

Limpet home depressions in Cretaceous ammonites

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LETHAIA



Kase, T., Shigeta, Y. & Futakami, M. 1994 06 15: Limpet home depressions in Cretaceous ammonites. *Lethaia*, Vol. 27, pp. 49–58. Oslo. ISSN 0024-1164.

Remarkable large pits were found on the shell surface of many ammonites from the Turonian–Maastrichtian sediments of Hokkaido, northern Japan, and Sakhalin, Russia. These pits are (1) round to elliptical in shape; (2) up to 20 mm (usually around 10 mm) in diameter; (3) shallow depressions to deep holes that almost penetrate the shell; (4) occasionally healed by a thin shell blister from inside the shell; (5) often overlapping one another; (6) several to more than 170 in number on one flank of the ammonites; (7) found on both flanks and predominantly on the body chamber and the final volution of the phragmocone; and (8) found only in the two families Pachydiscidae and Puzosiidae, predominantly of more than 300 mm in shell diameter. They can best be interpreted as the home depressions of patellogastropod limpets. The presence of pits on both flanks of the ammonites and those healed from inside the shell strongly suggest that the limpets were dwelling on mature swimming ammonites. Host specificity, their very small shell size compared with the host ammonites, and sparse occurrence in sediments favor a mode of life as obligate pseudoplankton. We suggest that this remarkable limpet–ammonite association was well established in northwestern Pacific bioprovinces during the late Cretaceous. Taking this live association and the depth limit of algal growth as food for the limpets into consideration, the mature ammonites dwelled or periodically visited the upper layer of the euphotic zone, probably less than around 20 m in depth. □ *Ammonite, limpet, home depression, life mode, pseudoplankton, Cretaceous.*

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A wide variety of organisms excavate depressions or drill boreholes in the hard substrates for the sake of habitation, predation, and protection from predators. Boreholes in fossil shelled assemblages have attracted attention because they illuminate part of the behavioral activities of past organisms (see Bromley 1978; Boucot 1990). Because boreholes are not usually preserved with the boring organisms, their origins are largely a matter for speculation. Particularly, the borers for the Paleozoic and early Mesozoic boreholes have largely remained unspecified (e.g., Carriker & Yochelson 1968; Rohr 1976, 1991; Smith *et al.* 1985).

Through our independent field observations and examination of many museum and institution collections of Cretaceous ammonites from Hokkaido, northern Japan, and South Sakhalin, Russia, we have become aware of the presence of remarkable, large pits in many ammonites. These pits are apparently similar to the incomplete boreholes drilled by naticid and muricid gastropods, but differ significantly in size and shape. The pits are also similar to the reptile and mosasaur bite-marks (Kauffman & Kesling 1960; Saul 1979;

Hewitt & Westermann 1990; Kauffman 1990; Ward & Hollingworth 1990), but are difficult to interpret in this way. We have concluded that they are the home depressions of patellogastropod limpets.

The purpose of this paper is to describe the distribution of the pit-bearing ammonites and the nature of the pits in detail, and to discuss their origin as well. Particularly, this paper focuses on discussing ecological implications of this remarkable limpet–ammonite association and ammonoid paleoecology. Limpet home depressions are an example of non-predatory boreholes preserved in fossil shelled organisms.

Repository. – The specimens illustrated are stored in the section of Invertebrate Paleontology, National Science Museum, Tokyo (NSM). Other pit-bearing specimens used in this study are housed in the same section of the NSM (under nos. NSM PM7569, 8254–8262, 8264–8268, 8270, 8272 and 8273), in the Geological Museum, Geological Survey of Japan (under nos. GSJ F4890 and F5159), in the University Museum, the University of Tokyo (under no. UMUT MM19015), and in Mikasa City Museum (under nos. MCM 5503.12, MCM YKC-570530, MCM KIC-561008.1, MCM YKC-A131-1, and MCM YKC-531007).



Fig. 1. *Canadoceras kossmati* Matsumoto. Left side view of a specimen (NSM PM8263) from the Upper Campanian in the Naiba area of South Sakhalin, showing the presence of more than 120 large pits and their typical preservation. Arrow indicates the position of the last suture. Scale bar 50 mm.

Distribution of pit-bearing ammonites

We found 30 pit-bearing ammonites from the Turonian–Maastrichtian, predominantly offshore sediments of Hokkaido and Sakhalin. Pits are found mostly on the body chamber and the final volution of the phragmocone, and number from several to more than 170.

