

First Record of the Northeastern Pacific Patellogastropod Genus *Acmaea* from the Miocene of Japan and Its Paleobiogeographic Implications

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Abstract. *Acmaea mitra* Rathke, 1833 is the sole species of the genus *Acmaea* and inhabits lower intertidal to subtidal rocky shores in the eastern side of the North Pacific Ocean from California to the Aleutian Islands. The discovery of *Acmaea mitra* from the Upper Miocene of central Japan represents the first fossil record of the species and genus in the western side of the North Pacific and the oldest record of the genus *Acmaea*. The Late Miocene specimens are definitely referred to *Acmaea mitra* on the basis of overall shell morphology and shell microstructure. The fossil records strongly suggest that *A. mitra* became regionally extinct in the western side of the North Pacific by the end of the Late Miocene. *A. mitra* represents a good additional example of northeastern Pacific restriction, an uncommon biogeographic distribution pattern of marine organisms in the middle-latitude North Pacific Ocean during the late Cenozoic. The causes of the regional extinction of *A. mitra* in the western side of the North Pacific remain uncertain.

INTRODUCTION

Both the western side of the North Pacific (WSNP) and the eastern side of the North Pacific (ESNP) have well-documented fossil records of Cenozoic marine mollusks that provide basic data for examining the historical development of marine biogeography in this bioprovince. An interesting distribution pattern seen in fossil and modern mollusks in this bioprovince is geographic restriction: taxa living on both sides of the North Pacific during the Neogene subsequently became restricted either to the WSNP (the northwestern Pacific restriction) or the ESNP (the northeastern Pacific restriction). Vermeij (1989) surveyed historical biogeographic patterns of cool-temperate mollusks during the Neogene and recognized 15 taxa that reflected the northwestern Pacific restriction. On the other hand, he recognized only a possible case of the northeastern Pacific restriction. Later, Amano (1998) and Kurihara (2007) added several taxa reflecting this pattern. In these studies, the causes of regional extinction in the WSNP have not been examined rigorously. In this study, we present another case of northeastern Pacific restriction recognized in the patellogastropod limpet genus *Acmaea*.

The genus *Acmaea* accommodates only the single species *Acmaea mitra* Rathke, 1833. Many species once allocated to *Acmaea* in the North Pacific have now been referred to other genera of Lottiidae (e.g.,

Lindberg, 1981, 1986; Sasaki, 1999), and those fossil species described as *Acmaea* were based solely on shell morphology, a highly convergent character among patellogastropods, so that they need further study for reliable generic allocation. *A. mitra* inhabits hard substrates from the low intertidal to a depth of 30 m along the ESNP and the eastern Aleutian Islands (Lindberg, 1981). The discovery of *A. mitra* from the Upper Miocene of Japan reported in this paper is twofold: (1) the fossil record of the genus *Acmaea* extends back to the Late Miocene, and (2) it shows regional extinction of *A. mitra* in the WSNP by the end of the Late Miocene.

The following institutional abbreviations are used: GMNH (Gunma Museum of Natural History, Tomioka, Gunma, Japan), NSM (National Museum of Nature and Science, Tokyo; formerly National Science Museum, Tokyo, Japan), SDSNH (San Diego Natural History Museum, California, U.S.A.) and UMUT (University Museum, the University of Tokyo, Japan).

STRATIGRAPHY AND ASSOCIATED FAUNA

The three *Acmaea* specimens described in this paper are found in the molluscan fossil collection of GMNH (PI2258–2260). They were collected at locality HN08 [= locality C of Kato (2001)], a right bank of the Usui River, Minakuchi, Annaka City, Gunma Prefecture

(36°19'11"N, 138°53'12"E) in a fossiliferous pebbly medium- to coarse-grained sandstone bed in the lower part of the Itahana Formation. The Itahana Formation is the uppermost regressive unit of the Miocene Annaka Group (Takahashi & Hayashi, 2004), and is stratigraphically divided into the lower marine and upper non-marine units (Oishi & Takahashi, 1990). Based on the radiometric and biochronologic analyses of the underlying Haraichi Formation, Takahashi & Hayashi (2004) estimated the Itahana Formation as early Late Miocene age (ca. 11.0 Ma).

