ARCTIC
VOL. 41, NO. 3 (SEPTEMBER 1988) P. 167-172

New Species of Limpets from the Neogene of Alaska (Patellogastropoda: Mollusca)

DAVID R. LINDBERG[1] and LOUIE MARINCOVICH, JR.[2]

(Received 11 March 1987; accepted in revised form 4 February 1988)

ABSTRACT. Two new species of patellogastropod limpets from the Miocene-Pliocene of Alaska are described — *Patelloida gradatus* new species from the Unga Conglomerate Member of the Bear Lake Formation at Cape Aliaksin, Alaska Peninsula, southwestern Alaska, and *Niveotectura myrakeenae* new species from the Yakataga Formation in the northeastern Gulf of Alaska. A third species from the Narrow Cape Formation of Kodiak Island may be referrable to *Patelloida sookensis* Clark and Arnold, 1923, a species previously known only from Vancouver Island, Canada. These and other species of Patelloidinae dominated the northeastern Pacific patellogastropod fauna for over 60 m.y. The presence in Alaska of these three warm-water limpet species may be related to the middle Miocene warm-water event that is well documented elsewhere in the North Pacific. However, regional cooling during the late Neogene drove this predominantly tropical group from higher latitudes, leaving them poorly represented in the Holocene boreal fauna.

Key words: paleontology, historical biogeography, paleoecology, fossil gastropods, Miocene, Patellogastropoda, *Patelloida*, limpets

RÉSUMÉ. On décrit deux nouvelles espèces de patelles gastéropodes trouvées dans le miocène-pliocène de l'Alaska: la nouvelle espèce *Patelloida gradatus* venant du conglomérat de l'Unga, membre de la formation Bear Lake au cap Aliaksin dans la péninsule de l'Alaska, au sud-ouest de l'Alaska, et la nouvelle espèce *Niveotectura myrakeenae* venant de la formation Yakataga dans la partie nord-est du golfe de l'Alaska. Une troisième espèce de la formation Narrow Cape de l'île Kodiak peut se rattacher à la *Patelloida sookensis* Clark et Arnold, 1923, une espèce qui n'avait été trouvée auparavant que dans l'île de Vancouver au Canada. Ces espèces et d'autres appartenant aux Patelloidinae ont dominé la faune des patelles gastéropodes du Pacifique Nord-Est pendant 60 millions d'années. On peut corréler la présence en Alaska de ces trois espèces de patelles d'eaux tempérées au fait, bien documenté ailleurs dans le Pacifique Nord, de la présence d'eaux tempérées au milieu du miocène. Cependant, le refroidissement de la région au cours de la fin du néogène fit fuir des latitudes élevées ce groupe appartenant en grande partie à la faune tropicale, ce qui explique sa faible représentation dans la faune boréale de l'holocène.

Mots clés: paléontologie, biogéographie historique, paléoécologie, fossiles gastéropodes, miocène, patelles gastéropodes, *Patelloida*, patelles

Traduit pour le journal par Nésida Loyer.

РЕЗЮМЕ. Описаны два новых вида пателлогастроподных блюдечек из миоцена-плиоцена Аляски. Первый - Patelloida gradatus n. sp. из унгинского конгломеративного пласта бэрлэйкской свиты на мысе Аляксине, на Аляскиском полуострове в югозаподной Аляске, и второй - Niveotectura myrakeenae n. sp. из ягатагинской свиты на северовосточном берегу Аляскинского залива. Третий вид, из нэрроукэпской свиты на острове Кодяке, может быть отнесен к Patelloida sookensis Clark & Arnold, 1923. До ныне этот вид встречался только на канадском острове Ванкувере. Эти три вида, вместе с другими видами Patelloidinae, господствовали в фауне пателлогастропод северовосточного Тихого океана в течение 90 мил. лет. Присуствие этих тепловодных видов блюдечек в Аляске может быть связано со среднемиоценовым тепловодным событием, которое весьма хорошо документированно в других пунктах Северного Тихого океана. Однако, региональное похолождение во время позднего неогена вытеснило эту преимущественно тропическую группу с высоких широт, оставляя ее слабое представительство в голоценовой бореальной фауне Северного Тихого океана.

INTRODUCTION

Cap-shaped or limpet shells are common components of some Tertiary fossil assemblages. However, because of the simple shell morphology and the reliance on soft part characters for most limpet classification schemes, fossil limpets are often tentatively assigned to a Holocene regional family or genus and are not further studied. This practice has contributed to a fossil record for limpets that lacks a historical biogeographical perspective.

Patellogastropod limpets, which typically occur in high-energy, rocky, nearshore environments, are usually represented in fossil assemblages by few individuals and often reflect the vagaries of post-mortem transport into more benign environments, where they were preserved. However, if some of the original material of the patellogastropod shell is preserved, identification of the specimen need not be uncertain. The use of shell microstructure in patellogastropod systematics has already been demonstrated (MacClintock, 1963, 1967; Lindberg, 1976, 1978, 1979, 1981a; Lindberg and McLean, 1981; Lindberg and Hickman, 1986), and its use in recognizing distributions of patellogastropod taxa in space and time is invaluable for understanding the evolution of members of the order. For example, although many of the specimens discussed herein are Miocene in age (24-5 Ma), their shell microstructure characters are in excellent condition and are readily apparent in cross section (Fig. 1).