The pits are found predominantly on the undersurface of the flat-lying ammonite shells in the outcrops. Their predominance on the lower flanks of the flat-lying ammonite shells is most likely due to preservational bias. Maeda (1987) has demonstrated that Cretaceous ammonites with a maximum shell diameter of more than 300 mm are usually embedded solitarily with the median plane parallel to the

stratification in the outcrops and are generally less well preserved than smaller specimens (e.g., collections from Hokkaido, Japan, and Sakhalin, Russia). He attributed this to strong dissolution and/or sediment compaction of the ammonite shells, particularly in the upper surface of the ammonites. As a consequence, the larger ammonites possess an upper flank that is strongly crushed or selectively dissolved ('half-ammonites' of Seilacher *et al.* 1976), or a 'ventral-tire preservation' in which only the ventral shell and both flanks of the last two whorls are preserved. Probably, the pits were excavated in both flanks of ammonites, but subsequent dissolution on the sea floors and sediment compaction after burial make it difficult to detect the presence of boreholes in the upper flank of the large, flat-lying ammonites. Support for this view is the presence of many pits on both flanks in those specimens free from strong compaction and dissolution.

The pits have been found predominantly in large and giant ammonites, more than 300 mm in maximum shell diameter, while they are uncommon in small ammonites. The sparsity of the pits in small ammonites is striking in spite of the fact that these are fairly common throughout the Upper Cretaceous of Hokkaido and Sakhalin. Since it should be expected that the pits can be seen more easily in the common small specimens, we suggest that they were preferably excavated on the large and gigantic ammonites.

The pits have only been found in two families (Pachydiscidae and Puzosiidae) and seven genera with large shells (*Pachydiscus*, *Canadoceras*, *Anapachydiscus*, *Puzosia*, *Mesopuzosia*, *Pachydesmoceras*, and *Pteropuzosia*). However, relatively large specimens of phylloceratid, acanthoceratid, texanitid, and the lytoceratid *Gaudryceras* are commonly well enough preserved to determine the presence or absence of pits. Some (e.g., phylloceratids and *Gaudryceras*) preserve an almost complete outer shell surface. Despite our extensive survey, we have not yet found pits in families other than the Pachydiscidae and Puzosiidae.

We found 30 pitted ammonites among more than 90 large to giant specimens examined. Because poor preservation of the larger specimens decreases the frequency of pitted ammonites, the real frequency appears to be higher. The highest frequency of pitted ammonites was seen in specimens collected from the Campanian–Maastrichtian deposits along the course of the Miho (Krasnoyarka) River in the Naiba area, South Sakhalin during field reconnaissance in 1990. On this occasion, 22 large to giant specimens were collected, 17 of them pitted.

Morphology of pits

The pits discussed here vary greatly in size and depth but never seem to penetrate the shell completely. Most of the shell and the surrounding matrix was normally peeled off during excavation of the ammonites from the calcareous

concretions, producing incomplete internal molds. In these ammonites, the detailed nature of the pits is difficult to observe. Here, we illustrate three representative pit-bearing ammonites and describe the nature of the pits.

A large specimen of *Canadoceras kossmati* Matsumoto (NSM PM8263) collected from the Ryugase Group (Matsumoto 1942) (=Krasnoyarka Formation of Zakharov *et al.* 1984) in Miho (Krasnoyarka) Valley, South Sakhalin, shows common preservation of the pits (Fig. 1). In the outcrop, the median plane of the specimen was almost parallel to the stratification, and the pits are only found in the undersurface of the ammonite. The pits are represented by at least 120 circular to slightly elliptical, shallow depressions or traces of depressions up to 13.6 mm in maximum diameter. They are present on the flank of the final volution of the phragmocone and the body chamber but are not found on the ventral surface and umbilical wall of the shell. Two or more pits are sometimes seen overlapping one another.

A medium-sized specimen of *Puzosia orientalis* Matsumoto (NSM PM8271), from the Lower Turonian in the Obira area of Hokkaido, reveals more details about the pits, although its outer prismatic shell layer is totally lost (Fig. 2). Although one flank of the shell is slightly compacted and dissolved and the body chamber is destroyed, the specimen preserves both flanks of the shell. The median plane was



Fig. 2. Stereo-paired close-up of a specimen (NSM PM8271) of *Puzosia orientalis* Matsumoto from the Lower Turonian in the Obira area, Hokkaido, Japan, showing the detailed nature of the pits. Scale bar 10 mm.

almost parallel to the stratification. More than 70 pits occur on the upper surface, and there are a few on the lower surface. The pits are variable in size: the largest attains 12 mm in longer diameter, and typically they are 5–8 mm in diameter. The outer margin is elliptical to circular in outline and indistinct. The wall of the pits is short, weakly inclined inwards, straight or slightly convex, and forms an obtuse angle with the wide and uneven bottom. The pits never penetrate the shell (Fig. 3B).

