THE VELIGER

The Veliger 38(1):47-53 (January 3, 1995)

An Extant Species of *Leptochiton* (Mollusca: Polyplacophora) in Eocene and Oligocene Cold-Seep Limestones, Olympic Peninsula, Washington

by

RICHARD L. SQUIRES

Department of Geological Sciences, California State University,
Northridge, California 91330, USA

AND

JAMES L. GOEDERT

15207 84th Ave. Ct. NW, Gig Harbor, Washington 98329, and
Museum Associate, Section of Vertebrate Paleontology,
Natural History Museum of Los Angeles County, 900 Exposition Boulevard,
Los Angeles, California 90007, USA

Abstract. Fossils of the chiton, *Leptochiton* (*Leptochiton*) *alveolus* (Lovén, 1846), are present in three localized cold-seep limestones on the Olympic Peninsula, Washington. One limestone is in the upper middle to upper Eocene Humptulips Formation near Humptulips; the second is in the lower Oligocene part of the Makah Formation at Shipwreck Point; and the third is in the lower upper Oligocene part of the Lincoln Creek Formation at Canyon River. The deep-sea limestones at the three localities contain dense concentrations of megabenthos that lived in association with subduction-related cold-methane seeps. Most of the chiton remains are disarticulated intermediate plates, but a well-preserved, fully articulated specimen that shows the dorsal surface was found at the Canyon River locality.

Leptochiton (*L.*) *alveolus* was previously known only as a living species with cosmopolitan distribution in deep waters. The presence of this species in the Eocene and Oligocene of Washington represents the earliest unquestionable record of this genus and the first report of an identified species of chiton from ancient cold-seeps.

INTRODUCTION

Chitons require hard substrate and commonly find it on wave-swept rocky coasts, a habitat poorly represented in the pre-Pleistocene rock record. Moreover, chitons from this high-energy environment seldom survive taphonomic processes intact. Chitons can live in deep water, and some 20 modern species are known to be endemic in depths between 200 and 6000 m (Ferreira, 1980). There is little information available on the types of substrate that deep-water chitons prefer, but most probably live on rocks. Wu & Okutani (1984) reported deep-sea chitons living on fragments of pumice probably exposed on a muddy floor. Wolff (1979) and Sirenko (1988) reported that a few species of modern deep-water chitons live on sunken fragments of wood. Saito & Okutani (1990) reported two species of chitons living attached to rocks at a deep-sea hydrothermal vent site in the Okinawa Trough and Kulm & Suess (1990) found chitons living on carbonate edifices, less than 1 m high, that formed around modern cold-seeps on uplifted submarine banks along the outer continental shelf-upper slope of Oregon.

Although the preservation potential for deep-water chitons seems to be good, reports of these chitons in the rock record are very rare. Only recently, Goedert & Campbell (1995) reported the first fossil chiton found associated with a deep-water, cold-seep limestone. This localized limestone is in the lower Oligocene part of the Makah Formation at Shipwreck Point, northern Olympic Peninsula, Washington. Recent collecting in other deep-water, Eocene and Oligocene rocks in Washington has yielded two additional localized, cold-seep limestone localities for this same chiton species. At all three localities, specimens of the chiton are associated with dense accumulations of worm tubes and bivalves that lived around subduction-zone related cold-methane seeps on the ocean floor. Evidently, the worm tubes and/or bivalves provided the necessary hard substrate for the chitons. At two of the localities, only disarticulated valves of the chiton were found, but at one locality, articulated specimens were found. One of these articulated specimens is remarkable because it shows the dorsal surface of all eight valves. Burial had to have been very rapid. It is the purpose of this paper to report that this chiton is the extant *Leptochiton* (*Leptochiton*) *alveolus* (Lovén, 1846). Goedert & Campbell (1995) identified this chiton as *Leptochiton* (?) sp.

