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NEW SPECIES OF PATELLOGASTROPODA (MOLLUSCA) FROM THE CRETACEOUS OF HOKKAIDO, JAPAN AND SAKHALIN, RUSSIA

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ABSTRACT—Rare patellogastropod limpets are described from the Cenomanian to Campanian (Cretaceous) age sediments in Hokkaido, northern Japan and Sakhalin, eastern Russia. Shell structure analysis has revealed the presence of five shell structure groups within six species, permitting the allocation of three of the species identified to modern clades. However, the other three species recorded belong to shell-structure groups not known at the present day. The species described in this paper are *Patella soyaensis* new species, *Patella* sp., *Patelloida obirensis* new species, ?*Patelloida miyauchii* new species, an indeterminate species of the Lottiinae, and an indeterminate species and belonging to an unknown family. Two species are recognized as belonging to the Patellidae and three species to the Lottiidae, demonstrating that two of the three major families found to inhabit present-day rocky shore environments already existed in the Cretaceous. The discovery of two *Patella* species belonging to a modern clade found in South Africa indicates that the fossil record of the clade dates back more than 80 Ma and the distribution of the clade has changed markedly since that time. The occurrence of *Patelloida* from the northwestern Pacific further elucidates the worldwide distribution for this genus during the Cretaceous.

INTRODUCTION

PATELLOGASTROPODS MIGHT have evolved as early as the Early Paleozoic, as they are thought to be among the most primitive of gastropods (e.g., Lindberg, 1988a; Haszprunar, 1988). The oldest purported patellogastropod has been recorded from the Middle Ordovician of Utah (Yochelson, 1988). Despite their long survival of about 450 million years, patellogastropod limpets are poorly represented in the fossil record throughout the world. This is primarily due to their peculiar habitats of high energy, erosional, rocky nearshore environments, but also to their featureless conical shells, which make recognition and identification difficult in highly consolidated sedimentary rocks, particularly when the shell is minute.

Suprageneric classification of living patellogastropods is based primarily on physiological characteristics (radular and gill morphologies) not preserved in fossil forms. In addition, convergence and parallelism are commonly encountered in the species, hindering reliable generic assignments for fossil forms. MacClintock (1967) was the first to use the results of the shell structure analysis to distinguish particular taxa within the group.

The patellogastropod shell consists of four to six layer including the myostracum. Each shell layer is of either a microstructure different from that of adjacent ones, or, where the structure is the same, the two layers' major structural elements are oriented perpendicular to each other. MacClintock (1967) recognized four basic microstructures (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 taxonomic boundaries previously accepted. Lindberg and McLean (1981) and Lindberg (1988a) have further emphasized the consistency between the classifications based on soft anatomy and shell structure. For example, 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 presence of an exterior prismatic and crossed-lamellar layer dorsal to the myostracum. Within the Lottiidae, the Lottiidae can be separated from the Patellidinae by the possession of a fibrous prismatic layer dorsal to the outer crossed-lamellar layer (Lindberg, 1988a, b).

The purpose of this paper is to describe the rare patellogastropod limpets from the Upper Cretaceous of Hokkaido, northern Japan and southern Sakhalin, Russia. The specimens are sufficiently well-preserved so that their original shell structures can be determined or inferred through binocular, thin-section, and SEM observations. This paper describes three new species and three unnamed species, which together belong to five different shell structure groups. This study therefore shows that the Cretaceous patellogastropod fauna was more diverse than was previously recognized and also provides additional information on the evolution and past distribution of this group.

Abbreviations used for catalog numbers are NSM (Invertebrate Paleontology, National Science Museum, Tokyo) and UMUT (Historical Geology and Paleontology, University Museum, the University of Tokyo).

OCCURRENCE

Predominantly offshore and deep-water sediments of the Late Cretaceous Middle- and Upper Yezo Groups and more regressive sediments of the Late Cretaceous Hakobuchi Group (=Krasnoyarka suite in Sakhalin) of Hokkaido and Sakhalin are characterized by the prolific occurrence of inoceramid bivalves and ammonites. Although patellogastropod limpets are a rarity in the Middle- and Upper Yezo and Hakobuchi Groups, six species were found from the Cenomanian to Campanian sediments at five localities in Hokkaido and at three localities in southern Sakhalin (Figure 1; detailed locality descriptions are listed in the Appendix).

The occurrence of patellogastropod limpets in offshore sediments of the Middle- and Upper Yezo Groups in Hokkaido appears to be anomalous when compared to their modern representatives. Living relatives dwell in rocky shores, but the shoreline during the Late Cretaceous in this area seems to have been far from each locality. The mode of occurrence of these limpets is noteworthy. They were all encased in calcareous concretions. Although limpet-bearing concretions are extremely rare, those so far discovered include a number of specimens. For example, about one hundred specimens of *Patelloida obirensis*

were found in an erratic, round calcareous concretion about 100 mm in diameter from locality 8, but none has been found in other concretions the same outcrop. The fossil-bearing concretion is most probably derived from the outcrop where it was found, and there is no bed that seems to have been deposited in a nearshore environment around the locality. Fossils found from the mudstone at this locality are *Inoceramus hobetsensis* Nagao and Matsumoto, *Scaphites planus* (Yabe), *Otoscaphites puerculus* (Jimbo), *Tetragonites glabrus* (Jimbo), *Gaudryceras denseplicatum* (Jimbo), *Neophylloceras subramosum* Shimizu, and *Mesopuzosia* sp. (Tanabe et al., 1977). The massive mudstone yielding the concretion shows neither evidence for strong current movement nor for transportation of the shells from remote places.

The mudstone bed is a part of the Saku Formation that intercalates sandstone beds of turbidite origin (Matsumoto and Okada, 1973). The depositional environment has been assumed to be an intermediate between nearshore, shelf environments and offshore, deep water environments (Matsumoto and Okada, 1973; Tanabe et al., 1977). Other facies analyses have shown that the Saku Formation represents outer shelf deposits in Cretaceous forearch basin (Hirano et al., 1992; Ando et al., 1994).

The concretions yielding *Patella* sp. (locality 7), an indeterminate lottiine species (locality 5), and an indeterminate patellogastropod species (locality 6) are from the mudstones that are assumed to have been deposited in environments deeper than those of the Saku Formation (Hirano et al., 1992; Ando, 1994).

Patella soyaensis was recovered from sandy siltstone beds in the Krasnoyarka suite in Sakhalin (localities 1 to 3) and the unit H of the Upper Cretaceous strata (local rock unit equivalent to the Hakobuchi Group; see Matsumoto, 1984) in the Wakkanai area of Hokkaido (locality 4). The formations represent the final regressive facies of the Cretaceous system in this area. This species was found in several cobble- to boulder-sized calcareous concretions that can contain a number of individuals. For example, one concretion of about 150 mm diameter from locality 1 include more than 200 individuals, the greatest accumulation we have ever encountered. ?*Patelloida miyauchii* was found in some calcareous concretions that were derived from sandy siltstone beds of the unit H in the Wakkanai area. Mode of occurrence is as same as that of *Patella soyaensis*.