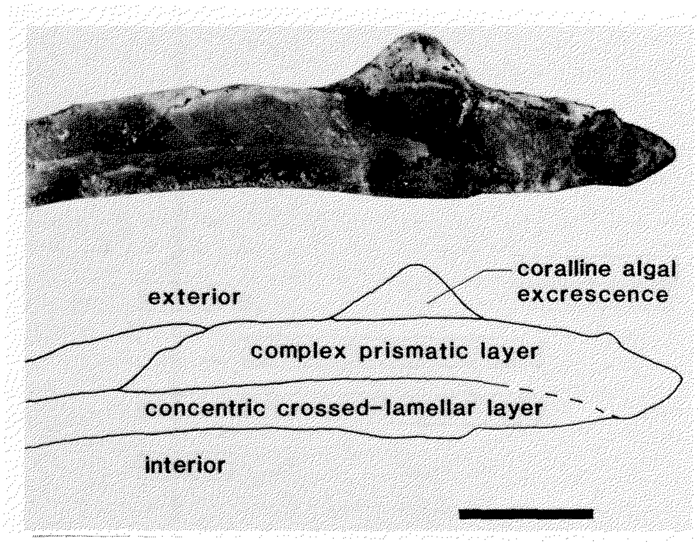

FIG. 1. Cross section through the shell of *Niveotectura myrakeenae* Lindberg and Marincovich, new species (holotype, USNM 414579). Scale bar = 2 mm.

[1]Museum of Paleontology, University of California, Berkeley, California 94720, U.S.A.
[2]U.S. Geological Survey, 345 Middlefield Road, Menlo Park, California 94025, U.S.A.

The three limpets from the Neogene of Alaska discussed here include two new species and are the first fossil members of the patellogastropod subfamily Patelloidinae known from Alaska. Members of this predominantly tropical clade were common in Tertiary limpet faunas along the west coast of North America (Vancouver to San Diego) for over 62 m.y. (Lindberg and Hickman, 1986). With the onset of regional cooling during the Neogene (Durham, 1950; Addicott, 1969), most *Patelloida* taxa were excluded from higher latitudes, and only two relict genera, *Erginus* Jefferys, 1877, and *Niveotectura* Habe, 1944, remain in the boreal Pacific Ocean today (Lindberg, 1983). *Patelloida gradatus* new species from the Alaska Peninsula and ?*Patelloida sookensis* (Clark and Arnold, 1923) from nearby Kodiak Island are members of a genus that was excluded from the region, while *Niveotectura myrakeenae* new species from the Bering Glacier region of southeast Alaska is the first fossil occurrence of this relict genus in Alaska.

The presence in Alaska of these three warm-water limpet species may be related to the middle Miocene warm-water event that is well documented elsewhere in the North Pacific. Evidence for this warm-water event in Alaska has recently been documented by the presence in the Bear Lake Formation of the warm-water gastropod *Turritella (Hataiella) sagai* Kotaka, 1951, previously known only from earliest middle Miocene (16-15 Ma old) faunas of Honshu, Japan (Marincovich and Kase, 1986). *Patelloida gradatus* new species, known from a Bear Lake outcrop inferred herein to be of middle Miocene age, is further evidence of a warm-water event that influenced the Bear Lake fauna. The less certain dating of the Miocene or Pliocene occurrence of *Niveotectura myrakeenae* new species in the Yakataga Formation makes it more debatable to ascribe the presence of this species to the earliest middle Miocene warm-water event. The same may be said for the presence of ?*Patelloida sookensis* in the Narrow Cape Formation of Kodiak Island. However, this formation on Kodiak Island is considered to be of early and middle Miocene age and contains several other warm-water molluscan genera (Allison, 1978), so the presence of ?*P. sookensis* there is possibly related to the same warm-water event that introduced *T.(H.) sagai* and *P. gradatus* into the Bear Lake fauna.

The higher classification used here follows Lindberg (1983, 1986a,b). The time scale is from Palmer (1983). Abbreviations in the text are as follows: CAS(S) — Stanford University Type Collection (now on permanent loan to Department of Invertebrates, California Academy of Sciences, San Francisco, California); LACM — Malacology Section, Natural History Museum of Los Angeles County, Los Angeles, California; UCMP — Museum of Paleontology, University of California, Berkeley, California; USGS — U.S. Geological Survey, Menlo Park, California; USNM — U.S. National Museum of Natural History, Washington, D.C.

SYSTEMATICS

Order Patellogastropoda Lindberg, 1986a
Family Lottiidae Gray, 1840
Subfamily Patelloidinae Chapman and Gabriel, 1923

Shell patelliform and composed of four layers. Outer surface of shell and interior margin complex prismatic. Next inner layer concentric crossed-lamellar, followed by myostracum, and radial crossed-lamellar layers.