The long geologic range of *L.* (*L.*) *alveolus* from Eocene to Recent should not be considered unusual. For example, the eastern Pacific, extant naticid gastropods *Neverita* (*Glossaulax*) *reclusiana* (Deshayes, 1839) and *Sinum scopulosum* (Conrad, 1849) have geologic records that extend back to the middle Eocene and early Oligocene, respectively (Marincovich, 1977). In addition, the eastern Pacific, extant thraciid bivalve *Thracia* (*Cetothrax*) *condoni* Dall, 1909, and the extant thyasirid bivalve *Conchocele disjuncta* Gabb, 1866, have geologic records that extend back to the Oligocene (Coan, 1990; Bernard, 1983).

Abbreviations used for catalog and/or locality numbers are: LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; LACM, Natural History Museum of Los Angeles County, Malacology Section.

STRATIGRAPHIC DISTRIBUTION AND GEOLOGIC AGES

Fragments of two valves of *Leptochiton* (*L.*) *alveolus* were found at LACMIP loc. 12385 in a localized limestone in the Humptulips Formation on the East Fork of the Humptulips River, southern Olympic Peninsula, Washington (Figure 1). The limestone was deposited in a subduction zone where subsurface methane-rich waters discharged onto the ocean floor (Goedert & Squires, 1990). The limestone is 15 m thick, 30 m long, and 15 m wide. It is highly

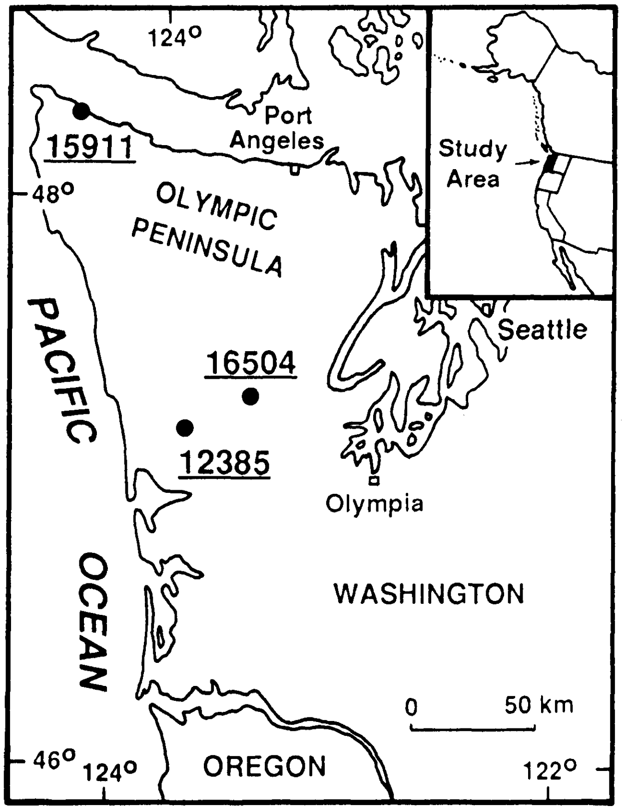


Figure 1

Index map to localities of fossil *Leptochiton* (*L.*) *alveolus*.

fossiliferous with dense concentrations of vestimentiferan? and serpulid worm tubes and numerous articulated specimens of the bivalves *Thyasira* (*Conchocele*) *folgeri* Wagner & Schilling, 1923, and *Modiolus* (*Modiolus*) *willapaensis* Squires & Goedert, 1991. Additional fossils are fissurellid?, patelliform, turbinid?, and naticid gastropods; other bivalves; a scaphopod; and decapod parts. The thyasirids and turbinids show growth series, and some of the vestimentiferan? worm tubes are vertically oriented (Goedert & Squires, 1990). Rau (1986) reported the age of the Humptulips Formation to range through much of the middle Eocene and into the late Eocene age. The exact age of the rocks at LACMIP loc. 12385 is not known, and until calcareous nannofossil studies are made on the surrounding siltstone, only a broad age range of late middle Eocene to late Eocene can be assigned (Goedert & Squires, 1990; Squires & Goedert, 1991) (Figure 2).