The sandy mudstone beds yielding *P. soyaensis* in Sakhalin are in the lower part of the unit II of the lower Krasnoyarka subsuite (Seimskian horizon) by Zhidkova et al. (1974) in the Makarov area and in the upper part of the unit II of the lower Krasnoyarka subsuite by Poyarkova (1987) in the Naiba area. The units are characterized mainly by coarse-grained sediments. Based on the lithologic composition, sedimentary structures, and fossil assemblages, these authors interpreted the units as shallow marine, upper to lower subtidal sediments. In spite of shallow water origin, the units lack fossils indicative of unequivocal intertidal, rocky shore habitats, rather fossil suites are characterized by such mollusks as *Canadoceras multicostatum* (dominant), *Tetragonites popetensis, Saghalinites teshioensis* and *Pachydiscus soyaensis* for the unit at locality 1 and *Inoceramus schmidti, Inoceramus saghalineisis, Tetragonites popetensis, Gaudryceras striatum* and *Gigantocapulus gitanteus* for the unit at locality 3 (our observations).

We suggest that the limpets were fossilized near the hard substrates that they clung to during life, and were not transported from the original, rocky shore habitats. Kase et al. (1994) have interpreted the limpets to be obligate pseudoplankton, attached to pelagic ammonites by producing deep home depressions, in the upper layer of the ocean. The limpets might have been carried on either living or post-mortem, drifting ammonite shells, then fall to the soft bottom when their host shells were water-

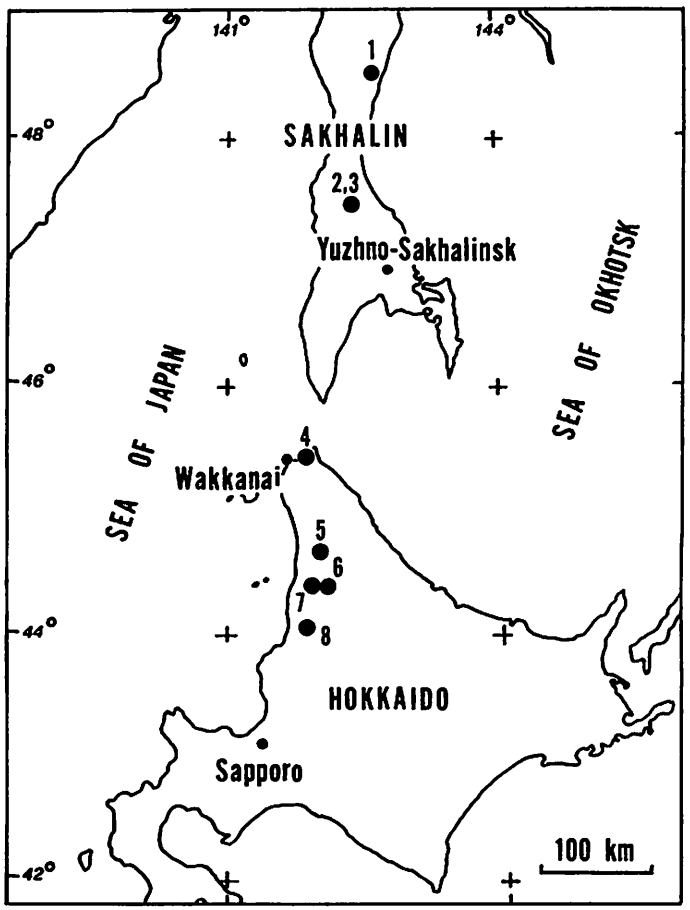


FIGURE 1—Index map showing the fossil localities.

logged. Many large pachydiscid ammonites with limpet home depressions have been found in localities 1 and 4.

SYSTEMATIC PALEONTOLOGY

Order PATELLOGASTROPODA Lindberg, 1986
Suborder PATELLINA von Ihering, 1876
Superfamily PATELLOIDEA Rafinesque, 1915
Family PATELLIDAE Rafinesque, 1915
Genus PATELLA Linné, 1758
PATELLA SOYAENSIS new species
Figure 2.1, 2.2, 2.6, 2.7

Diagnosis.—Small *Patella* having exterior foliated layer, followed by concentric crossed-lamellar layer, myostracum, inner radial crossed-lamellar layer; aperture elliptical; sculpture of regular growth lines with fine axial threads.

Description.—Shell small (longer apertural diameter 11.5 mm in largest specimen). Apex in anterior third of shell; profile moderately high (height/length ratio about 0.6). Aperture oval (width/length ratio 0.7 to 0.8); anterior margin more narrowly rounded than posterior. Anterior slope almost straight, lateral slopes weakly convex, posterior slope convex. Shell surface sculptured by fine, regular-spaced growth increments, fine, irregular-spaced radial threads. Shell consists of four layers including myostracum; exterior layer (M+2) of radial crossed-foliated structure, followed by concentric crossed-lamellar layer (M+1), myostracum (M), radial crossed-lamellar layer (M−1) (Figure 3.1–3.3). Muscle scar of horseshoe-shaped, symmetrical bundles.