Genus *Patelloida* Quoy and Gaimard, 1834
Patelloida Quoy and Gaimard, 1834:349

Shell of low to high profile; typically stout, with thick intermediate area composed of concentric crossed-lamellar layer. Sculpture variable, but radial components usually present and concentric growth line sculpture typically threadlike and pronounced in complex prismatic layer. Lateral teeth variable in size and shape, cusps complex; marginal teeth in two pairs (radular tooth formula: 2-3-0-3-2). Radular ventral plates complex; sutures, anterior processes and lateral extensions present in most taxa. Gut looping complex; two excretory organs, one on either side of the rectum; single gill present on left side of nuchal cavity. Pericardial sac triangular, positioned on anterior left side of visceral mass. Oral lappets present in some species. Mantle edge often thickened with large tentacle/gland complexes. Broadcast spawning.

Age. Cretaceous to Holocene.

Distribution. Past and present tropical and warm temperature seas in both hemispheres.

Remarks. Modern species of the monophyletic taxon (or clade) *Patelloida s.l. (sensu lato)* live in tropical and subtropical regions. As now defined, the group consists of at least two subclades (Lindberg and Vermeij, 1985). One subclade includes those species with low to medium shell profiles, strong radial ribs or many fine riblets, reduced third lateral radular teeth, and that occur on various substrata. The type species of the genus, *Patelloida rugosa* Quoy and Gaimard, 1834, is a member of this subclade; hence members of this subclade are assigned to *Patelloida s.s.* (*sensu stricto*). The other subclade, which has been called the *Patelloida profunda* group by Christiaens (1975) and Lindberg and Vermeij (1985), includes species with medium to high shell profiles, many ribs, equal-sized lateral radular teeth, and typically limited to calcareous substrata. Both groups have Tethyan distributions and are recognizable in the Cretaceous; the *Patelloida s.s.* group dates from the Late Cretaceous (Campanian, about 75 Ma) of California (MacClintock, 1967), and the *Patelloida profunda* group from the Early Cretaceous (Albian, about 100 Ma) of England (Lindberg, in press). These clades are defined by, and can be recognized in the fossil record by, shell morphology (Lindberg and Vermeij, 1985), shell structure (MacClintock, 1967; Lindberg, in press), and preserved features of soft part anatomy such as gill morphology (Hickman and Lindberg, 1985) and radular morphology (Akpan *et al.*, 1982).

Patelloida gradatus Lindberg and Marincovich, new species (Fig. 2a)

Shell medium sized (aperture diameter about 20 mm). Apex subcentral, positioned in anterior third of shell; profile high (length/height ratio approximately 1.5). All slopes convex, with strong concentric shell sculpture. Concentric sculpture consists of alternating opaque and translucent growth increments that are grouped into distinct, approximately 1-mm-wide bands around the shell. Aperture oval.

Holotype dimensions. Length 19.9 mm, width 16.7 mm, height 12.4 mm.

Type locality. ALASKA: USGS Cenozoic locality M8028, sea cliff on northwest shore of Cape Aliaksin, Alaska Peninsula; Port Moller (B-3) quadrangle; 55°30′10″N, 160°50′07″W (Fig. 3). Unga Conglomerate Member of the Bear Lake Formation. Collected by Louie Marincovich, Jr., August 1982.

Type material. USNM 414578, holotype.

