the Mizunami Group.

Remarks.—Although the holotype is a fragmentary specimen, it reveals the characteristic radial ribs over the shell surface. ITOIGAWA *et al.* (1981) illustrated a complete shell of this species, on which the description of the shell is largely based. Unfortunately, this species has not been found in the collection of Mizunami Fossil Museum, and I selected the specimen from the same locality as the holotype.

This species differs distinctly from other species of *Patella* belonging to the same shell structure group by its possession of a higher shell profile and the presence of numerous scaly radial ribs of variable prominence.

Discussion

The occurrence of three species of *Patella* from the Miocene and early Pliocene of Japan is important from the viewpoints of both patellogastropod paleobiogeography and the evolutionary origin of Japanese Cenozoic molluscan faunas.

Rocky shore patellogastropod limpets show characteristic distribution patterns today. The most characteristic is the fauna of the coast of southern Africa, where the patellogastropod fauna consists mainly of the Patellidae (MACCLINTOCK, 1967; POWELL, 1973, BRANCH, 1981). The fauna along the West Coast of America is also characteristic as it is composed primarily of the Lottidae (MACCLINTOCK, 1967; LINDBERG, 1988 b). In contrast, the fauna in the Indo-West Pacific is a mixture of the Patellidae, Nacellidae and Lottiidae (MACCLINTOCK, 1967; POWELL, 1973; LINDBERG, 1988 b). However, shell microstructural analysis of fossil species has revealed that the distribution patterns have changed markedly through geologic time. For example, the Eocene fauna of the Pacific coast of North America, consisting of *Cellana*, *Patelloida*, and a pulmonate limpet *Siphonaria*, is similar to modern Australian limpet assemblages. Similarly, *Patelloida* was distributed along the Tethys during the Cretaceous and Cenozoic but has disappeared from Europe since the Eocene and from the Pacific coast of North America since the Miocene (LINDBERG, 1988; LINDBERG & HICKMAN,

Table 1. Preliminary summary of assignment of Miocene patellogastropods from Japan.

Old assignment	New assignment	Locality	Age	References
Acmaea sp. 1	*Patelloida* sp.	Mizunami	Early Middle Miocene	ITOIGAWA *et al.* (1981)
Acmaea sp. 2	*Patelloida* sp.	Mizunami	Early Middle Miocene	ITOIGAWA *et al.* (1981)
Acmaea sp. 3	*Tectura*? sp.	Mizunami	Early Middle Miocene	ITOIGAWA *et al.* (1981)
Acmaea sp. 4	*Patella itoigawai* sp. nov.	Mizunami	Early Middle Miocene	ITOIGAWA *et al.* (1981)
Penepatella cf. *stellaeformis* (REEVE)	*Patella mizunamiensis* sp. nov.	Mizunami	Early Middle Miocene	ITOIGAWA *et al.* (1981)
Cellana depressa ITOIGAWA *et al.* (1976)	*Cellana depressa*	Mizunami	Early Middle Miocene	ITOIGAWA *et al.* (1976)
——	*Patella yajimai* sp. nov.	Tanzawa	Early Pliocene (or Late Miocene)	herein
——	*Cellana* sp.	Izu Peninsula	Late Miocene	——

1986; LINDBERG & MARINCOVICH, 1988; LINDBERG & SQUIRES, 1990). KASE and SHIGETA (in preparation) have recorded additional three species of *Patelloida* from the Cretaceous of Hokkaido, Japan and Sakhalin, Russia.