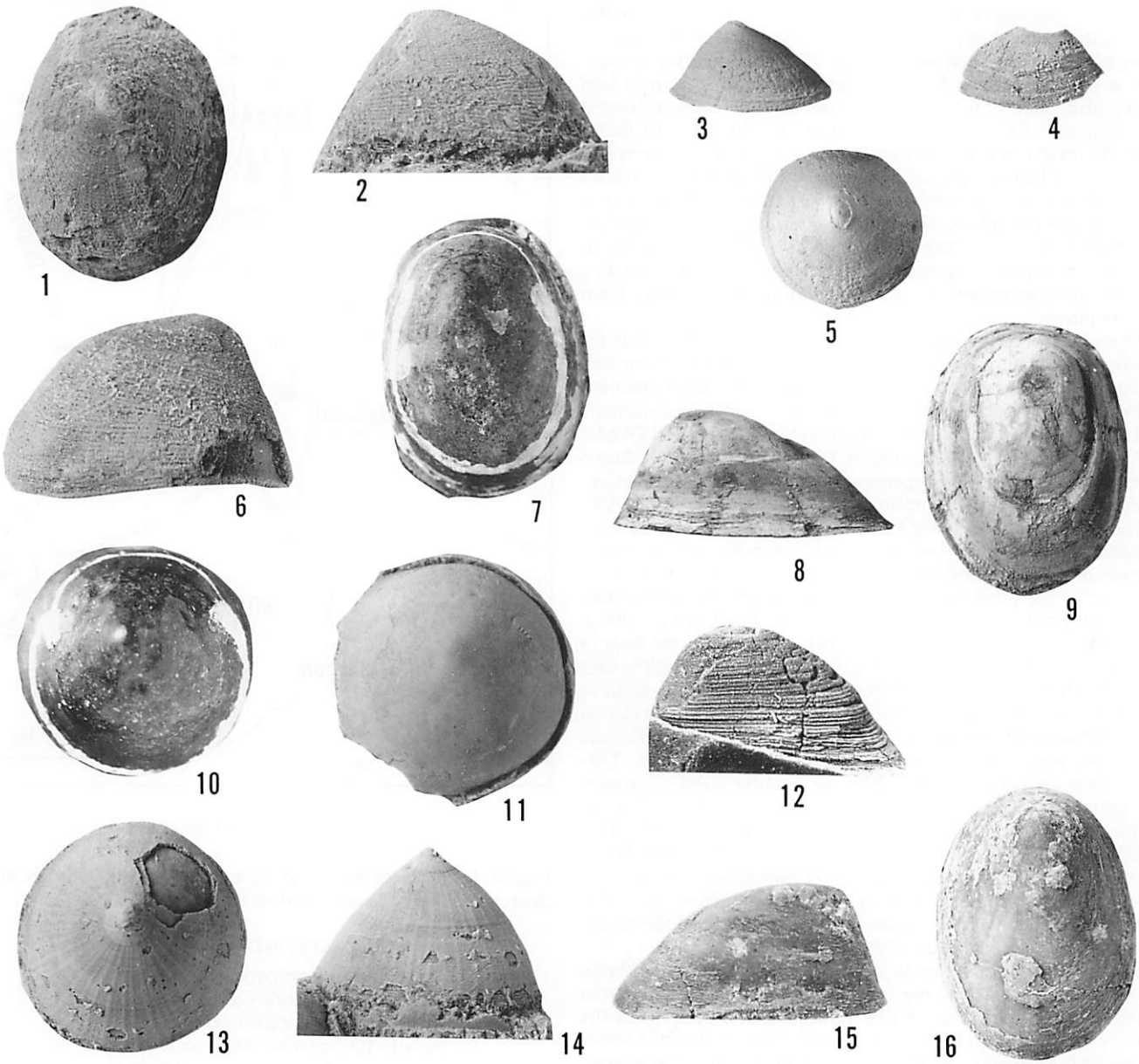


FIGURE 2—*1, 2, 6, 7, Patella soyaensis* new species, *1, 2,* holotype, NSM PM15460, apical and lateral views, locality 4; length, 9.9 mm, width, 8.3 mm, height, 4.8 mm; *6,* paratype, UMUT MM19016, lateral view, locality 2; length, 10.7 mm, width, 9.0 mm, height, 6.3 mm; *7,* paratype, NSM PM15461, apical view of an inner mold showing the muscle scar pattern, locality 4; length, 11.5 mm, width 8.5 mm, height, 6.0 mm. *3–5,* Lottiinae, genus and species indeterminate, *3, 5,* lateral and apical views of a specimen NSM PM15462, locality 5, length, 5.0 mm, width 5.0 mm, height, 2.6 mm; *4,* exterior view of a shell fragment of the same specimen showing the shell surface ornamented by fine radial striae and fine growth lines, NSM PM15463, locality 5. *8, 9, 12, Patella* sp., NSM PM15464, lateral and apical views of an inner mold, and lateral view of silicon rubber impression, locality 7; length, 8.7 mm, width, 7.0 mm, height, 3.5 mm. *10, 11, 13, 14, ?Patelloida miyauchii* new species, *10, 11,* paratype, NSM PM15466, locality 4, apical views of an inner mold with or without ammonium chloride coating, showing the muscle scar pattern; length, ca. 8 mm, width, ca. 7.5 mm, height, 5.7 mm; *13, 14,* holotype, NSM PM15467, locality 4, apical and lateral views; length, 8.2 mm, width, 7.9 mm, height, 5.5 mm. *15, 16, Patelloida obirensis* new species, holotype, NSM PM15468, locality 8, lateral and apical views; length, 8.5 mm, width, 6.2 mm, height, 3.9 mm.

Discussions.—This species is represented by more than fifty specimens from the Campanian part of the Krasnoyarka suite and the upper Campanian part of the Upper Cretaceous in the Wakkanai area; the formations represent a regressive facies. Most specimens are incomplete internal molds and casts; specimens showing the outer shell surface are extremely rare. The holotype and one of the paratypes (Figure 2.6) reveal the presence of fine radial threads over the shell surface. An ontogenetic change of shell form is evident in that the slopes of the shell become steeper and the lateral shell profile becomes mammilated in later growth (e.g., Figure 2.6).

Patella soyaensis belongs to MacClintock's (1967) shell structure group 10 (Table 1), which is represented by the single extant species *Patella* (*Olana*) *cochlear* Born, 1778, from South Africa. *Patella* (*O.*) *cochlear* is a moderately large limpet with an anterior end characteristically constricted and strong radial ridges

TABLE 1—Shell microstructure combinations and systematic positions of the six patellogastropods from the Cretaceous of Hokkaido, Japan and Sakhalin, Russia. m+3, outermost layer; m+2, outermost layer or second layer dorsal to the myostracum; m+1, layer dorsal to the myostracum; m-1, layer ventral to the myostracum; RCF, radial crossed-foliated; RCL, radial crossed-lamellar; CCL, concentric crossed-lamellar; CP, complex prismatic; SP, simple prismatic; FI, fibrous prismatic; FO, foliated.

Species	Number of shell layers excluding myostracum		Shell microstructure				MacClintock's (1967) shell structure group	Family and/or subfamily allocation
			outer layer			inner layer		
	outer	inner	m+3	m+2	m+1	m-1		
Patella soyaensis new species	2	1		RCF	CCL	RCL	10	Patellidae
Patella species	2	1		RCF	CCL	RCL	10	Patellidae
Patelloida obirensis new species	2	1		CP	CCL	RCL	2	Lottiidae, Patelloidinae
?*Patelloida miyauchii* new species	2	1		SP	CCL	RCL	none	Lottiidae, Patelloidinae
Lottiinae genus and species indeterminate	3	1	CP	FI	CCL	RCL	?3	Lottiidae, Lottiinae
Patelloidea genus and species indeterminate	3	?1	SP	FO	CCL	unknown	?15	unknown

over the shell surface, whereas *P. soyaensis* is a small limpet, with an elliptical aperture and fine radial threads.

Etymology.—The species is named for Soya, the type locality of this species.

Material.—Holotype, NSM PM15460; paratypes, NSM PM15461, UMUT MM19016.

Type locality.—Locality 4.

Occurrence.—Campanian; Krasnoyarka suite at localities 1–3; the Upper Cretaceous at locality 4.