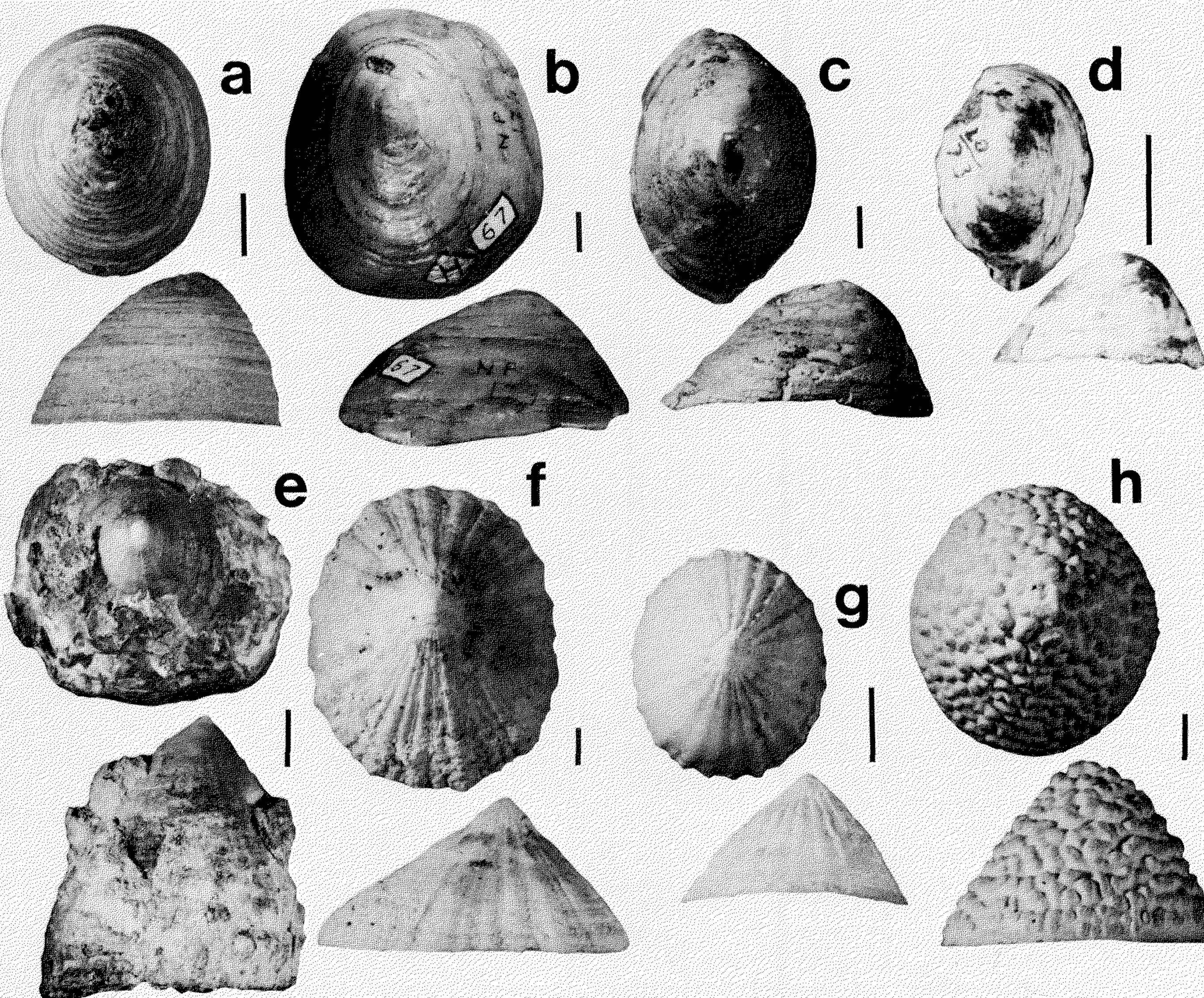

FIG. 2. Fossil and Holocene Patellogastropoda of the boreal Pacific Ocean. Scale bars = 5 mm. a) *Patelloida gradatus* Lindberg and Marincovich, new species (holotype, USNM 414578). Unga Conglomerate Member of the Bear Lake Formation, Alaska Peninsula, Alaska. b) *Patelloida sookensis* (Clark and Arnold, 1923) (holotype, CAS(S) 67). Sooke Formation, Vancouver Island, British Columbia, Canada. c) ?*Patelloida sookensis* (hypotype, USNM 414580). Narrow Cape Formation, Narrow Cape, Kodiak Island, Alaska. d) *Patelloida sookensis*? (hypotype, UCMP 35251). Quimper Sandstone, Discovery Bay, Jefferson County, Washington. e) *Niveotectura myrakeenae* Lindberg and Marincovich, new species (holotype, USNM 414579). Yakataga Formation, northeastern Gulf of Alaska, Alaska. f) *Niveotectura pallida* (Gould, 1859) (LACM Loc. No. 82-12). Mutsu Bay, Aomori Prefecture, Japan. g) *Niveotectura funiculata* (Carpenter, 1864) (LACM Loc. No. 60-24). Carmel, Monterey County, California. h) *Acmaea mitra* Rathke, 1833 (UCMP Loc. No. A-6601). Moss Beach, San Mateo County, California.

Distribution. Known only from the type locality.

Age. Middle Miocene. The Cape Aliaksin strata are overlain by a lava flow that yields a potassium-argon age of 10.4 Ma (F. Wilson, USGS, pers. comm. 1986) and contain molluscan species whose oldest inferred age in the Bear Lake Formation is earliest middle Miocene or 16-15 Ma (Marincovich and Kase, 1986; L. Marincovich, Jr., unpub. data).

Etymology. The specific name is derived from the Latin noun *gradus*, or step, and refers to the stepped arrangement of the growth phases of this species.

Discussion. The distinct bands of growth lines that encircle the shell distinguish *P. gradatus* from all other known Holocene and fossil species of *Patelloida*. The gross shell morphology of *P. gradatus* is similar to *Discurria insessa* (Hinds, 1842) and *Scurria orbignyi* (Dall, 1909). *Discurria insessa* ranges from Wrangell, southeastern Alaska, to southern Baja California, Mexico, and lives on the stipes of the brown alga *Egregia* spp. (Lindberg, 1981b). The curved rather than parallel lateral shell margins of *P. gradatus* argue against a similar habitat for the Miocene species. *Scurria orbignyi* occurs on rocky shores between Paita, Peru, and Talcahuano, Chile (Marincovich, 1973). The apertures of both *S. orbignyi* and *P. gradatus* are only slightly irregular and are not similar to the apertures of patellogastropods that home to specific sites on the substratum after foraging.

The wavy, grouped growth increments of *P. gradatus* are also present in *Patelloida sookensis* from the late Oligocene or early Miocene Sooke Formation of Vancouver Island, Canada (Fig.