The lower unit of the Itahana Formation contains well-preserved marine mollusks of about 80 species (Kurihara, 2000). This assemblage is typical of Shiobara-type molluscan fauna (Iwasaki, 1970; Chinzei, 1978). Late Miocene temperate shallow-water associations characteristic in central and northern Honshu, Japan (Chinzei, 1986). Mollusks associated with *Acmaea* occupied various shallow marine habitats and include species of the gastropods *Charonia*, *Chlorostoma* and *Kelletia* indicative of temperate, subtidal rocky shores.

SYSTEMATIC PALEONTOLOGY

Order PATELOGASTROPODA Lindberg,
1986

Superfamily PATELLOIDEA Rafinesque, 1815

Family LOTTIIDAE Gray, 1840

Genus *Acmaea* Eschscholtz in Rathke, 1833

Type species: *Acmaea mitra* Rathke, 1833, subsequent designation by Dall, 1871.

Discussion: Lindberg (1986) revised familial and generic level classification of species traditionally assigned to "Acmaeidae." Major changes in his classification are subdivision of "Acmaeidae" into Acmaeidae and Lottiidae and the restricted usage of Acmaeidae to a small monophyletic group that includes the monotypic, shallow-water genus *Acmaea* and the deep-water genus *Pectinodonta*. The members of this group share three pairs of uniform lateral teeth arranged in a posteriorly diverging inverted V-shape, identical ventral plate morphology, an absence of marginal teeth, similar gross anatomy and the same shell structure belonging to MacClintock's (1967) shell structure group 15 (Lindberg, 1986). However, Nakano & Ozawa (2004) recently demonstrated that *A. mitra* and *Niveotectura pallida* (Gould, 1859) constitute a monophyletic group on the basis of molecular data and similarity of radula, and also that *Pectinodonta* is clearly unrelated to *A. mitra*. Nakano & Ozawa (2007) classified *A. mitra* and *N. pallida* as a clade within Lottiidae and regarded

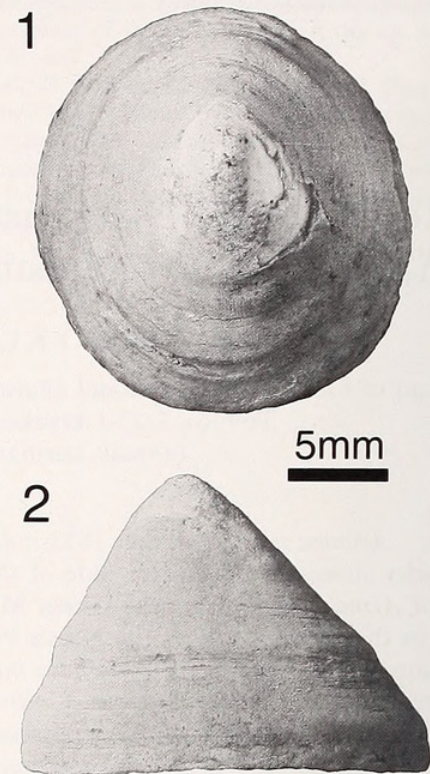


Figure 1. 1, 2, *Acmaea mitra* Rathke from the Upper Miocene Itahana Formation, apical and lateral views, GMNH PI2258, locality HN08, length, 21.0 mm, width, 19.0 mm, height, 15.3 mm.

Acmaeidae as a junior synonym of Lottiidae. The validity of this new systematic change needs to be confirmed by rigorous anatomical study because *A. mitra* and *N. pallida* belong to different shell structure groups and the anatomy of *A. mitra* has never been studied (Fuchigami & Sasaki, 2005). In this paper, we follow the classification proposed by Nakano & Ozawa (2007) for the familial assignment of *Acmaea*.