PATELLA sp.
Figure 2.8, 2.9, 2.12

Discussion.—Two incomplete, indeterminate specimens are available. Like *Patella soyaensis*, this species belongs to MacClintock's (1967) shell structure group 10, indicating allocation to *Patella* (Table 1). In shell size and profile this species is similar to *Patella soyaensis* in that the aperture is elliptical and attains 8.7 mm in length, the apex is positioned at one quarter of the total length of the shell from the anterior apertural margin, and the width/length and height/length radios are about 0.8 and 0.4, respectively. However, *Patella* sp. differs from *P. soyaensis* in having lamellar concentric growth rugae and lacking axial ornament over the shell surface.

Material.—NSM PM15464, 15469.

Occurrence.—Lower Santonian: Upper Yezo Group at locality 7.

Superfamily ACMAEOIDEA Forbes, 1850
Family LOTTIIDAE Gray 1840
Subfamily PATELLOIDINAE Oliver, 1926
Genus PATELLOIDA Quoy and Gaimard, 1834

PATELLOIDA OBIRENSIS new species
Figure 2.15, 2.16

Diagnosis.—Small species belonging to *Patelloida profunda* group; aperture elongate, shell profile moderately high, apex anterior. Surface sculpture of concentric rugae, fine radial threads.

Description.—Shell small (longer apertural diameter, 9.1 mm in the largest specimen), moderately high, conical (height/length ratio about 0.4), with almost straight anterior, posterior slopes, weakly convex lateral slopes. Aperture elliptical, with width/length ratio slightly greater than 0.7. Apex positioned submarginally, at 1/5 of apertural length from anterior apertural margin. Shell surface appears to be sculptured by fine, slightly lamellar, concentric growth increments, fine radial threads. Shell consists of four layers: outermost shell of moderately thick, complex prismatic layer (M+2), followed by thick, concentric crossed-lamellar layer (M+1), myostracum (M), thick, radial crossed-lamellar layer (M−1).

Discussion.—More than a hundred specimens were recovered from a calcareous nodule approximately 100 mm in diameter. All specimens are represented by incomplete molds and casts. Some polished sections cut radially from the apex show that this species possesses concentric ornamentation similar to that of *Patella soyaensis*. This species belongs to MacClintock's (1967) shell structure group 2 and can be confidently referred to *Patelloida* (Table 1). In addition, its moderately high shell profile and fine radial ornamentation without strong axial ribs suggests that *P. obirensis* belongs to the *Patelloida profunda* group, an old subclade within the genus *Patelloida* defined by Lindberg and Vermeij (1985).

Patelloida obirensis differs from *Acmaea tenuistriata* (Michelin, 1838) (Akpan et al., 1982) from the Gault of Folkestone (middle to upper Albian), the single known species of the *Patelloida profunda* group from the Cretaceous (Lindberg, 1988a; Lindberg and Marincovich, 1988), in having a more elongate aperture and a more anteriorly located apex.

Etymology.—The specific name refers to Obira, the type locality of the species.

Material.—Holotype, NSM PM15468.

Type locality.—Locality 8.

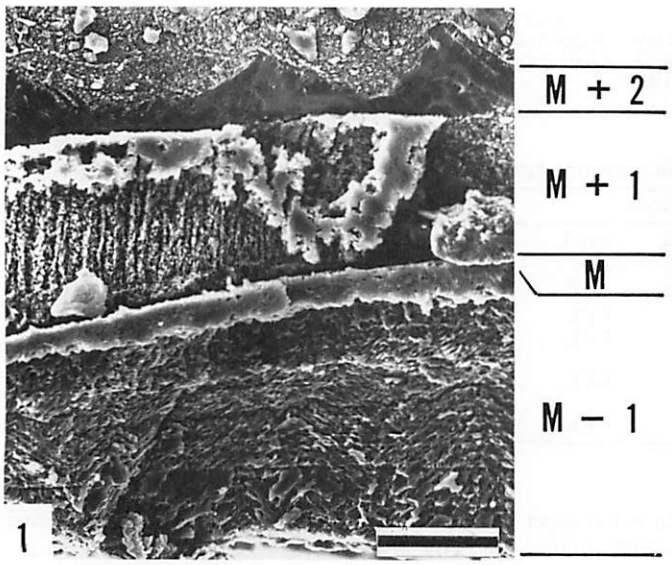
Occurrence.—Middle Turonian; Middle Yezo Group at the type locality.

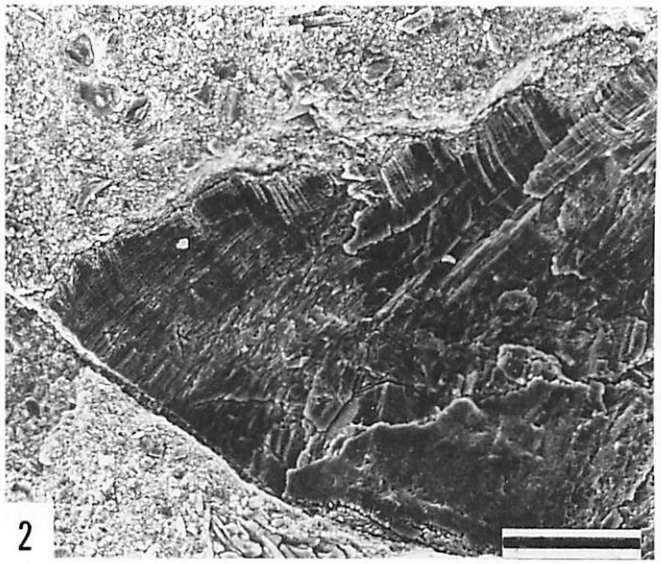
?PATELLOIDA MIYAUCHII new species
Figure 2.10, 2.11, 2.13, 2.14

Diagnosis.—Small *Patelloida* having simple prismatic outermost layer, shell profile high, aperture circular, apex centrally located, sculpture of fine radial riblets and fine growth lines.

Description.—Shell small (length of aperture 8.4 mm in the largest specimen), aperture circular (width/height ratio about 0.95). Apex central, slightly anterior of shell center; profile high (height/length ratio about 0.5 to 0.9). All slopes almost straight abapically, then convex. Shell surface sculptured by approximately 50 fine radial riblets; interspaces of riblets two to three times wider than riblets. Concentric growth lines very fine. Shell consists of four layers including myostracum: exterior simple prismatic layer (M+2), concentric crossed-lamellar layer (M+1), myostracum (M), radial crossed-lamellar layer (M−1) (Figure 3.4–3.6). Muscle scar of horseshoe-shaped symmetrical bundles.