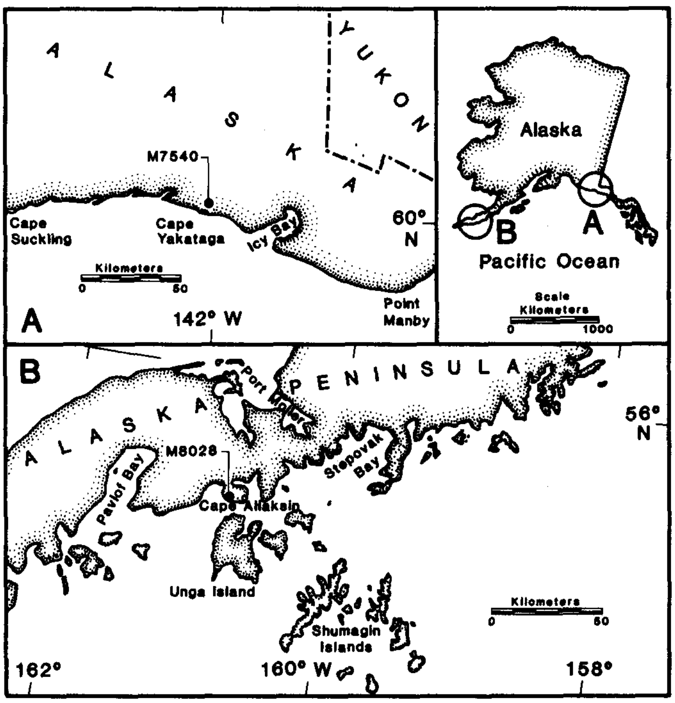

FIG. 3. Location of Alaskan fossil localities.

2b). However, unlike *P. gradatus, P. sookensis* has weak radial ribs. *Patelloida sookensis* may be represented in Alaskan strata of approximately late early to early middle Miocene age by a single, deformed limpet from the Narrow Cape Formation, Kodiak Island, Alaska (Fig. 2c).

Remarks. Patelloida gradatus, P. sookensis and a third specimen from the Quimper Sandstone of Washington (Durham, 1944) (Fig. 2d), which is probably not referrable to *P. sookensis*, all share similar gross shell morphology. They all have medium-high shell profiles, lack strong radial ribbing, have apexes positioned at or in the anterior third of the shell and, when preserved, have characteristically coarse, wavy growth lines. Although the gross shell morphology of these species is not known in Holocene species of *Patelloida*, it was present in Oligocene and Miocene species of the northeastern Pacific. Whether these extinct species are all members of a third subclade within the *Patelloida* cannot be determined from the available data.

Genus *Niveotectura* Habe, 1944

Niveotectura Habe, 1944:185

Shell of high profile, large (to 50 mm long), white; sculpture of strong radial ribs. Pericardial sac triangular, positioned on anterior left side of visceral mass; single gill present on left side of nuchal cavity. Radular tooth formula: 0-3-0-3-0.

Remarks. Niveotectura appears to be intermediate in shell form and anatomy between *Patelloida* and *Erginus*. *Niveotectura* and *Patelloida* species have similar anatomical organizations (radulae excepted) and exterior shell sculpture. *Niveotectura* and *Erginus* species typically have white shells with medium to high profiles, lack marginal radular teeth, have similar radular basal plate morphologies, equal-sized lateral teeth, and occur on calcareous substrates in subtidal habitats; all are characters shared by subtidal Patellogastropoda. *Niveotectura* and *Erginus* species are restricted to the Northern Hemisphere and reach their greatest diversity in the boreal Pacific Ocean; *Patelloida* species occur worldwide in tropical and warm-temperate seas. Members of the genus *Erginus* differ from *Niveotectura* species by having markedly different anatomical organizations and by brooding their young (Lindberg, 1983).

Like the *Patelloida profunda* group discussed above, *Niveotectura* is primarily subtidal and restricted to calcareous substrata. However, these similarities appear to result from convergence rather than from common ancestry. One difference between these two groups is found in the relative thicknesses of the outer two shell layers. In the genus *Niveotectura* the outer complex prismatic layer is equal to or thicker than the inner concentric crossed-lamellar layer (Fig. 1); in members of the *Patelloida profunda* group the concentric crossed-lamellar layer is substantially thicker than the complex prismatic layer.

Almost every known patellogastropod clade has subtidal taxa that have converged on common shell and radular morphologies (McLean, 1966; Lindberg and McLean, 1981; Lindberg, 1983). The genus *Niveotectura* probably represents this expansion into the subtidal habitat by early Neogene North Pacific *Patelloida s.s.* species. *Erginus* was either subsequently derived from *Niveotectura* or represents an earlier or later second invasion of the North Pacific Ocean subtidal habitat by a *Patelloida s.s.* species (Fig. 4).