A large specimen of *Pachydiscus sahekii* Matsumoto & Miyauchi (NSM PM8253) from the Upper Campanian in the Wakkanai area, Hokkaido, shows another aspect of the pits (Fig. 4). This is a fragmentary 'half-ammonite', consisting of the phragmocone and a third of the body chamber. The reconstructed shell diameter is about 700 mm. Some 130

pits are concentrated on the body chamber, and several are also found on the final volution of the phragmocone. As in other pit-bearing ammonites, the pits do not preserve their complete outer shape, because most of the shell was peeled off during excavation from the calcareous concretion. However, several are well preserved (Fig. 4). They are elliptical to circular in shape, 4.7–12.4 mm in larger diameter, and penetrate the shell almost vertically (Fig. 3A). The wall of the pits is steep, short, slightly parabolic, and smooth, and the bottom is uneven. No pit penetrates the shell completely, but many are deeply excavated as to reach the thickness of the ammonite shell (ca. 2 mm in the area between the axial ribs). An interesting aspect of the pits is that some are healed by a very thin shell deposited from inside the body chamber (Figs. 3A, 4B). Such pits can easily be recognized by the presence of weak depressions on the steinkern. However, recrystallization prevents microstructural determination of the healed shells. The high incidence of healed pits strongly suggests that the borers excavated the pits when the ammonite was living.

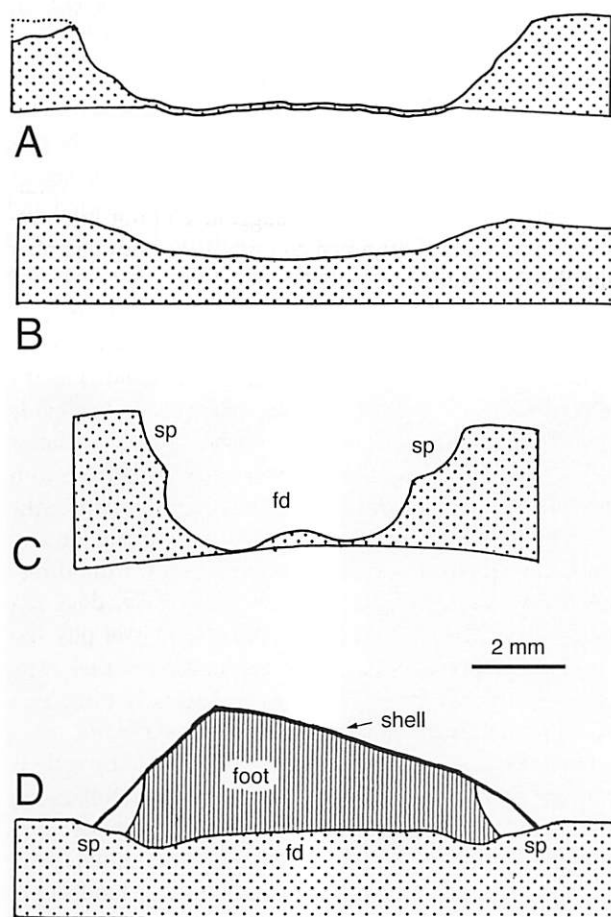


Fig. 3. Cross sections of fossil and modern limpet home depressions. □A. A deep home depression by a patellogastropod limpet healed by a thin shell blister from the inside in the body chamber of *Pachydiscus sahekii* Matsumoto & Miyauchi in Fig. 4. □B. A shallowly excavated home depression by a patellogastropod limpet found in *Puzosia orientalis* Matsumoto in Fig. 2. □C. A deep home depression of *Sabia conica* (Schmacher) in the body chamber of *Harpago chiragra* (Linnaeus), showing two distinct levels of excavation, sp (shell platform) and fd (foot depression). Note that the depression almost penetrated the shell. □D. An idealized home depression of patellogastropod limpets showing two levels of excavation; sp = shell platform; fd = foot depression; modified from Bromley (1978); terminology after Lindberg & Dwyer (1983).