Discussion.—This small limpet is known so far only from the Late Cretaceous deposits of the Wakkanai area in Hokkaido. The small shells show a simple low cap-shape profile, but be-


M + 2
M + 1
M
M − 1
1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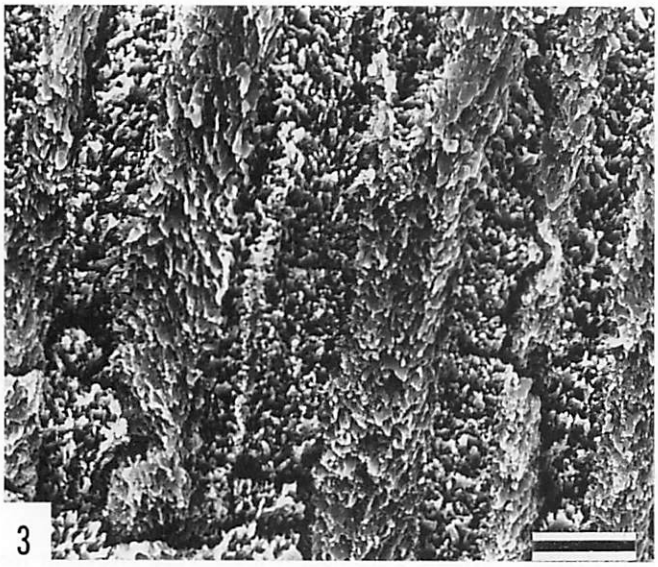
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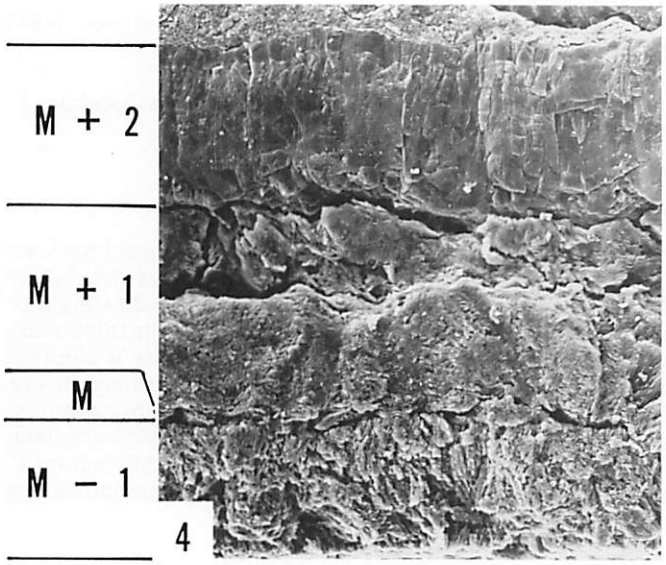
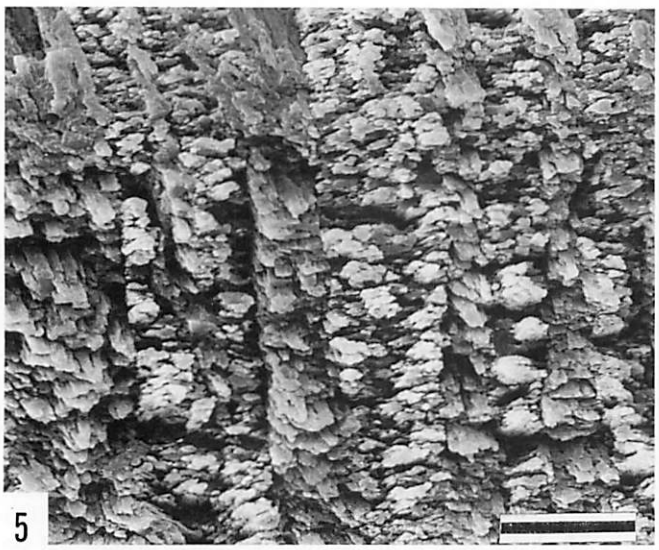

M + 2
M + 1
M
M − 1
4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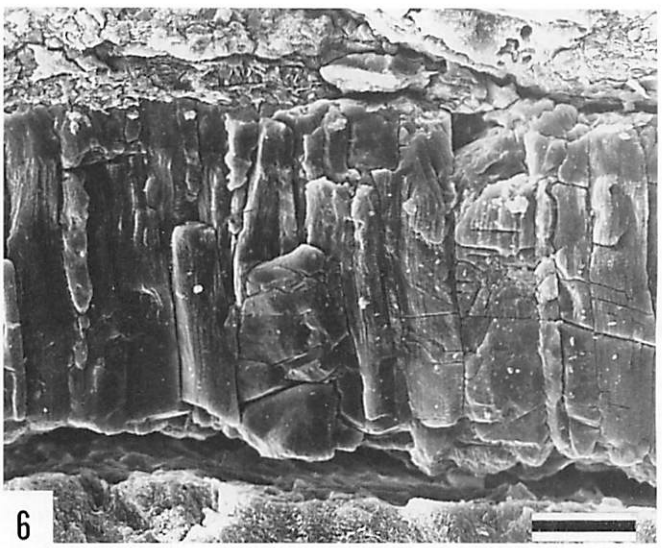
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come mammilate as the shell grows. All available specimens show the same pattern of surface ornamentation, consisting of fine radial riblets and fine concentric growth lines.

To the best of our knowledge, no species having this combination of shell structures is known among the fossil and living limpets. The species of the genus *Patelloida* have a thick outermost complex prismatic layer instead of simple prismatic layer (Table 1). Thus, the assignment of this species to *Patelloida* is tentative.

This new species somewhat resembles *Acmaea tenuistriata* (Michelin, 1838) (Akpan et al., 1982) from the Gault of Folkestone, but differs from *A. tenuistriata* in its small shell size, centrally located apex, and high shell profile, in addition to the differences in shell structure.

Patella traskii (Gabb, 1864) from the upper Campanian of California is the other species that has been confidently assigned to *Patelloida* based upon its shell structure (MacClintock, 1967; Lindberg, 1988a). ?*Patelloida miyauchii* can easily be distinguished from *P. traskii* by its small shell size, circular aperture, highly elevated shell, centrally located apex, and the absence of strong radial ribs.

Etymology.—This species is named for Mr. Toshiya Miyauchi, whose collection from the Orannai Formation at Soya has been very useful.

Material.—Holotype, NSM PM15467; paratypes, NSM PM15466.

Type locality.—Locality 4.

Occurrence.—Upper Campanian at the type locality.

Subfamily LOTTIINAE Gray, 1840
Genus and species indeterminate
Figure 2.3–2.5

Description.—Shell small in size, apertural length 5.0 mm, aperture circular (width/length ratio 1.0). Apex at 2/5 of apertural length from anterior apertural margin. Shell profile high, height/length ratio about 0.5. Anterior slope almost straight, lateral, posterior slopes weakly convex. Sculpture of fine growth lines, fine radial striae. Shell consists of five layers: exterior shell very thin, complex prismatic layer (M+3), followed by moderately thick fibrous prismatic layer (M+2), concentric crossed-lamellar layer (M+1), myostracum (M), radial crossed-lamellar layer (M−1) (Figure 4).

Discussion.—This distinctive patellogastropod limpet is represented by several incomplete specimens collected from a cobble-sized concretion. This concretion contains shell fragments of *Inoceramus schmidti,* an index fossil of the lower Campanian rocks of the northwestern Pacific.