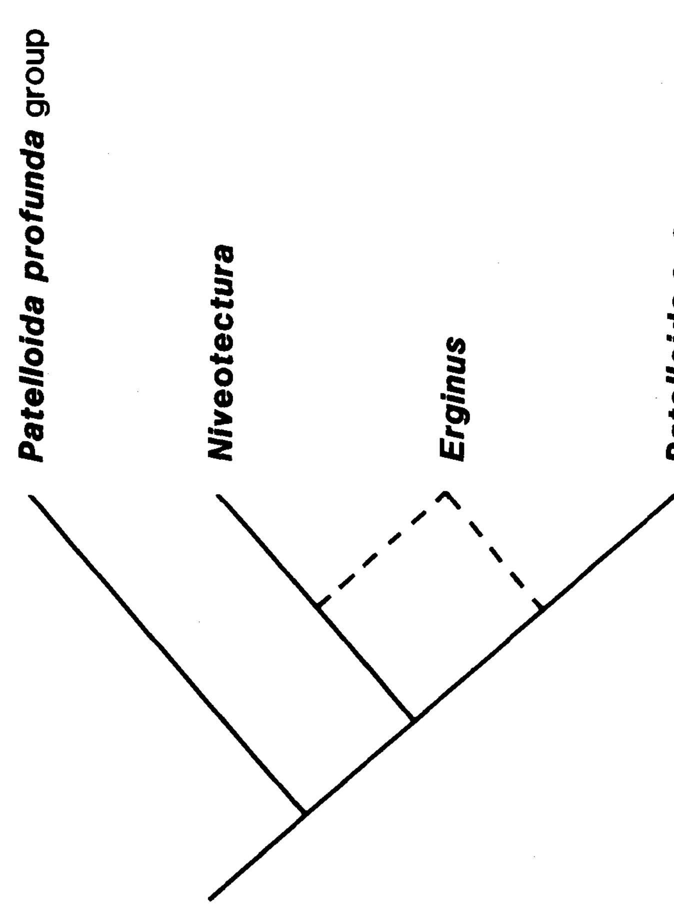

FIG. 4. Hypothesized relationships of subclades within the patellogastropod subfamily Patelloidinae Chapman and Gabriel, 1923. Each branch represents a monophyletic taxon.

Niveotectura myrakeenae Lindberg and Marincovich, new species (Fig. 2e)

Shell medium sized (aperture diameter about 25 mm). Apex central; profile high (length/height ratio approximately 1.0). All slopes straight or slightly convex, with both radial and concentric shell sculpture. Radial sculpture consists of approximately 28 primary and secondary radial riblets; concentric sculpture of weaker concentric cords that cross the radial riblets and produce pustules at the intersections. Interspaces between ribs about three times as wide as ribs. Concentric growth lines distinct. Most of the exterior of the shell is covered by a crustose coralline alga that forms excrescences.

Holotype dimensions. Length 21.3 mm, width 25.7 mm, height 24.5 mm. Shell has been secondarily deformed by compression in the anterio-posterior axis.

Type locality. ALASKA:USGS Cenozoic locality M7540, on slope south of and below 1139 m (3737 ft) benchmark of unnamed peak that is immediately east of White River Glacier; northeastern Gulf of Alaska; Bering Glacier (A-3) quadrangle; about 60°04′43″N, 142°00′00″W (Fig. 3). 1669 ±6 m(5475 ±20 ft) above base of Yakataga Formation. Coll. John Armentrout, 1974.

Type material. USNM 414579, holotype.

Distribution. Known only from type locality.

Age. Mioicene or Pliocene.

Etymology. We are pleased to name this species in honor of the late Dr. A. Myra Keen, of Stanford University, an exemplary paleontologist and malacologist, who taught the importance of interfacing the present with the past.

Discussion. Niveotectura myrakeenae differs from the Holocene northwestern Pacific *Niveotectura pallida* (Gould, 1859) (Fig. 2f) by having fewer and narrower radial ribs and much wider interspaces between ribs. In *N. pallida* the ribs are broad, almost flat topped in profile, and the width of the interspaces between ribs is equal to or slightly less than the width of the ribs. The Holocene northeastern Pacific species *Niveotectura funiculata* (Carpenter, 1864) (Fig. 2g) differs from *N. myrakeenae* by having more numerous ribs and narrower interspaces between ribs. The individual ribs on the shell of *N. funiculata* are not as broad as those on *N. pallida*, but they are substantially broader than those on *N. myrakeenae*. Like *N. pallida* and unlike *N. myrakeenae, N. funiculata* has interspaces between ribs that are equal to or less than rib width. *Niveotectura myrakeenae* differs from both of the Holocene *Niveotectura* species by having pustules where radial and concentric sculptures cross on the exterior surface of the shell and a substantially higher shell profile.

Niveotectura myrakeenae differs from other Alaskan Tertiary Patelloidinae discussed herein by having moderately strong radial ribbing and by lacking the distinctly convex shell slopes that characterize the other species. Instead, the slopes of the shell are straight or only slightly convex, which gives the shell a classical conical shape.