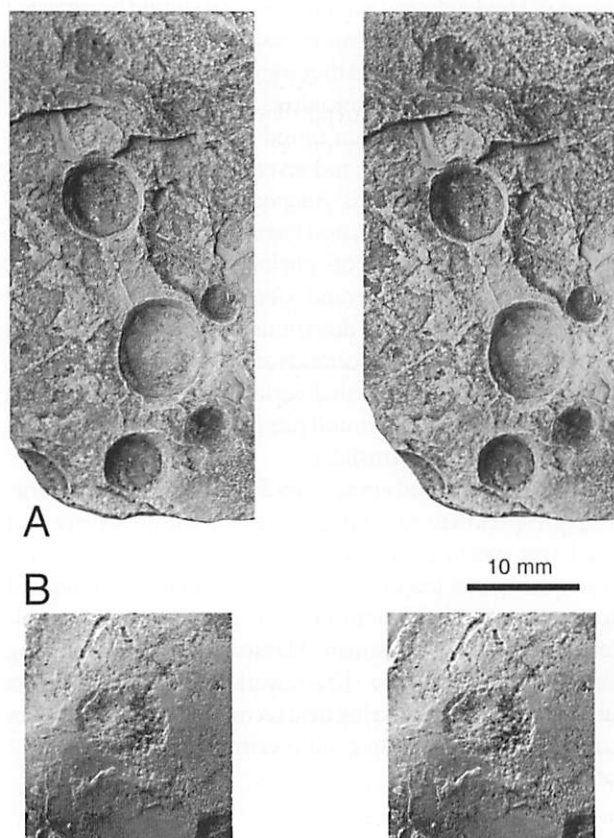


Fig. 4. Stereo-paired close-up of the pits in a specimen (NSM PM8253) of *Pachydiscus sahekii* Matsumoto & Miyauchi from the Upper Campanian in the Wakkanai area of Hokkaido, Japan. □A. Five deeply penetrated pits showing the steeply inclined walls and almost flat bottoms; the outermost shell layer (prismatic layer) is lacking, such that the outer shelves of the pits are lost. □B. A shallow depression covered with thin shell material in the steinkern, indicating a healing of the pit from the inside.

Origin of pits

It is obvious from our observations that the pits were not the results of physical destruction, nor of chemical dissolutions after the ammonites were exposed from the calcareous concretions. The pits are found in many ammonites collected from calcareous concretions in the field. It is also obvious that the pits were not the results of predatory activities by naticid and muricid gastropods nor by octopods. It is difficult to imagine that these animals would drill multiple, incomplete pits on a large live ammonite.

The pits discussed here are similar to 'mosasaur bite-marks' in *Placenticer* and *Pachydiscus* species from the Late Cretaceous of North America (Kauffman & Kesling 1960; Saul 1979; Hewitt & Westermann 1990; Kauffman 1990). The presence of fine radial or concentric cracks around the holes and some alignments of the holes that appear to correspond to the placement of teeth in the mosasaur jaw constitute principal arguments for the 'mosasaur-bite' hypothesis. However, it is evident that the pits are not the results of mosasaur-bite, because their unpenetrated and healed nature and the presence of so many small pits aggregated in a limited area in a single specimen are difficult to explain by this mechanism.

We suggest that the pits discussed here are the home depressions (home scars) of patellogastropod limpets. These gastropods are inconspicuous in fossil molluscan assemblages because of their high-energy, erosional habitats but are found sporadically from the offshore, fairly deepwater Cretaceous sediments of Hokkaido and Sakhalin. Analysis of shell features and shell microstructures has revealed six species whose living relatives mostly dwell in rocky shores of modern seas (Kase & Shigeta, unpublished). The occurrence of such limpets in offshore sediments is anomalous but can reasonably be explained by taking this remarkable mode of life into account. Kase & Shigeta (unpublished) have observed that the limpets occur in aggregation in some calcareous concretions rather than randomly in the outcrops. They have suggested that the limpets were fossilized near to the hard substrates on which they clung during life. It may be that the hard substrates were, as discussed below, the limpet-carrying ammonites that sank to the bottom from their original habitats after death.

Patellogastropod limpets are sometimes closely associated with the ammonites that bear the pits. The calcareous nodule encasing the *Pachydiscus sahekii* specimen (NSM PM8253) from the Wakkanai area, Hokkaido, includes the shells of two limpet species, *?Patelloida* sp. and *Patella* sp. The former species has an elliptical aperture with a maximum apertural diameter of 15 mm in the largest specimen, while the latter species has a circular aperture with a maximum apertural diameter of 10 mm in the largest specimen. The size and shape of the apertures of the two species approximate those of the pits (Fig. 5).