Acmaea mitra Rathke, 1833

(Figures 1, 2)

Acmaea mitra RATHKE IN ESCHSCHOLTZ, 1833, p. 18, pl. 23, fig. 4; ABBOTT, 1974, p. 29, fig. 145; LINDBERG, 1981, p. 63, fig. 64; LINDBERG & MARINCOVICH, 1986, fig. 2h; LINDBERG, 1988a, fig. 6d.

Description: Shell up to 21.0 mm in length, high conical, moderately thick, cap-shaped, with height about 3/4 of major apertural diameter. Apex in anterior 2/5, not curved anteriorly. Aperture subcircular, with length/width ratio 1.23. Anterior slope very weakly convex and other slopes almost straight. Surface devoid of any sculpture except for some concentric, knobby bulges indicative of growth halts, and concentric

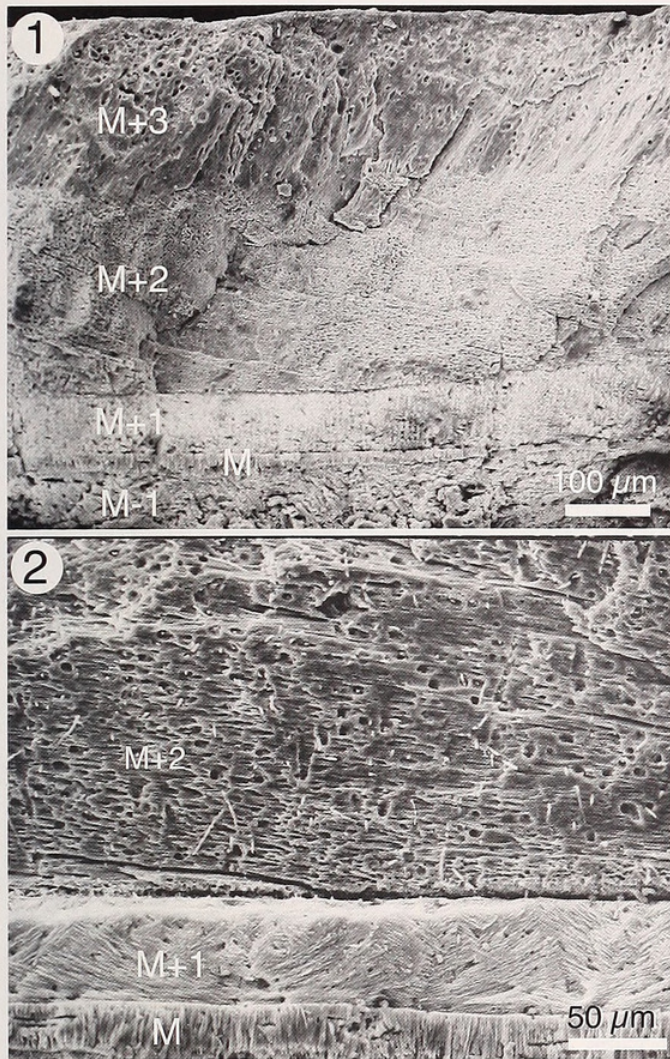


Figure 2. SEM micrographs of the shell walls in *Acmaea mitra* Rathke from the Itahana Formation, GMNH PI2259, locality HN08, etched by 1% HCl for 30 sec. 1, fractured section cut almost radially from the apex to shell margin showing the outermost complex prismatic layer (M+3), followed by the foliate layer (M+2), outer concentric crossed-lamellar layer (M+1), myostracum layer (M) and inner radial crossed-lamellar layer (M-1); 2, polished surface cut almost commarginally showing the foliate layer (M+2), followed by the outer concentric crossed-lamellar layer (M+1) and myostracum layer (M).

growth lamellae. Shell consists of five layers; outermost layer (M+3) of complex prismatic structure, followed by foliate layer (M+2), concentric crossed-lamellar layer (M+1), myostracum (M), radial crossed-lamellar layer (M-1).