Remarks. The presence of encrusting calcareous algae with elaborate excrescences on the holotype suggests minimal aerial exposure for this species. Holocene subtidal species are commonly encrusted with coralline algae (McLean, 1966; Lindberg, 1981b), and elaborate patterns of algal excrescences are not uncommon on some living individuals (Fig. 2h). The presence of a coralline alga with developed excrescences on the shell of *N. myrakeenae* argues for a tide pool or subtidal habitat during the life of this individual; both Holocene members of the genus *Niveotectura* are predominantly subtidal species.

Based on present correlations, *N. myrakeenae* and *N. pallida* were contemporary species on either side of the North Pacific Ocean during the early Neogene. The oldest specimens referrable to *N. pallida* are reported from the "Shirado beds" of the Joban coal field of northeastern Honshu, Japan, by Yokoyama (1925b). These strata are now referred to the Nakayama Formation of the Shirado Group (Kamada, 1962) and are of earliest middle Miocene age (equivalent to planktonic foraminiferal zones N8 or N9; S. Ohara, pers. comm. 1986). A Late Miocene specimen is known from Sakae (Yokoyama, 1925a) (Ogawa Formation [Makiyama, 1958]), and Pliocene specimens have been reported from the Shigarami Formation (Yokoyama, 1925a), the Omma Formation (Kaseno and Matsuura, 1965), the Sawane Formation (Yokoyama, 1926), and the Imaizumi Formation (Shikama and Masujima, 1969). Pleistocene specimens are known from the Koshiba Formation of Yokohama (Yokoyama, 1920).

Niveotectura myrakeenae could be ancestral to *N. funiculata*, which first appears in the lower Pleistocene Lomita Marl Member of the San Pedro Formation in San Pedro, southern California (Woodring *et al.*, 1946).

ACKNOWLEDGEMENTS

We thank S. Ohara, of Chiba University, Chiba, and T. Kase, of the National Science Museum, Tokyo, Japan, for discussions of the modern ages of the older literature records of Japanese fossil limpets; R. Allison, University of Alaska, T. Kase, and S. Stone (USGS) for reviewing the manuscript; G. Shkurkin (UCMP) for preparing the Russian abstract; H. Schorn (UCMP) for photographing the specimens illustrated in Figure 2; and M. Krup (UCMP) for preparing Figures 1 and 3.

REFERENCES

ADDICOTT, W.O. 1969. Tertiary climatic change in the marginal northeastern Pacific Ocean. Science 165:583-586.

AKPAN, E.B., FARROW, G.E., and MORRIS, N. 1982. Limpet grazing on Cretaceous algal-bored ammonites. Palaeontology 25(2):361-367.

ALLISON, R.C. 1978. Late Oligocene through Pleistocene molluscan faunas in the Gulf of Alaska region. Veliger 21(2):171-188.

CARPENTER, P.P. 1864. Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Report of the British Association for the Advancement of Science for 1863:517-686.

CHAPMAN, F., and GABRIEL, C.J. 1923. A revision and description of the Australian Tertiary Patellidae, Patelloididae, Cocculinidae, and Fissurellidae. Proceedings of the Royal Society of Victoria 36:22-40.

CHRISTIAENS, J. 1975. Revision provisoire des mollusques marins recents de la famille des Acmaeidae (seconde partie). Informations de la Société belge de Malacologie 4:91-116.

CLARK, B.L., and ARNOLD, R. 1923. Fauna of the Sooke Formation, Vancouver Island, with description of a new coral by T.W. Vaughan. University of California Publications, Bulletin of the Department of Geological Sciences 14(5):123-234.

DALL, W.H. 1909. Report on a collection of shells from Peru, with a summary of the littoral marine Mollusca of the Peruvian zoological province. Proceedings of the United States National Museum 37(1704):147-294.

DURHAM, J.W. 1944. Megafaunal zones of the Oligocene of northwestern Washington. University of California Publications, Bulletin of the Department of Geological Sciences 27:101-212.

———. 1950. Cenozoic marine climates of the Pacific coast. Geological Society of America Bulletin 61:1243-1246.

GOULD, A.A. 1859. Descriptions of shells collected in the North Pacific Exploring Expedition under Captains Ringgold and Rogers. Proceedings of the Boston Society of Natural History 7:161-166.

GRAY, J.E. 1840. Synopsis of the contents of the British Museum. 42nd ed. London: G. Woodfall and Son. 370 p.