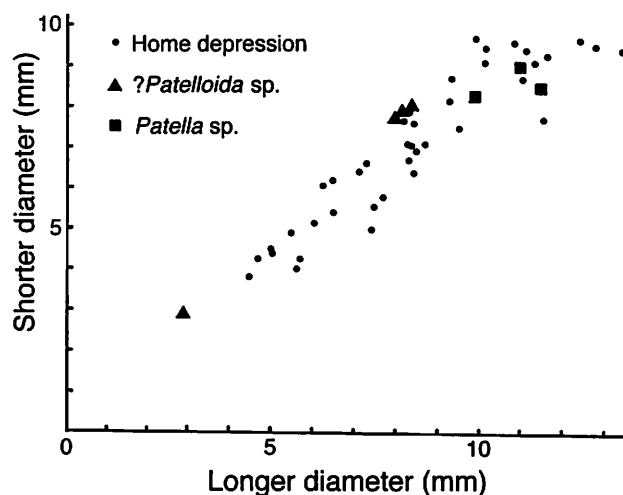


Fig. 5. Scatter plots of the longer and shorter diameters of 40 home depressions in NSM PM8253, and the longer and shorter apertural diameter of seven limpets collected from the same concretion as the ammonites.

A specimen of *Canadoceras* sp. from the Upper Campanian in the Wakkanai area is suggestive of our interpretation (Fig. 6). This specimen comprises the body chamber and the final volutions of the phragmocone and preserves both flanks of the shell. The reconstructed shell diameter is about 120 mm, suggesting that it is the smallest known pit-bearing ammonite. It bears 10 pits on one flank and 21 on the other. The pits are small, shallow, and circular to slightly elliptical in shape: the largest one reaches 4.4 mm in diameter. Three small specimens of *Patella* sp. are affixed with their aperture to the shell surface of the ammonite besides the pits, and the size and shape of the pits approximate those of the limpet aperture. Removal of these two (of the three) specimens from the ammonite shell, however, does not ascertain whether the limpets are positioned over pits, because of the powdery nature of the ammonite shell. The example suggests that the limpets were closely associated with ammonites and most probably preserved *in situ*.

Home depressions are known to be produced by various limpetiform gastropods, including haliotids (e.g., Koike *et al.* 1970; Lindberg & Dwyer 1983), patellogastropods (e.g., Branch 1971, 1975; Lindberg & Dwyer 1983), capulids (e.g., Orr 1962; Matsukuma 1978), hipponicids (e.g., Lindberg & Dwyer 1983), and siphonariids (e.g., Abe 1940). These limpets produce home depressions widely varying in shape and depth. Patellogastropod limpets cling on various substrates such as rocks, shells, and wood, and deep home depressions are usually produced by homing and/or territorial species (Branch 1975). Lindberg & Dwyer (1983) documented home depressions produced by the extant *Collisella scabra* that are composed of two distinct levels: the outer level (or shell platform) and the inner, deeper depression. The outer and inner levels correspond to the shell margin and the foot

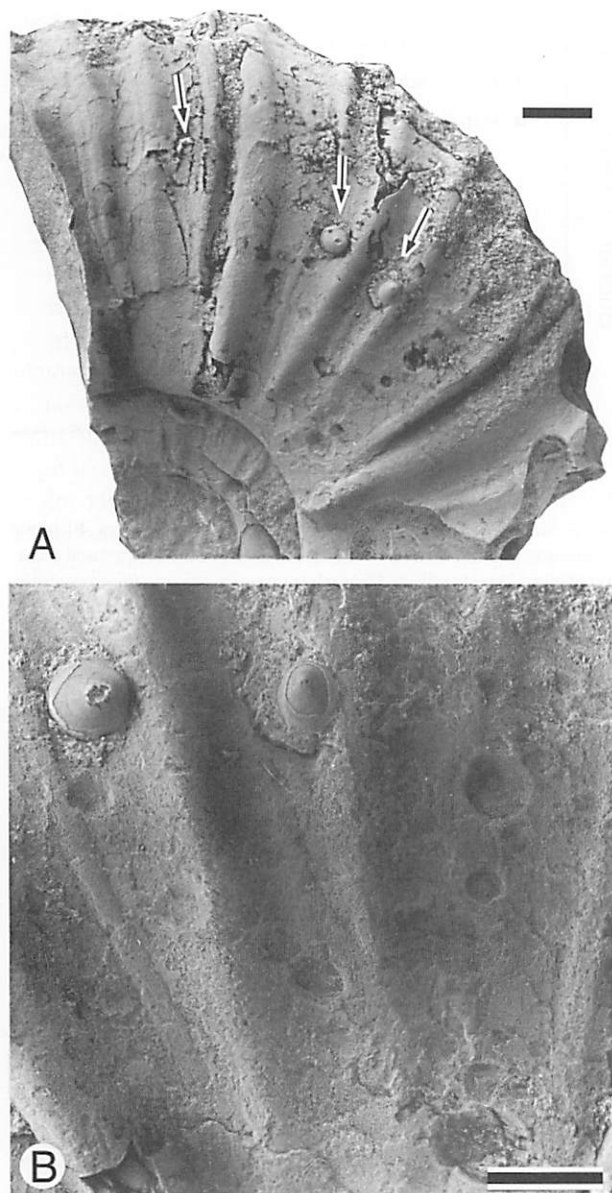


Fig. 6. *Canadoceras* sp. NSM PM8269 from the Upper Campanian in the Wakkanai area, Hokkaido. □A. Right-side view showing small circular home depressions and two shells and one fragmented shell of *Patella* sp. (arrows) tightly affixed to the ammonite with their apertures. Scale bar 10 mm. □B. Close-up of A. Scale bar 5 mm.