Discussion: The suprageneric classification of living patellogastropods is primarily based on radular, gill and other anatomical characters, not preserved in fossil shells. However, shell morphology frequently exhibits convergence and parallelism, which makes the generic classification difficult. Analysis of shell microstructures

is a powerful method for classification of fossil species (e.g., Lindberg & Hickman, 1986; Lindberg, 1988a, b; Lindberg & Marincovich, 1988; Lindberg & Squires, 1990; Kase, 1994; Kase & Shigeta, 1996; Lindberg & Hedegaard, 1996). Patellogastropod shells consist of four to six successive layers including the myostracum, and each layer is composed of one of four basic microstructures (prismatic, foliated, crossed, and complex crossed) and also of either a microstructure different from adjacent layers, or, where the structure is the same, the two layer's major structural elements are oriented perpendicular to each other (MacClintock, 1967). This study demonstrated a general consistency between the classification based on soft anatomy and shell structure (MacClintock, 1967), who recognized 17 shell structure groups within the Patellogastropoda. Recently, Fuchigami & Sasaki (2005) added some deep-sea taxa recently accessible by submersible vessels and recognized 20 shell structure groups. They further emphasized the general, but not complete, consistency between the soft anatomy and shell structure. Among the 20 shell structure groups recognized by Fuchigami & Sasaki (2005), the specimens described here belong to their shell structure group P, diagnosed by an outermost irregular spherulitic prismatic layer, followed by a concentric regular foliated layer, concentrically arranged crossed-lamellar layer, the myostracum, and an inner radially arranged crossed-lamellar layer, clearly demonstrating allocation to the genus *Acmaea*.

The Late Miocene specimens from the Itahana Formation do not exhibit any difference in overall shell morphology from those of the modern specimens of *Acmaea mitra*. The periodic concentric and knobby bulges are seen both in the fossil and modern specimens. The largest specimen from the Itahana is slightly smaller than the common adult size of the modern specimens, but it appears not to be an important distinguishing character.

Acmaea sookensis Clark & Arnold (1923) from the Upper Oligocene Sooke Formation of Vancouver Island, British Columbia, Canada is the only fossil form that is sculptured only by concentric and periodic increments similar to those of the present species. This species, however, was reassigned to the genus *Patelloida* by Lindberg & Marincovich (1988) and therefore their resemblance is only superficial.

Distribution: *A. mitra* inhabits hard substrates of the low intertidal to a depth of 30 m along the Pacific side of North America from the warm-temperate sea of Isla San Martin, Baja California, Mexico (30°30'N) in the south to the cool-temperate sea of Umnak Island, eastern Aleutian Islands, Alaska (53°N) to the north (Lindberg, 1981; Vermeij et al., 1990). Recently, Golikov et al. (2001) recorded this species from the Sea of Okhotsk for the first time, but this record is

Table 1

Comparisons of shell and radular characters, habitat and feeding between *Acmaea mitra* and *Niveotectura pallida*.

	<i>Acmaea mitra</i>	<i>Niveotectura pallida</i>
Shell		
Color	White ¹	White ²
Maximum diameter	ca. 30 mm ¹	ca. 60 mm ²
Profile	High ¹	High ²
	Subcentral ¹	Subcentral ²
Structure group	Group P ³	Group C ³
Sculpture	Concentric growth lines ¹	Radial ribs and concentric growth lines ²
Radula formula	0-3-0-3-0 ¹	0-3-0-3-0 ⁴
Habitat		
Substratum	Hard bottom ¹	Hard bottom ²
Bathymetric range	Lower intertidal to 30 m ¹	Lower intertidal to 70 m ⁵
Geographic range	Aleutians to Baja California ¹	Sakhalin and Kuriles to central Japan, Korea, Maritime Territory ²
Food	Coralline algae ⁶	Coralline algae ⁷

References: ¹Lindberg (1981); ²Sasaki (2000); ³Fuchigami & Sasaki (2005); ⁴Sasaki (1998); ⁵Sasaki (2006); ⁶Padilla (1985); ⁷Fujita (1992).

based on the misidentification of *Erginus moskalevi* (Golikov and Kussakin, 1972) (B. Sirenko, pers. comm.). Therefore, the geographic distribution of this species is currently restricted to the eastern North Pacific.