Two articulated specimens, as well as seven separate valves and two clusters of several valves, of *Leptochiton* (*L.*) *alveolus* were found at LACMIP loc. 16504 in a small limestone block in the upper part of the Lincoln Creek Formation at Canyon River, in the Satsop River area, southern Olympic Peninsula, Washington (Figure 1). Prothero & Armentrout (1985) reported that the Lincoln Creek Formation in the Canyon River area is late Eocene

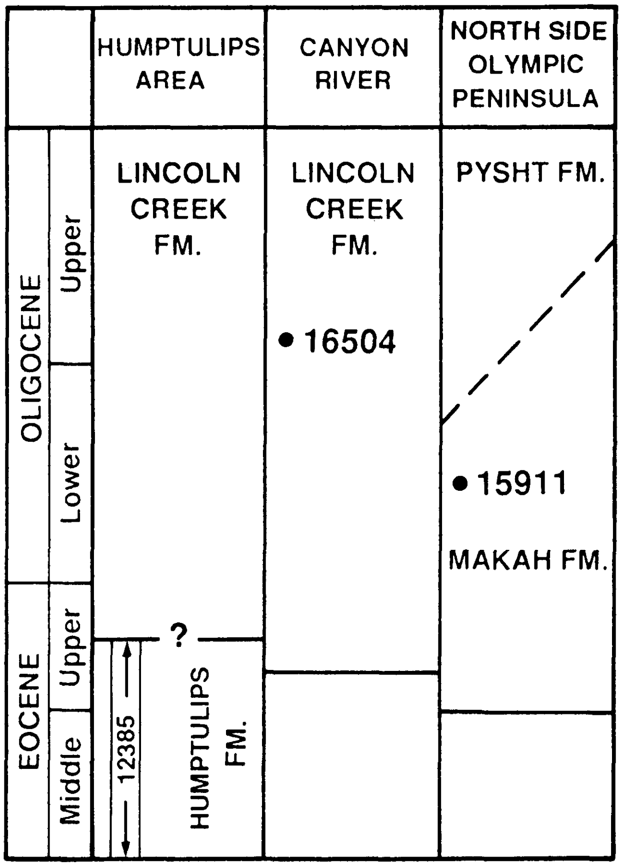


Figure 2

Chronostratigraphic chart showing position of localities for fossil *Leptochiton* (*L.*) *alveolus*.

to late Oligocene in age. The limestone at LACMIP loc. 16504 is a cold-methane-seep deposit containing a diverse chemosynthetic community with numerous specimens of the gastropod *Provanna antiqua* Squires, 1995. The rocks at the locality are earliest late Oligocene in age (Squires, 1995) (Figure 2). The details of the petrology and taxonomic composition of the limestone are under study by the junior author and K. L. Kaler.

Twenty separate valves of *Leptochiton* (*L.*) *alveolus* have been found at LACMIP loc. 15911 in a one-meter-thick limestone block in the Makah Formation at Shipwreck Point, northern Olympic Peninsula, Washington (Figure 1). Snavely et al. (1980) reported that the Makah Formation is late Eocene to late Oligocene in age. Most of the *Leptochiton* specimens were found during the study by Goedert & Campbell (1995) of the paleoenvironment of the limestone. The limestone is a cold-methane-seep deposit containing abundant specimens of the bivalves *Modiolus* (*M.*) *willapaensis* and *Calyptogena chinookensis* Squires & Goedert, 1991, in association with vestimentiferan? worm tubes, scaphopods, many archaeogastropods and other gastropods (including *Provanna antiqua*), other bivalves, crustacean fragments, and wood fragments (Goedert & Campbell, 1995). Goedert & Campbell (1995) and Squires (1995) reported that the rocks at LACMIP loc. 15911 are early Oligocene in age.

SYSTEMATIC PALEONTOLOGY

Class Polyplachophora Gray, 1821

Order Neoloricata Bergenhayn, 1955

Suborder Lepidopleurina Thiele, 1910

Family Leptochitonidae Dall, 1889

Genus *Leptochiton* Gray, 1847

Type species: *Chiton cinereus* Montagu, 1803 [= *Leptochiton asellus* (Gmelin, 1791)], by subsequent designation (Gray, 1847).

Discussion: There has been considerable confusion regarding whether or not *Leptochiton* should stand as a genus, be put in synonymy with *Lepidopleurus* Risso, 1826, or be made a subgenus of *Lepidopleurus*. Ferreira (1979) reviewed the nomenclatural history of *Leptochiton* and concluded that it should have full generic rank. Kaas & Van Belle (1985) also recognized *Leptochiton* as a distinct genus.