of the limpet, respectively. They attributed the mechanism to chemical dissolution, assisted by radular rasping action. As a consequence of abundant secretion from the foot margin and less secretion in the sole of the foot, the bottom of the depression is slightly more convex than the margin itself (Bromley 1978; Lindberg & Dwyer 1983) (Fig. 3D). Lindberg & Dwyer (1983) suggested that this mechanism is common among other prosobranch limpets.

The home depressions in the Cretaceous ammonites do not exactly fit the ideal morphology seen in extant patellogastropods: none show two distinct levels, and the foot

depressions are usually uneven, sometimes convex and sometimes concave (Fig. 3A, B). This is mainly due to the diagenetic destruction of the original depressions. We usually see incomplete home depressions because the outer shell layer of the ammonites has been peeled off. Such home depressions do not preserve their delicate topography.

To the best of our knowledge, there are no examples of patellogastropod home depressions healed from inside the shell. In general, modern limpets excavate shallow home depressions, but Vermeij (1978, p. 143) pointed out that the depth of the home depressions changes geographically in relation to predation pressure. For example, an Indo-Pacific hipponicid limpet, *Sabia conica*, excavates deep home depressions on the shells of gastropods. This limpet sometimes penetrates the host shell almost completely (Fig. 3C). It may be possible to assume that *Sabia conica* excavates the host shell completely, then the host animal seals off the home depressions by depositing a shell blister from inside the shell. Such a shell repair is known in *Haliotis gigantea* and *Haliotis sieboldii*, in which many pits drilled by the pholadid *Navea subglobosa* are healed by a shell blister from inside the shell (Hamada & Okutani 1967).

Discussion

Limpet paleoecology. – Modern patellogastropod limpets are inhabitants of intertidal to shallow marine rocky shores throughout the world. Exceptions to this include two groups living in deep waters: *Pectinodonta* of the Acmaeidae and a species of the Lepetidae. The former dwells on and ingests water-logged wood (Wolf 1979), and the latter dwells on pebbles (Hickman 1983) and feeds on detritus (Branch 1985). To the best of our knowledge, however, pseudoplanktic patellogastropod limpets do not occur today.

Some pelagic organisms provide the substrate for pseudoplankton in modern seas. A whale's belly provides a substrate for barnacles (Baer 1971), a marine turtle's carapace a substrate for algae, barnacles, bryozoans, isopods, crabs, amphipods, hydrozoans, and bivalves (Frazier *et al.* 1984). No pseudoplanktic patellogastropod limpet has been recorded living on these marine vertebrates. Living nautili are another example of pelagic substrates for marine invertebrates. Landman *et al.* (1987) observed that live shells of *Nautilus* are utilized as substrate by such epibionts as bryozoans, serpulids, and foraminifers, but they did not record patellogastropod limpets there. Carlson *et al.* (1984), Ward *et al.* (1984) and Saunders & Ward (1987) demonstrated that living *Nautilus* stay in deep waters (150–500 m) during daytime, while they migrate to shallower depth at night. Below the upper layer of the euphotic zone, herbivorous patellogastropods may find it difficult to survive because plant growth is not abundant enough to maintain herbivorous organisms.

The line of evidence described above suggests that some patellogastropod limpets adopted a pseudoplanktic mode of

life by dwelling on swimming ammonites during the Cretaceous. Also, the deep penetration of the home depressions in the Cretaceous ammonites strongly suggests that the limpets were homing, and most probably territorial, species. The limited space on the host ammonites favored such an adaptation (Branch 1975). Although examples showing life associations of limpets and ammonites are extremely rare, the common occurrence of ammonites bearing numerous home depressions strongly suggests that this association was well established and widespread among large pachydiscid and puzosiid ammonites at least in the northwestern Pacific bioprovince during the Cretaceous.