The Patellidae, in contrast, are only poorly represented in the fossil record. POWELL (1973) listed five species from the Cretaceous, Oligocene, Miocene and Pliocene which he identified as belonging to the Patellidae. Of these *Patella fuenzalidai* HERN (1969) from the Pliocene of Chile was reassigned to *Cellana* by LINDBERG and HICKMAN (1986) as a result of shell microstructure analysis. Because they were described soley on shell morphology, the generic assignment of these Mesozoic and Cenozoic species are much in doubt. Exceptions are the two species of *Patella* which KASE and SHIGETA (in preparation) have described from the Cretaceous (Santonian and Campanian) of Hokkaido, northern Japan and Sakhalin, Russia. Both species also belong to MACCLINTOCK's (1967) shell structure group 10. The occurrence of the three *Patella* species of the same clade demonstrates that this clade of *Patella* distributed throughout the northwestern Pacific during late Cretaceous, Miocene and early Pliocene periods, although it is not known whether this clade of *Patella* existed in the Pacific during Paleogene time. Today, *Patella* with the same shell microstructure combination is represented in South Aftrica by a single species *Patella* (*Olana*) *cochlear* BORN, 1778, suggesting that the clade became extinct from the Pacific after early Pliocene time.

Japanese Cenozoic patellogastropod faunas are not well understood. Pliocene, Pleistocene and Holocene species, mostly from the northern half of Japan, are relatively well documented and studied when compared with older ones. These species

have been primarily identified by direct comparison to living species (*e.g.*, OYAMA, 1973; OGASAWARA, 1977; TAKAYASU *et al.*, 1986). The present-day distribution of this latter group coincides almost exactly with the known fossil occurrences.

In contrast, occurrence from strata older than the Pliocene are extremely rare and have generally been tentatively referred to *Acmaea* or *Patella* without any reliable evidence. The early Middle Miocene strata of the Mizunami Group in central Japan is exceptional as it has yielded nine species of patellogastropods (ITOIGAWA *et al.*, 1981). Also, there is an undescribed species from the Miocene of Izu Peninsula, central Japan. Molluscan assemblages associated with these limpets are characterized by tropical and subtropical elements (*e.g.*, CHINZEI, 1986; ITOIGAWA & SHIBATA, 1986; KASE & KATAYAMA, 1981). Revisions of the Miocene patellogastropods by shell microstructure analysis are now in progress by the author. As shown in Table 1, the Miocene patellogastropod fauna includes species of *Patella*, *Cellana*, *Patelloida*, and a generically undetermined species which belongs to MACCLINTOCK's (1967) shell structure group 3 (Table 1). Thus, as is found today, the Miocene patellogastropod fauna of Japan comprised a diverse generic composition.

As with the Miocene species, modern patellogastropods along the coast of the Japanese Islands include species of Patellidae, Nacellidae and Lottiidae (*e.g.*, HABE, 1944; OKUTANI & HABE, 1975; SASAKI & OKUTANI, 1992). The Patellidae are represented in Japan by the sole species *Patella flexuosa* QUOY and GAIMARD, 1843, which differs from the three Miocene species in shell microstructure. Today, the Patellidae are diverse and widespread in the Indo-West Pacific province (POWELL, 1973).

Other Miocene species exotic in Japan are two patellogastropod limpets illustrated by ITOIGAWA *et al.* (1981) as *Acmaea* sp. 1 and *Acmaea* sp. 2. They belong to MACCLINTOCK's (1967) shell structure group 2 and, from the shell characteristics, appear to be members of the *Patelloida profunda* group, an old Tethyan clade distributed today in the tropical Pacific and Austral provinces (CHRISTIAENS, 1975; LINDBERG & VERMEIJ, 1985). Species of *Cellana* are present in the Miocene of the Mizunami and Izu peninsular areas. Modern species of *Cellana* are diverse on the rocky shores of the Indo-West Pacific region (*e.g.*, POWELL, 1973). Furthermore, modern species belonging to MACCLINTOCK's (1967) shell structure group 3 are common along the coast of Japanese Islands (SASAKI & OKUTANI, 1993; personal observation). It is concluded that the Miocene patellogastropod fauna from the Mizunami and Izu peninsular areas, aside from the three species of *Patella*, comprise species whose modern relatives are distributed in the warm waters of the northwestern Pacific.

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