Subgenus *Leptochiton sensu stricto*

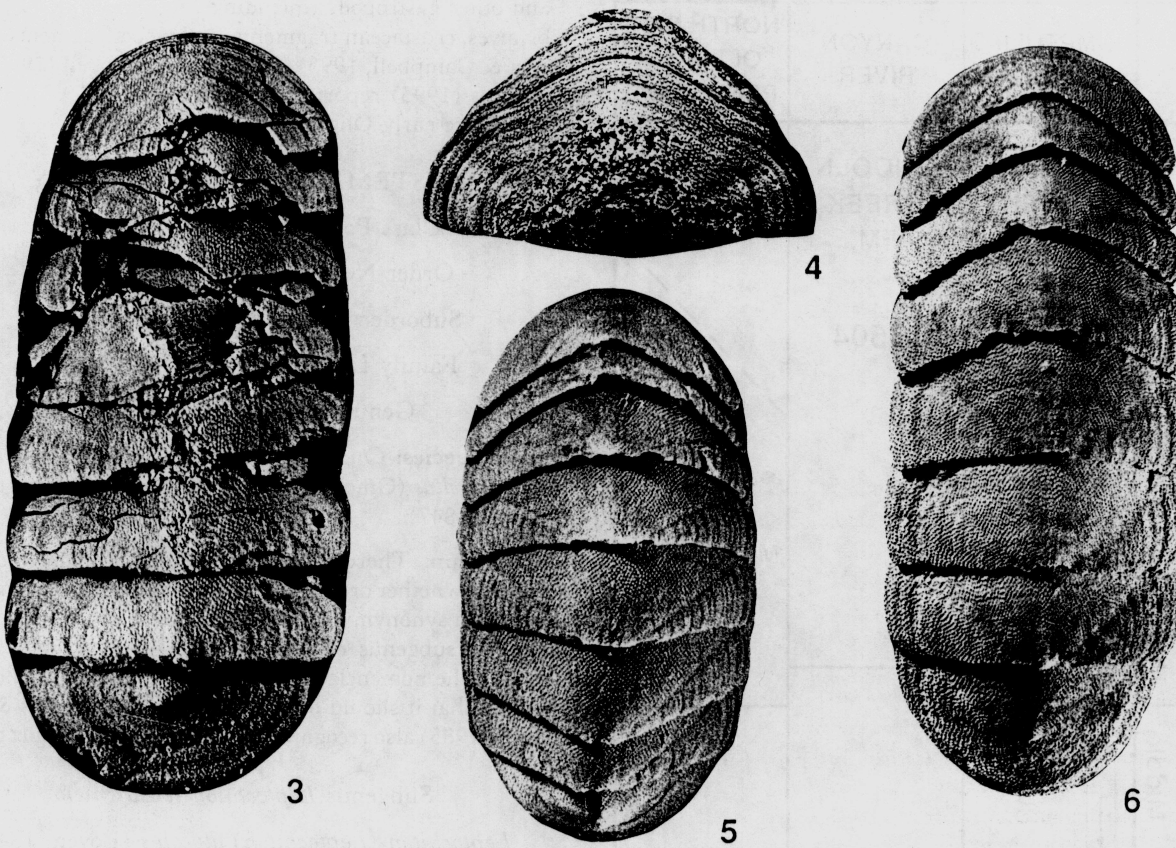
Leptochiton (*Leptochiton*) *alveolus* (Lovén, 1846)

(Figures 3–6)

Chiton alveolus M. Sars MS, Lovén, 1846:159. [For synonymies of this species, see Ferreira (1979) and Kaas & Van Belle (1985).]

Discussion: Three articulated specimens and 37 separate valves were found. The best preserved specimen (Figure 3) is extremely unusual for a fossil chiton because it is fully articulated. It shows the dorsal surface, but the ventral surface is encased in hard limestone. Chitons commonly curl up after death, but this specimen is flat and, most likely, was buried while alive. The specimen has suffered some fracturing and mild crushing, and its length seems to have been shortened slightly due to the valves having been pushed together. A second fully articulated specimen is very crushed.