Wignall & Simms (1990) classified pseudoplanktic species into three categories: obligate pseudoplankton, facultative pseudoplankton, and accidental pseudoplankton. Obligate pseudoplankton spend all of their adult stage as pseudoplankton by developing highly specialized structural and behavioral devices, thereby inhibiting them from returning to a benthic existence. Good examples are lepadomorph barnacles such as *Conchoderma* and *Coronula*. In contrast, facultative pseudoplankton are normally benthic epifaunal species potentially capable of settling successfully on floating objects but limited in number of settlements. Modern examples are common, including boring bryozoans, byssate, cemented and boring bivalves, balanomorphs, etc. Finally, accidental pseudoplankton include benthic forms that settle accidentally on the objects when they are floating near the bottom.

Separation of obligate and facultative pseudoplankton in fossil assemblages is a difficult task. However, Wignall & Simms (1990) provided some criteria for this distinction: obligate pseudoplankton differ from facultative pseudoplankton in being host-specific and nearly always associated with a floating object. They normally have thin-shelled skeletons, a lightweight body plan and commonly a pendant attachment strategy. The latter adaptive strategy is a particularly useful indication of obligate pseudoplankton, in which the load of heavy epifaunal species would cause floating objects to sink to the bottom, causing damage among the epifauna.

We suggest that the limpets responsible for the home depressions of the Cretaceous ammonites from Hokkaido and Sakhalin were obligate pseudoplankton rather than facultative pseudoplankton, even though they do not fulfill the criteria provided by Wignall & Simms (1990). Although it is not well known which limpets utilized which ammonites as substrate, the presence of home depressions exclusively in pachydiscid and puzosiid ammonites suggests that the limpets were host-specific and supports a mode of life as obligate pseudoplankton. The extremely rare occurrence of limpets in Cretaceous sediments from Hokkaido and Sakhalin also favors this lifestyle.

The rare occurrence of limpets on the host ammonites refutes an obligately pseudoplanktic mode of life for the limpets. The attachment mechanism of limpets by tenacity

of the sole of the foot differs greatly from the cementation and byssal attachment of other obligate pseudoplankton. The limpets might easily have been released from the ammonite shell when they died. During post-mortem drift of the ammonite near the sea surface, the limpets could still have survived on the shell. However, the empty ammonite shell might have rapidly become water-filled and sunk to the bottom through penetration of seawater into the air chambers (Chamberlain *et al.* 1981). The density of such a water-filled, empty ammonite shell might have been much less than that of thick-shelled mollusks. Therefore, they should be quite mobile and may be transported for a considerable distance along the sea floor in a manner similar to that of plant remains (Maeda 1987, 1991). During transportation along the sea floor, the limpets could have survived for a short time, in spite of unfavorable conditions, but might have been released from the ammonite shell by a weakening of their muscles and friction against the bottom sediments. This may be another reason why *in situ* associations of limpets and ammonites are so rare in the fossil records. Sparsity of *in situ* associations does not reject the possibility of a life as obligate pseudoplankton for these limpets.

The patellogastropod limpets found in the Cretaceous of Hokkaido and Sakhalin are characteristically small compared with common modern species found on rocky shores (Kase & Shigeta, unpublished). The size of the home depressions also indicates that the limpets were small. Some home depressions attain a length of 20 mm, but such large depressions are not so common; most being about 10 mm in length. Although the limpets are not as thin-shelled as modern species of similar size, their small shell size seems to represent a lightweight body plan. A modern limpet shell of 10 mm apertural length approximates to 100 mg in shell weight. Therefore, the total weight of several hundred limpets merely attains a few tens of grams, approximating that of a medium-sized oyster shell. Meischner (1968) concluded that a large *Ceratites semipartitus* (about 400 mm in diameter) encrusted by more than a hundred *Placunopsis ostracina* could swim normally in seawater. The total weight of the limpets seems to have been equivalent to or less than that of the *P. ostracina* shells on *C. semipartitus*. We suggest that the incrustation of many small limpets did not significantly prevent the swimming activity of the ammonite.

An intriguing problem to be clarified is when such a remarkable association began and why such an association is unknown between patellogastropod limpets and pelagic organisms today. The possible producers of the home depressions described in this paper include at least six species that represent at least two of the three major patellogastropod families of modern rocky shores (Kase & Shigeta, unpublished). This suggests that the adaptation did not originate in a particular clade but developed independently from different stocks within the Patellogastropoda. Giant ammonites are also known from the Jurassic and early Cretaceous (Stevens 1988), and the Patellogastropoda have existed since

the early Paleozoic (Yochelson 1988), but despite extensive search we have not yet found home depressions in Jurassic and early Cretaceous ammonites. It is tempting to assume that the epipelagic mode of life of patellogastropods appeared when some clades of ammonites began to adopt pelagic environments near the sea surface during the Late Cretaceous, and that it disappeared after the extinction of ammonites at the end of the Cretaceous owing to the lack of other suitable pelagic organisms as the substrates.