The combination of the five shell layers suggests the subfamily Lottlinae (Table 1), in which Lindberg (1988b) recognized two tribes, the Scurriini and Lottiini, based on shell structure and radular and intestinal characteristics. In view of shell structure alone, the species described here is an intermediate between the two tribes. In the Lottiini, the outer shell consists of a thin, simple prismatic layer (about 40 percent of the prismatic layer) and an inner, thick, fibrous prismatic layer, whereas in the Scurriini, the outer shell consists of an outer, thick, complex prismatic layer (more than 80 percent of the prismatic layer) and an inner, thin, fibrous prismatic layer. This indeterminate species has an outer complex prismatic layer like the Scurriini, but its thickness is slightly less than 20 percent of the prismatic layer.

Although it has not been possible to determine the genus or species to which these specimens belong, their occurrence within Cretaceous sediments is important, as it demonstrates that the Lottiinae is a clade as old as the Patelloidinae. Previously, the oldest record of the Lottiinae was from the Pliocene of the North American Pacific (Lindberg, 1988b). The recording of this indeterminate species therefore extends the fossil record of the Lottiinae back by about 70 million years.

Material.—NSM PM15462, NSM PM15463.

Occurrence.—Lower Campanian; Upper Yezo Group at locality 5.

Family, genus and species indeterminate
Figure 5

Description.—Shell moderately elevated, apex at 1/3 of apertural length from anterior apertural margin, height/length ratio of about 0.4. Aperture elliptical, 10.6 mm in longer diameter, width/length ratio of 0.75. Surface sculpture unknown. Shell consists of five layers including myostracum; exterior shell of a very thin simple prismatic layer (M+3) followed by moderately thick foliated layer (M+2), concentric crossed-lamellar layer (M+1), myostracum (M), but inner layer not determined.

Discussion.—Several fragmentary specimens represent small, limpetiform shells similar to the other Cretaceous patellogastropod limpets described here. Because the specimens are composed of incomplete internal and external molds, the surface ornamentation is unknown. Although the specimens are all recrystallized to some extent, SEM observation shows that the shell surface is composed of a very thin simple prismatic layer (M+3) followed by a moderately thick foliated layer (M+2) (Figure 6). The shell layer further inside (M+1) and the innermost layer (M−1) are severely recrystallized. However, binocular observation reveals a concentrically arranged, alternating light-dark pattern in the inner surface of the M+2 layer, suggesting a concentric crossed-lamellar structure for this layer. This shell layer covers most of the ventral surface outside the muscle scar. Shell structure of the innermost layer (M−1) is unknown.

This species is enigmatic and cannot be referred definitely to any known genus or family within the Patellogastropoda, as it possesses a combination of shell layer unknown among living species. The combination of shell layers seen in this species appears to indicate that it belongs to MacClintock's (1967) shell structure group 15 (Table 1). Included in this shell structure group are *Acmaea mitra* Rathke, 1833, and the predominantly subtidal Lepetidae and subtidal *Pectinodonta* (MacClintock, 1967; Lindberg, 1981). These forms possess a thick outermost

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FIGURE 3—SEM micrographs of the shell walls in two patellogastropod limpets from Hokkaido. Scale bars represent 10 μm for *3, 5* and *6*; 50 μm for *1* and *4*, and 100 μm for *2*. *1–3, Patella soyaensis* new species, from locality 4, etched by 0.5% HCl; *1,* cross section cut radially from the apex to shell margin showing the outermost radial crossed-foliated layer (M+2), followed by outer concentric crossed-lamellar layer (M+1), the myostracum layer (M), and the inner radial crossed-lamellar layer (M−1); *2,* enlargement of the outermost crossed-foliated layer at shell margin showing slightly fused calcite blades; *3,* enlargement of M+2 layer showing strongly etched surface of concentric crossed-lamellar layer. *4–6,* ?*Patelloida miyauchii* new species, from locality 4, etched by 0.5% HCl; *4,* cross section cut almost radially from the apex to shell margin showing the outermost simple prismatic layer (M+2), followed by the concentric crossed-lamellar layer (M+2), the myostracum layer (M), and the inner radial crossed-lamellar layer (M−1); *5,* enlargement of M+2 layer showing clearly the first, second, and third order lamellae; *6,* enlargement of the outermost layer showing that each simple prism is oriented perpendicularly to the shell surface.

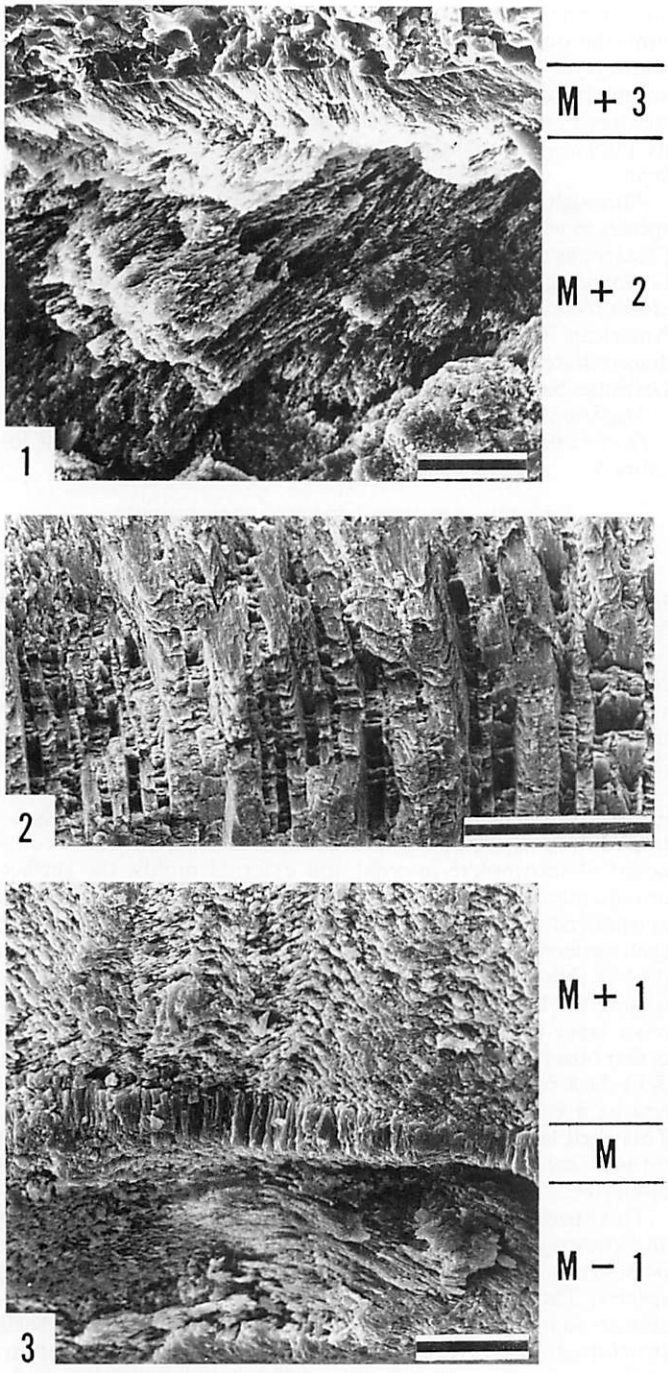

FIGURE 4—SEM micrograph of the shell walls of Lottiinae, genus and species indeterminate. Scale bars represent 10 μm for *1* and *3*, and 50 μm for *2*. *1*, cross section cut radially from the apex to shell margin showing the outermost complex prismatic layer (M+3) and the inner fibrillar layer (M+2); *2*, section cut radially from the apex to shell margin showing concentric crossed-lamellar layer (M+1); *3*, section showing the outer concentric crossed-lamellar layer (M+1), the myostracum layer (M) and the inner radial crossed-lamellar layer (M−1).

complex prismatic layer, whereas the outermost shell layer of the Cenomanian form is seen to be very thin and most probably composed of a simple prismatic structure.