PALEOBIOGEOGRAPHIC IMPLICATIONS

Acmaea mitra is a subtidal species widely distributed along the ESNP from California to the eastern Aleutian Islands (Lindberg, 1981). In contrast, the fossil record of the genus *Acmaea* is represented only by *A. mitra* and was considered restricted to the ESNP. *A. mitra* occurs in the Pleistocene deposits of California (Grant & Gale, 1931; Valentine, 1961; Marincovich, 1976), and its oldest form is a well-preserved specimen (SDSNH 24351) from the lower part of the San Diego Formation of California, which is dated as middle Pliocene (ca. 3.5 Ma; T. A. Deméré, pers. comm.). Putative oldest forms of *Acmaea* in the ESNP are *Acmaea clarki* Van Winkle (1918) from the Oligocene of Washington and *Acmaea?* cf. *A. mitra* in the faunal list of the Upper Miocene Towsley Formation, the Ventura Basin of California (Winterer & Durham, 1962), but their identification cannot be confirmed because both species have never been studied rigorously. Therefore, the Late Miocene specimens in Japan represent the oldest fossil record and the first occurrence in the WSNP of this unique genus and species, and the most parsimonious view is that *A. mitra* originated in the WSNP during the Late Miocene and later migrated to the ESNP.

On the other hand, there is no reported occurrence of *A. mitra* in the Pliocene and Pleistocene of Japan, in spite of the presence of many fossiliferous localities yielding patellogastropod limpets as stated below. This

strongly suggests that *A. mitra* in the WSNP might have become extinct by the end of the Miocene. Vermeij (1989) discussed the origins of various biogeographic patterns seen today among late Neogene cool-water marine mollusks in the North Pacific and North Atlantic. The distribution pattern of *A. mitra* can be categorized into his "northeastern Pacific restriction," where species previously with an amphipacific distribution have become restricted to the ESNP. Molluscan taxa showing this distribution pattern include the lucinid bivalve *Epilucina californica* (Conrad, 1837), the venerid bivalves *Humilaria* Grant & Gale, 1931 and *Compsomyx* Stewart, 1930, the myid bivalve *Platyodon* Conrad, 1837, and the muricid gastropod *Nucella shiwa* (Chinzei, 1961) (Amano, 1998; Kurihara, 2007). As far as we are aware, the following genera can be added to the northeastern Pacific restriction taxa: the turrid gastropod *Megasurcula* Casey, 1904 and the cymatiid gastropod *Mediargo* Terry, 1968. *Megasurcula* is still extant in the ESNP, but in the WSNP this genus became extinct by the end of the Late Miocene (Oyama, 1954). *Mediargo* became extinct by the Pliocene in the ESNP, whereas it persisted only until the end of the Late Miocene in the WSNP (Smith, 1970). From the biostratigraphic point of view, the majority of cool- and mild-temperate marine molluscan clades in Japan range from the Late Miocene to Pliocene, suggesting that only a few clades became extinct during the Late Miocene. Aside from *Acmaea*, *Megasurcula* and *Mediargo*, the only molluscan groups extinct during the Late Miocene are the pectinid genera *Nanaochlamys* Hatai & Masuda, 1953 and *Miyagipecten* Masuda, 1952 (Masuda, 1986; Matsubara, 1996).