HABE, T. 1944. On the Japanese Lottiidae (= Acmaeidae). Japanese Journal of Malacology (Venus) 13:171-187.
HICKMAN, C.S., and LINDBERG, D.R. 1985. Perspectives on Molluscan Phylogeny. In: Broadhead, T.W., ed. Mollusks. Notes for a Short Course. University of Tennessee, Department of Geological Sciences, Studies in Geology 13:13-16.
HINDS, R.A. 1842. Descriptions of new shells. Annals and Magazine of Natural History 10:81-84.
JEFFERYS, J.G. 1877. New and peculiar Mollusca of the Patellidae and other families of Gastropoda procured in the 'Valorous' expedition. Annals and Magazine of Natural History 19:231-243.
KAMADA, Y. 1962. Tertiary Mollusca from the Joban coal-field. Paleontological Society of Japan, Special Papers, No. 8. 187 p.
KASENO, Y., and MATSUURA, N. 1965. Pliocene shells from the Omma Formation around Kanazawa City, Japan. Kanazawa University, Science Reports 10(1):27-62.
LINDBERG, D.R. 1976. Cenozoic phylogeny and zoogeography of the Acmaeidae of the eastern Pacific. Annual Report of the Western Society of Malacologists 9:15-16.
——. 1978. On the taxonomic affinities of *Collisella edmitchelli*, a late Pleistocene limpet from San Nicolas Island, California. Bulletin of the Southern California Academy of Sciences 77:65-70.
——. 1979. *Problacmaea moskalevi* Golikov and Kussakin, a new addition to the eastern Pacific limpet fauna (Archaeogastropoda: Acmaeidae). The Veliger 22(1):57-60.
——. 1981a. Rhodopetalinae, a new subfamily of Acmaeidae from the boreal Pacific: anatomy and systematics. Malacologia 20:291-305.
——. 1981b. Acmaeidae. Pacific Grove, California: Boxwood Press. 122 p.
——. 1983. Anatomy, systematics, and evolution of brooding acmaeid limpets. Unpubl. Ph.D. thesis, Biology Board, University of California, Santa Cruz, California. 277 p.
——. 1986a. Radular evolution in the Patellogastropoda. American Malacological Bulletin 4:115.
——. 1986b. Name changes in the "Acmaeidae." Veliger 29:142-148.
——. In press. The Patellogastropoda. In: Ponder, W.F., ed. Prosobranch Phylogeny. Proceedings of the 9th International Malacological Congress, Edinburgh, 1986. Malacological Review, Supplement.
—— and HICKMAN, C.S. 1986. A new anomalous giant limpet from the Oregon Eocene (Mollusca: Patellida). Journal of Paleontology 60:661-668.
LINDBERG, D.R., and McLEAN, J.H. 1981. Tropical eastern Pacific limpets of the family Acmaeidae (Mollusca: Archaeogastropoda): generic criteria and descriptions of six new species from the mainland and the Galápagos Islands. Proceedings of the California Academy of Sciences 42:323-339.
LINDBERG, D.R., and VERMEIJ, C.J. 1985. *Patelloida chamorrorum* spec. nov.: a new member of the Tethyan *Patelloida profunda* group (Gastropoda: Acmaeidae). The Veliger 27:411-417.
MACCLINTOCK, C. 1963. Reclassification of gastropod *Proscutum* Fischer based on muscle scars and shell structure. Journal of Paleontology 37:141-156.
——. 1967. Shell structure of patelloid and bellerophontoid gastropods (Mollusca). Bulletin Peabody Museum of Natural History, Yale University 22:1-140.
MAKIYAMA, J. 1958. Matajiro Yokoyama's Tertiary fossils from various localities in Japan. Part 2. Palaeontological Society of Japan, Special Paper, No. 4. 6 p., 57 plates.
MARINCOVICH, L., Jr. 1973. Intertidal mollusks of Iquique, Chile. Natural History Museum Los Angeles County Science Bulletin 16:1-49.
—— and KASE, T. 1986. An occurrence of *Turritella (Hataiella) sagai* in Alaska: implications for the age of the Bear Lake Formation. Bulletin of the National Science Museum, Tokyo, Series C, 12(2):61-66.
McLEAN, J.H. 1966. West American prosobranch gastropods: superfamilies Patellacea, Pleurotomariacea, and Fissurellacea. Unpubl. Ph.D. thesis, Department of Zoology, Stanford University, Stanford, California. 262 p.
PALMER, A.R. 1983. The Decade of North American Geology 1983 Geologic Time Scale. Geology 11(9):503-504.
QUOY, J.R.C., and GAIMARD, J.P. 1834. Voyage de découvertes de l'Astrolabe, exécuté par ordre du Roi, pendant les années 1826-29, sous le commandement de M.J. Dumond d'Urville. Zoologie, Mollusca, Vol. 3. Paris. 712 p.
SHIKAMA, T., and MASUJIMA, A. 1969. Quantitative studies of the molluscan assemblages in the Ikego-Nojima formations. Yokohama National University, Science Reports, Section 2, 15:61-94.
WOODRING, W.P., BRAMLETTE, M.N., and KEW, W.S.W. 1946. Geology and paleontology of Palos Hills, California. U.S. Geological Survey Professional Paper 207. 145 p.
YOKOYAMA, M. 1920. Fossils from the Miura Peninsula and its intermediate north. Journal of the College of Science, Imperial University of Tokyo 39(6):1-198.
——. 1925a. Tertiary Mollusaca from Shinano and Echigo. Journal of the Faculty of Science, Imperial University of Tokyo, Section 2, 1(1):1-23.
——. 1925b. Molluscan remains from the middle part of the Jô-Ban coal-field. Journal of the College of Science, Imperial University of Tokyo 45(7):1-23.
——. 1926. Fossil shells from Sado. Journal of the Faculty of Science, Imperial University, Tokyo, Section 2, 1(8):249-312.