Implication for ammonite paleoecology. – There is general consensus that planispirally coiled ammonoids, like living *Nautilus*, were swimmers in the offshore shelf seas. However, their precise distribution patterns within the water column is not well understood. In order to infer their spatial and bathymetric distributions, a large number of studies have been made, mainly focusing on analyses of distribution patterns in local stratigraphic intervals (e.g., Scott 1940; Kauffman 1967; Obata & Futakami 1977; Tanabe *et al.* 1978; Tanabe 1979; Batt 1989) and on hydrodynamic and hydrostatic examinations of ammonoid shells (e.g., Chamberlain 1981; Saunders & Shapiro 1986). We have presented evidence that the patellogastropod limpets lived on the live shell of *Pachydiscus sahekii* and formed home depressions on it. We have also suggested that such a relationship was commonly established between ammonoids and limpets during the Cretaceous. If our interpretation is correct, then it provides a clue to the bathymetric distribution pattern of ammonoids.

With the exception of the deepwater *Pectinodonta* and some lepetids, patellogastropods feed on small pieces of macroalgae and/or detritus containing microalgae, such as diatoms and blue-green algae on the surface of hard substrates. Because the Cretaceous limpets are mostly referred to the extant genera or clades inhabiting intertidal marine systems, and because they lived on the shells of swimming ammonoids, they probably fed on algal films and/or diatom-containing detritus on the surface of the ammonoid shells. Growth of such vegetation is principally nourished by photosynthesis, and for this reason they would be confined to the upper layers of the ocean where there is an adequate light intensity. The depth of this layer may vary to some extent from place to place. Farrow & Clockie (1979) documented the depth limit of grazing patellogastropod limpets to be less than 20 m in the Firth of Clyde, Scotland. We speculate that the ammonoids were living at or periodically visited the near-surface seawater in the daytime, at least when the limpet attached to them.

One may assume that the infestation by limpets was dangerous for ammonites, because the deep excavation would have caused the phragmocone to implode, causing instant death (e.g., Kanie *et al.* 1980). The species of the Pachydiscidae and Puzosiidae documented here possess a body chamber that occupies about two-thirds of the last whorl. Because the umbilicus was almost free from limpet encrusta-

tion, the danger area was a relatively small portion of the total shell surface in these ammonites. Furthermore, the contact of the soft animal inside the body chamber and the movement of the tentacles could have prevented the attachment of limpets on the umbilical and phragmocone surfaces situated near the aperture (Landman *et al.* 1987).

The limpets preferred to live on large and giant ammonites and disregarded small and presumably rapidly growing specimens of the Pachydiscidae and Puzosiidae. Marine encrustation is generally more common on larger (older) individuals than in smaller (younger) ones. This is probably due to the reduced growth rate and larger surface area of older individuals. For example, *Sabia conica* (Schmacher) produces home depressions on large (50 mm in height) specimens of *Turbo argyrostoma* Linnaeus from shallow waters around Okinawa, southern Japan (personal observation by T.K.).

The absence of home depressions in ammonites other than pachydiscids and puzosiids is an intriguing but difficult problem to answer. One possible explanation is that the other ammonites, like living *Nautilus*, dwelled below the upper layer of the euphotic zone. The presence of a thick periostracum over the shell surface would also prevent encrusters from boring into the shell (Bottjer 1982). *Gaudryceras*, a common genus from the Upper Cretaceous of Hokkaido and Sakhalin, is a good example (Birkelund 1981): even if *Gaudryceras* species were shallow divers and were inhabited by limpets, the limpets would not have produced home depressions.

Acknowledgments. – We are greatly indebted to R.A. Hewitt for his critical review of the manuscript and language correction. Kase and Shigeta thank K.F. Sergeev, Yan Youn Bin, and the staff of the Institute of Marine Geology and Geophysics, Yuzhno-Sakhalinsk, for their enthusiastic support of our field program in Sakhalin, and also K. Kodama, H. Maeda, and T. Takeuchi for their help during the fieldwork. We further thank H. Maeda for discussion and identification of the ammonites and T. Miyauchi for providing material from Wakkanai. K. Muramoto (Mikasa City Museum) and T. Chitoku (Hobetsu Museum) allowed the senior author to examine the specimens under their care. This study was supported by Grant-in-Aid for Scientific Research (C) (no. 0240616) and International Scientific Research Program (Field Research) (nos. 02041062 and 05041068), the Ministry of Education, Science and Culture, Japan.

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