Patterns of geographical restriction provide a clue for understanding the causes of extinction. If a species

persisted in one area while it disappeared in another, the possible causes of extinction can be attributed to the factors or events by which the two areas differ (Vermeij, 1989). Similarly, if a species disappeared in one area while its close relative persisted in the same area, the possible causes of extinction can be attributed to the factors by which the two species differ. *A. mitra*, now restricted to the ESNP, occupies the same habitat with, and is the closest relative to *N. pallida*, which is restricted to the WSNP (Nakano & Ozawa, 2004). Although these two species belong to different shell structure groups and have different external sculpture, they are almost identical in shell form and color, radular morphology, and feeding strategy (Table 1). Therefore, both *A. mitra* and *N. pallida* are regarded as ecological counterparts and may have responded similarly to changing environments in the geological past.

We undertook an extensive survey of the geographic and stratigraphic distributions of *N. pallida* in Japan (Figure 3). In this survey we treated *Niveotectura shigaramiensis* (Makiyama, 1927) as a junior synonym of *N. pallida*. Miocene specimens assignable to *N. pallida* are from the Ginzan Formation of Yamagata Prefecture (Nomura & Zinbo, 1937; NSM PM18322) and the Koshitomezawa Formation of Iwate Prefecture (NSM PM17596), both in northeast Honshu. The Ginzan Formation has been dated as the late Middle Miocene by planktonic foraminifera and diatom biostratigraphy (Sato, 1986), and the Koshitomezawa Formation as the Middle Miocene or the early Late Miocene based upon radiometric dating of its overlying unit (Suto & Ishii, 1987). The shell of the Ginzan specimen consists of a thick, outer complex prismatic layer and a thin, inner concentric crossed-lamellar layer that belongs to Fuchigami & Sasaki's (2005) Group P as does the modern *N. pallida*. The specimen described by Yokoyama (1925b) from Sakae in Nagano Prefecture, which Marinovich & Lindberg (1988) regarded as from the Upper Miocene Ogawa Formation, is now believed to be from the Lower Pliocene Shigarami Formation (e.g., Amano & Koike, 1993). Lindberg & Marinovich (1988) noted that the oldest example of *N. pallida* was from the Joban coalfield of northeast Honshu, Japan. Yokoyama (1925a) recorded *N. pallida* from three localities in the Joban coalfield, of which Yunami (Tozenji) is known as a classic (now destroyed) fossil locality of the lower Middle Miocene Kokozura Formation of the Takaku Group (Yanagisawa, 1996). If the occurrence of *N. pallida* from Yunami is correct, it represents the oldest form of this species. However, we cannot confirm Yokoyama's (1925a) record because the specimen of *N. pallida* from Yunami was not illustrated by him and has not been found in the UMUT collection. Therefore, we excluded the occurrence from Yunami in this discussion. The Pliocene and