Material.—NSM PM15477, and several fragmentary specimens.

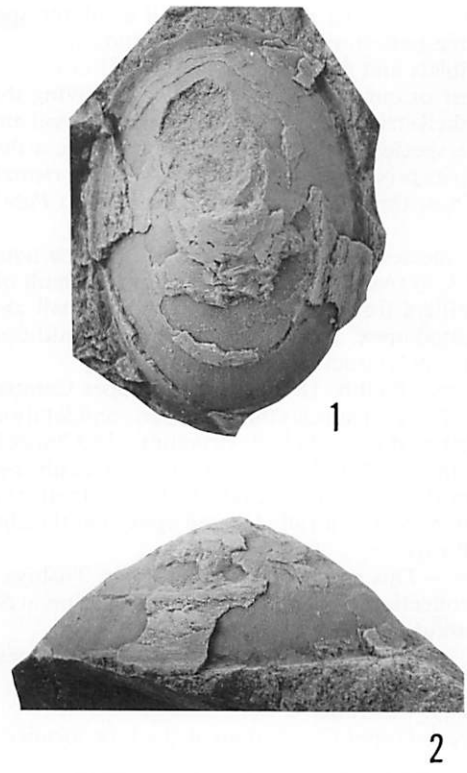

FIGURE 5—Patellogastropoda, family, genus and species indeterminate, NSM PM15477, locality 6; length, 10.6 mm, width, 8.0 mm, height, 4.5 mm; *1*, apical view; *2*, lateral view.

*Occurrence.*Lower Cenomanian; Middle Yezo Group at locality 6.

DISCUSSION

Compared with the high diversity and abundance of modern patellogastropod limpets in littoral rocky shore systems, the fossil record is very sparse, particularly in pre-Tertiary rocks. Pre-Tertiary species have been described solely on the basis of shell form, resulting in an indefinite generic allocation. Only three pre-Tertiary species have been assigned by examining shell structures. Lindberg (1988a) reallocated *Patella traskii* Gabb (1864) from the Campanian of California and *Acmaea tenuistriata* (Michelin, 1838) (Akpan et al., 1982) from the Albian of England to the *Patelloida* sensu stricto group and the *Patelloida profunda* group, respectively. Kase (personal obser.) referred a Campanian species from the Pierre Shale of South Dakota to *Patelloida*. The discovery documented in this paper of six species from the Cretaceous of Hokkaido and southern Sakhalin reveals a pattern of evolution and past distribution of patellogastropod limpets not previously documented.

The order Patellogastropoda consists of five families: Patellidae, Nacellidae, Lepetidae, Acmaeidae, and Lottiidae. This study shows that patellogastropod limpets were diverse in terms of shell structure, and at least two of the five families (Patellidae and Lottiidae) existed during the Cretaceous. The presence of species having shell structure combinations unknown today suggests that the Cretaceous patellogastropods include some extinct clades. Lindberg (1988a) hypothesized that the Patellidae is the most primitive of the five patellogastropod families recognized today. His hypothesis predicted the discovery of patellid species from geologically older rocks, although the family was represented by only Holocene species at the time. The discovery of

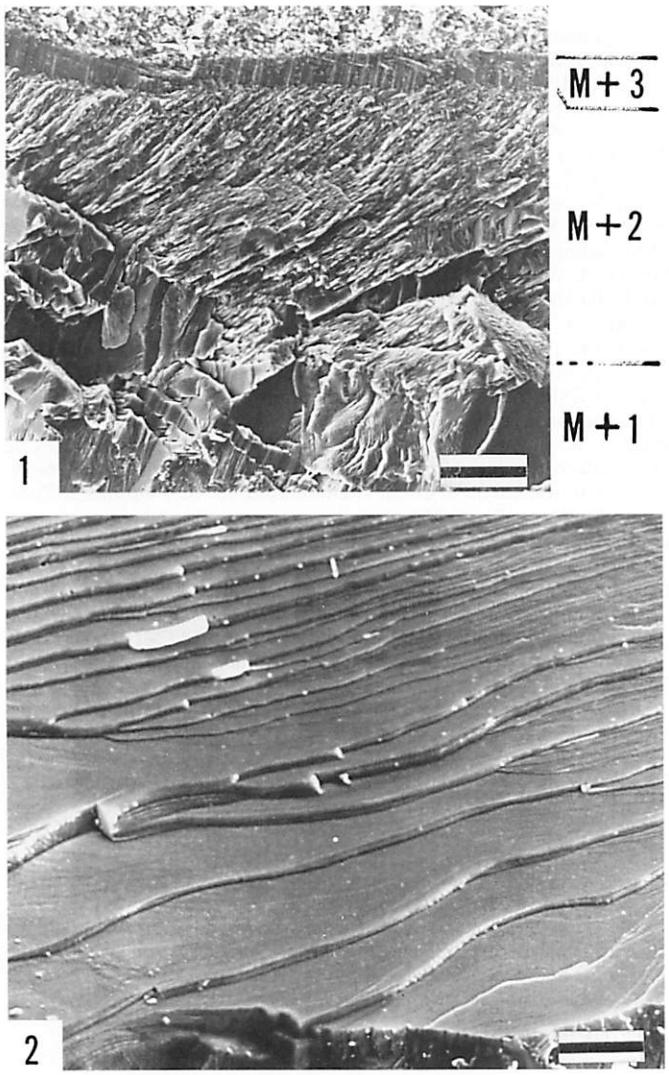

FIGURE 6—SEM micrograph of the shell wall of Patellogastropoda; family, genus, and species indeterminate from locality 6. Scale bars represent 20 μm for *1* and 5 μm for *2*. *1*, cross-section cut radially from the apex to shell margin showing the outermost simple prismatic layer (M+3), followed by foliated layer (M+2), and recrystalized concentric crossed-lamellar layer (M+1); *2*, oblique section cut parallel to growth lines showing slightly fused sheets of foliated layer (M+2).

two species of *Patella* from the Cretaceous of Hokkaido and southern Sakhalin extends the fossil record of the Patellidae back approximately 85 million years further than previously known, into the Santonian of the Cretaceous, suggesting Lindberg's hypothesis.