The fossils from Washington were compared to every known fossil and Recent species of *Leptochiton*. The fossil species of *Leptochiton* are listed by Van Belle (1981) and the Recent species are discussed in Kass & Van Belle (1985). The fossil specimens from Washington are morphologically indistinguishable from *Leptochiton* (*L.*) *alveolus*, heretofore known only as an extant species. The Washington fossil specimens are like *L.* (*L.*) *alveolus* in the following features: arched, thin valves with convex slopes; the head valve is semicircular; the intermediate valves seem to be weakly keeled although crushing has



Explanation of Figures 3 to 6

Figures 3–6. *Leptochiton* (*Leptochiton*) *alveolus* (Lovén, 1846). Figures 3, 4. Fossil specimens. Figure 3. LACMIP 12334, LACMIP loc. 16504, upper part of the Lincoln Creek Formation at Canyon River, dorsal view, ×6.1. Figure 4. LACMIP 12322, LACMIP loc. 15911, lower Oligocene Makah Formation at Shipwreck Point, dorsal view of an intermediate plate, ×7.4. Figures 5, 6. Recent specimens. Figure 5. LACM 49-309.9, Bering Sea, Alaska, dorsal view showing a partially enrolled specimen, ×7.1. Figure 6. LACM 66-85.1, Peru, dorsal view showing a slightly enrolled specimen, ×4.5.

made this feature difficult to distinguish; and the tegmentum is covered with evenly disposed, minute granules whose size can vary slightly from place to place. The articulated fossil (LACMIP 12334) in Figure 3 is 16.1 mm long and 6.9 mm wide, whereas modern specimens of *L.* (*L.*) *alveolus* have been reported by Kaas & Van Belle (1985) up to 30 mm, and rarely, 40 mm long. An examination of the LACM collection of Recent specimens of *L.* (*L.*) *alveolus* from Alaska to Peru revealed the following variations in morphology: degree of elongation of the shell (length/width ratios vary from approximately 1.7 to 2.5), strength of the granules (from weak to moderately coarse), spacing of the granules (usually evenly disposed, but on some valves, the granules are coarser on the central area), strength of the lateral area (weakly defined to distinct), strength of the mucro (from low to prominent), and location of the mucro (from medially to anterior). Two Recent specimens, one from LACM lot 49-309 (Bering Sea, Alaska) and the other from LACM lot 66-85 (Peru), are shown in Figures 5 & 6, respectively. The specimen in Figure 5 is less elongate than the one in Figure 6 and has a more anteriorly located mucro. The articulated fossil of *L.* (*L.*) *alveolus* (LACMIP 12334) is moderately elongate (length/width ratio of 2.3), weakly granulate with slight variations in granule size, and has a prominent mucro very anteriorly located. It may be that the anterior position of the mucro in the fossil is due to post-burial compression although the mucro's location is within the observed range in Recent specimens.

Leptochiton (*L.*) *alveolus* was not known from the eastern Pacific until Ferreira (1979) expanded the definition of *L.* (*L.*) *alveolus* and put the eastern Pacific *L.* (*L.*) *belknapi* Dall, 1878, into synonymy with *L.* (*L.*) *alveolus.* According to Wu & Okutani (1984), and as accepted by Kaas & Van Belle (1987), there is slight but significant morphological distinction between *L. alveolus,* which they claim is restricted to the Atlantic Ocean, and *L. belknapi,* which they claim is confined to the Pacific and Indian Oceans. We examined five lots of eastern Pacific *Leptochiton* in the LACM collection and found specimens that have features of both species. For example, we observed specimens from lot 49-309 (Bering Sea) whose anterior margin of the tail valve is almost straight (a feature of *alveolus*) and whose intermediate valves are keeled (a feature of *belknapi*). In addition, a specimen from this lot has one pair of sulci radiating from the apex (a feature of *alveolus*) on intermediate valves 4 and 7 and two pairs of these sulci (a feature of *belknapi*) on the others intermediate valves. Our observations indicate that these two species intergrade and that Ferreira (1979) was justified in regarding them as the same species.