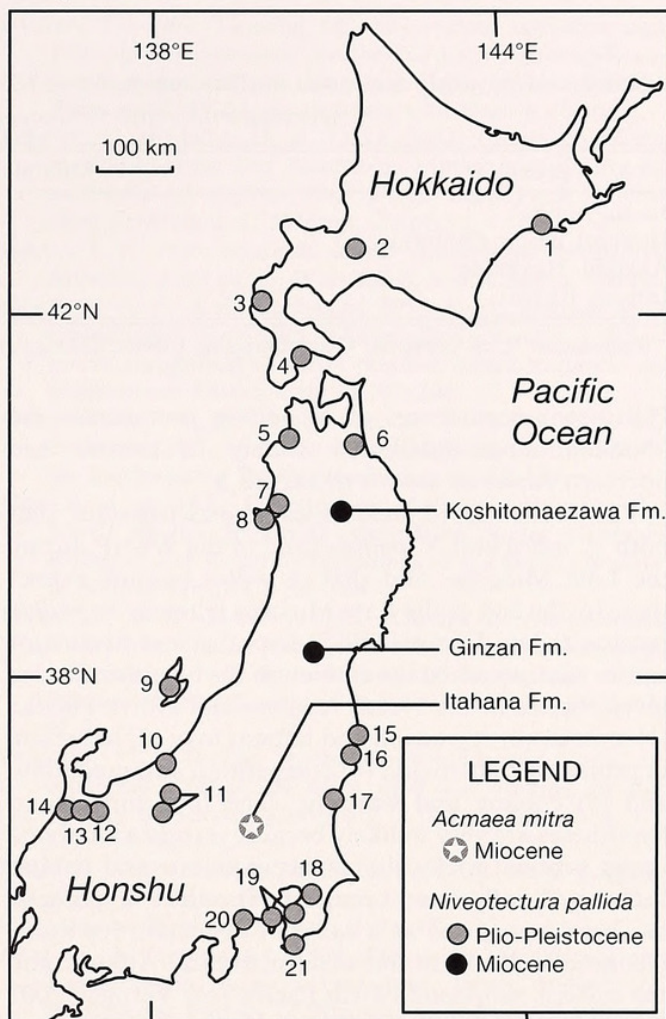


Figure 3. Geographic and stratigraphic distribution of fossil *Acmaea mitra* and *Niveotectura pallida* in Japan. Sources of fossil records of *Niveotectura pallida* are as follows: 1, Otanoshike Fm. (Akamatsu, 1988); 2, Otoebetsugawa Fm. (Akamatsu, 1987); 3, Setana Fm. (Suzuki, 2002, 2003); 4, Tomikawa Fm. (Sakagami et al., 1966); 5, Narusawa Fm. (Iwai, 1960); 6, Noheji Fm. (Iwai and Siobara, 1969); 7, Sasaoka Fm. (Nomura and Hatai, 1938); 8, Shibikawa and Katanishi Fms. (Ogasawara et al., 1986); 9, Sawane Fm. (Yokoyama, 1926; Omori, 1977); 10, Tanihama Fm. (Amano et al., 1987); 11, Shigarami Fm. (Yokoyama, 1925b; Makiyama, 1927; Nagamori, 1998); 12, Mita Fm. (Fujii and Shimizu, 1991); 13, Zukawa Fm. (Fujii and Shimizu, 1992); 14, Omma Fm. (Yokoyama, 1927; Kaseno and Matsuura, 1965; Matsuura, 1985); 15, Tomioka Fm. [= Dainenji Fm.] (Nemoto and O'Hara, 2005); 16, Taga Group [= Dainenji Fm.] (Nemoto and O'Hara, 1979); 17, Hitachi Fm. (Yokoyama, 1925a; Noda et al., 1995); 18, Shimosa Group (Yokoyama, 1922; O'Hara, 1982); 19, Kazusa Group (Yokoyama, 1920; Shikama and Masujima, 1969; Baba, 1990); 20, Ninomiya Group (Okumura, 1980); 21, Toyofusa Fm. (Baba, 1990). Records from the Kazusa and Shimosa Groups are too numerous, so some representative works are cited.

Table 2

Ranges of monthly mean sea surface temperature (SST) near the southern and northern distribution limits of *Acmaea mitra* and *Niveotectura pallida* in the North Pacific.

Locations	Monthly mean SST ranges (°C)	Remarks
Jueau, Alaska	2.2–10.6 ¹	Northern limit of <i>A. mitra</i>
Newport Beach, California	14.1–21.1 ¹	Southern limit of <i>A. mitra</i>
Akkeshi, Hokkaido	0.7–19.1 ²	Northern limit of <i>N. pallida</i>
Isozaki, Ibaraki	9.1–21.2 ²	Southern limit of <i>N. pallida</i>

References: ¹U.S. National Oceanographic Center (2006); ²Japan Oceanographic Data Center (2007).

Pleistocene occurrences of *N. pallida*, in contrast, are abundant and distributed widely in central and northern Japan as shown in Figure 3.