Along the west coast of North America, the patellogastropod community consists exclusively of acmaeoideans, whereas in South Africa the community consists primarily of patellids, and in the Indo-Pacific region, *Cellana*, patellids and lottiids are characteristic (MacClintock, 1967; Powell, 1973; Lindberg, 1988a). However, the compositions of the communities have changed markedly through geologic time. For example, *Patelloida* is found in the Cretaceous of England, South Dakota, and California. During the Eocene, *Patelloida* is still found in France, California and Oregon, but by the Oligocene in Europe and by the Pliocene along the North American Pacific coast, *Patelloida* disappeared from these areas (Lindberg and Marincovich, 1988; Lindberg and Squires, 1990). Today, it is mostly restricted to tropical to temperate, Indo-west Pacific and western Pacific seas (Lindberg and Vermeij, 1985). Lindberg and Hickman (1986) documented a species of *Cellana* from the Eocene of Oregon, but otherwise this genus is not known from the western coast of North America.

Patelloida obirensis from the middle Turonian of Hokkaido is the second Cretaceous species of the *Patelloida profunda* group, an old stock of the Patelloidinae (Lindberg, 1988a; Lindberg and Marincovich, 1988; Lindberg and Vermeij, 1985). In addition, *Scurriopsis* (s.s.) *moshiensis* Kase (1984) and *Acmaea? moshiensis* Kase (1984) from the Aptian of Japan, described solely from gross shell morphology, seem to belong to the Patelloidinae because both species have an outermost complex prismatic layer followed by an inner, concentric, crossed-lamellar layer (Kase, personal obser.). The presence of these species from Japan and Sakhalin supports the idea that *Patelloida* was most probably widespread during the Cretaceous.

Patella soyaensis from the Campanian of Hokkaido and Sakhalin and *Patella* sp. from the Santonian of Hokkaido belong to MacClintock's (1967) shell structure group 10 and to Lindberg's (1988a) *Patella* II group. Fossil species belonging to this shell structure group are also represented by two species from the lower middle Miocene Mizunami Group of central Japan and one species from the lower Pliocene (or uppermost Miocene) Ochiai Conglomerate of central Japan (Kase, 1994). The occurrence of these species in the Cretaceous and Neogene rocks of the northwestern Pacific is surprising because the only modern species of the same shell structure group [*Patella* (*Olana*) *cochlear* Born, 1778] is restricted to South Africa (MacClintock, 1967). The fossil record strongly suggests that the subgroup of *Patella* having this shell structure is an old clade within the Patellidae and that this clade was well represented in the northwestern Pacific bioprovince during Late Cretaceous and Neogene times, but has been absent from this area since Pliocene time. The paucity of fossil evidence from other areas, however, precludes the clarification of the migration history that resulted in the observed, discrete distribution pattern.

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APPENDIX
LOCALITY INFORMATION

The following localities are entered in the National Science Museum, Paleontological Collection Locality (NSM PCL) and in the National Science Museum, Sakhalin Expedition Locality (NSM SE) register.

Locality 1 [NSM SE MK2014; 142°40′18.1″E, 48°40′56.0″N]; calcareous concretions obtained in the stream bed of the River Akatsiya, a tributary of the River Makarova, Makarov, southern Sakhalin, Russia; the Unit II in the lower part of the lower Krasnoyarka subsuite by Zhidkova et al. (1974); Late Campanian (*Schlueterella kawadai* Subzone defined by Matsumoto, 1984).

Locality 2 [NSM SE NB7011; 142°29′55″E, 47°21′44″N; = locality N428 in Matsumoto (1942)]; one specimen is from Kawada's Cretaceous collection of Naiba area, southern Sakhalin, Russia in the University Museum, the University of Tokyo; the label attached to this specimen indicates that the specimen was collected from *Inoceramus schmidti* Zone (Early Campanian: age and inocermid zonation see Matsumoto, 1977, 1984) in the middle course of the River Seam, a tributary of the River Naiba, Naiba, southern Sakhalin; the fossil locality may be within the lower part of the lower Krasnoyarka subsuite by Poyarkova (1987).

Locality 3 [NSM SE NB1057; 142°30′14.3″E, 47°22′21.1″N; = locality N467 in Matsumoto (1942)]; calcareous concretion in the stream bed of the River Naiba, Naiba, southern Sakhalin; lower part of the lower Krasnoyarka subsuite by Poyarkova (1987); Early Campanian (*Inoceramus schmidti* Zone).

Locality 4 [NSM PCL3-4.5-8; 141°52'55"E, 45°29'03"N; = locality W7A in Matsumoto and Miyauchi (1984)]; calcareous concretions were obtained from an exposure during the large scale excavation for the reconstruction of the Soya Harbour at Soya, Wakkanai, Hokkaido; Unit H in the Upper Cretaceous strata defined by Matsumoto and Miyauchi (1984); Late Campanian (*Schlueterella kawadai* Subzone defined by Matsumoto, 1984).

Locality 5 [NSM PCL3-23-3; 142°01'10"E, 44°42'40"N]; an erratic pebble-sized calcareous concretion in the stream bed of Rubeshibe-zawa, a small tributary of the Abeshinai river, Saku, Nakagawa-cho, Hokkaido; most probably from the Upper Yezo Group; an Early Campanian age is suggested by the presence of *Inoceramus schmidti* within the concretion.

Locality 6 [NSM PCL3-35-1; 142°05'29"E, 44°15'54"N]; an erratic cobble-sized calcareous concretion from the stream bed of Sakinzawa valley, Horokanai-cho, Hokkaido; Middle Yezo Group; lowermost Cenomanian suggested by the occurrence of *Desmoceras kossmati* Matsumoto in the same concretion (ammonite zoning see Matsumoto, 1977).

Locality 7 [NSM PCL3-35-2; 141°00'54"E, 44°17'54"N]; an erratic cobble-sized calcareous concretion from the bottom of Sakasazawa valley, Haboro-cho, Hokkaido; most probably derived from the Upper Yezo Group; an Early Santonian age is suggested, as the concretion includes fragments of *Polyptychoceras* sp. and *Inoceramus naumanni* Yokoyama (age and inoceramus zonation see Matsumoto, 1977).

Locality 8 [NSM PCL3-38-1; 141°55'36", 44°03'55"N; = locality R4018 in Tanabe et al. (1977)]; southern bank of the Obirashibe river, about 10 m lower stream at the junction with the Nakakinenbetsu river, Tappu, Obira-cho, Hokkaido; the Mm-n Unit of the Middle Yezo Group in Tanabe et al. (1977); a Middle Turonian age is suggested by the occurrence of *Inoceramus hobetsensis* Nagao and Matsumoto (age and inoceramid zonation see Matsumoto, 1977).