The fossil record mentioned above indicates that both *A. mitra* and *N. pallida* lived in the WSNP during the Late Miocene, and that *A. mitra* became extinct there by the end of the Late Miocene whereas *N. pallida* persists today. Vermeij (1989) hypothesized five major causes that governed the extinction for Neogene marine invertebrates in the North Atlantic and North Pacific: (1) anoxia; (2) regression and habitat loss; (3) reduction in primary productivity; (4) competition and predation; and (5) cooling and warming. The first and second hypotheses are very unlikely because *A. mitra* inhabited upper subtidal rocky shores where anoxia and habitat loss may hardly have occurred. The third hypothesis has been recognized as a cause of extinction for many Neogene mollusks in the western tropical Atlantic and the eastern temperate North Pacific (see Vermeij, 2001 for review). Vermeij (1989) found that large suspension-feeding bivalves in the ESNP became extinct more than those in the WSNP during the Pliocene, and suggested that reduction or interruption of primary productivity was a possible cause of this extinction in the ESNP. This hypothesis evidently contradicts the distribution pattern of *A. mitra*. The fourth hypothesis—predation and competition as agents of extinction—is well known to be possible causes of extinction for terrestrial organisms but no convincing example has been proposed for marine organisms (Vermeij, 1987, 1989, 2004).

The last hypothesis, especially cooling, seems to be the most plausible for the regional extinction of amphipacific marine biota in the WSNP, because the cool-temperate WSNP shows wider annual temperature fluctuations than the ESNP with extensive development of winter ice (Vermeij, 1978, 1989). However, this hypothesis is unlikely for the selective extinction of *A. mitra* from the WSNP because this species has wide temperature tolerances the same as *N. pallida* in modern seas. The available monthly mean sea surface temperature near the northern- and southernmost distribution areas of *A. mitra* and *N. pallida* are almost the same (*A. mitra*, 2.1–21.1°C; *N. pallida*, 0.7–21.2°C;

Table 2). If *A. mitra* in the WSNP had become extinct by cooling or warming, *N. pallida* would have also become extinct at the same time. In the WSNP, cooling and warming events occurred at the latest Miocene (ca. 6–5 Ma) and the Early Pliocene (ca. 5–4 Ma), respectively (e.g., Ogasawara, 1994; Suzuki & Akamatsu, 1994), but *N. pallida* survived even under these paleoclimatic conditions. G. J. Vermeij (pers. comm.) suggested that cooling is still a possible cause of the regional extinction of *A. mitra* from the WSNP if this species had a limited geographic range during the Late Miocene in the WSNP: such a small population(s) might have been affected by the environmental deterioration more severely than widely distributed species. However, the poor fossil record of *A. mitra* and *N. pallida* during the Late Miocene does not allow us to justify this possibility.

In summary, any major hypotheses previously proposed cannot interpret explicitly the development of the unique distribution pattern shown here in *A. mitra*. However, documentation and accumulation of such examples may contribute toward further understanding of the origin of various distribution patterns of marine organisms in the North Pacific.

Acknowledgments. We thank H. Nakajima (Annaka City) for donation of the fossil specimens of *A. mitra* to GMNH, Y. Takakuwa (GMNH) for the loan of the specimens in his care, T. A. Deméré (SDSNH) for providing photos and necessary information on the specimens in his care, and L. Marinovich, Jr. (California Academy of Sciences) and B. Sirenko (Zoological Institute of Russian Academy of Science) for sharing their knowledge of fossil and Recent limpets. We also thank G. J. Vermeij (University of California, Davis) for comments improving this paper. This study was supported by grants from the National Museum of Nature and Science, Tokyo and from the Ministry of Education, Science, Sports and Culture, Japan (18253007).

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Kurihara, Yukito and Kase, Tomoki. 2008. "First record of the northeastern Pacific patellogastropod genus *Acmaea* from the miocene of Japan and its paleobiogeographic implications." *The veliger* 50, 39–47.

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