Modern *L.* (*L.*) *alveolus* is one of the two known cosmopolitan species of chiton. Clark (1994) reported the other species to be the mopaliid *Placiphorella atlantica* (Verrill & Smith, 1882). *Leptochiton* (*L.*) *alveolus* is present in the Pacific, Atlantic, and Indian Oceans, and in the Mediterranean Sea, and the latitudinal range of this species is approximately 72°N (Point Barrow, Alaska) to 50°S (Kerguélen Islands, southern Indian Ocean) (Van Belle, 1975; Ferreira, 1979; Kaas, 1981). It is rarely found in depths of less than 100 m, and its favored habitat is in bathyal to abyssal depths (as deep as 4825 m) (Ferreira, 1979; Kaas & Van Belle, 1985). There is scant information about the types of substrate that this species lives on in modern oceans. Specimens of *Leptochiton* (*L.*) *alveolus*? have been found living on manganese nodules and crusts dredged from 4500 m in the equatorial north Pacific Ocean (D. J. Eernisse, personal communication). So far *L.* (*L.*) *alveolus* has not been reported as a member of a modern chemosynthetic community, but there is a good likelihood that this species will be found based on its habitat in the past and on its modern cosmopolitan distribution in deep waters. In addition, chemosynthetic habitats commonly contain benthic invertebrates whose ancestries are long ranged (Newman, 1985).

The only living species of *Leptochiton* that has been reported from a chemosynthetic community is *L. tenuidontus* Saito & Okutani (1990), which has been found at a hydrothermal vent site at 1395 m depth in the Okinawa Trough, east China Sea. *Leptochiton tenuidontus,* which is known from only a single eroded specimen, differs from the *L.* (*L.*) *alveolus* by having the following features: wider shell, coarser granules, and more rows of transverse radular teeth.

Previously, the earliest geologic record of *Leptochiton sensu stricto* was questionable. Van Belle (1981), in his very useful catalog of fossil species of chitons, listed *Leptochiton* ? *deshayesi* (Terquem, 1852) from Lower rocks of Early Jurassic age in France and *Leptochiton* ? *fischeri* (Rochebrune, 1883) from rocks of late middle Eocene age (Bartonian Stage) in France. His only other Eocene record of this genus is *L. magnogranifer* (Ashby, 1925) from Muddy Creek, Victoria, southeastern Australia; however, an Eocene age for Ashby's species cannot be corroborated. Ashby (1925) reported that the horizon for *L. magnogranifer* is unknown. There are no Eocene rocks in the Muddy Creek area, but there are Miocene through Pleistocene rocks (Spencer-Jones, 1971). The fossil specimens of *L.* (*L.*) *alveolus* from the late middle Eocene to late Eocene Humptulips Formation in Washington, therefore, represent the earliest known record of *Leptochiton sensu stricto.*

The only other reports of Eocene chitons from the Pacific coast of North America are from the middle Eocene (molluscan "Transition Stage") basal part of the Tejon Formation, Tehachapi Mountains, southern California. Squires (1989) and Lindberg & Squires (1990) reported unidentified chiton fragments associated with abundant rocky intertidal mollusks in these rocks. The chiton fragments, which are poorly preserved, are probably referable to genus *Stenoplax* (R. N. Clark, personal communication).

All Oligocene records *Leptochiton sensu stricto,* other than those in the Makah and Lincoln Creek Formations of Washington, are in Europe (Van Belle, 1981), but none is *L.* (*L.*) *alveolus. Leptochiton sensu stricto* was also present in Europe during the Miocene and was present in Australia during the Miocene and Pliocene (Van Belle, 1981), but none of these species is conspecific to *L.* (*L.*) *alveolus.*

The only other fossil species of *Leptochiton* reported from the Pacific coast of North America is *L. clarki* Berry (1922: 427-430, pl. 1, fig. 10, text figs. 1-4) from the Pleistocene at Santa Monica, California. *Leptochiton clarki* differs from *L.* (*L.*) *alveolus* by having distinct rows of small granules, weak longitudinal riblets on the central area, and radial riblets laterally. Today, numerous species of *Leptochiton* live off the Pacific coast of North America (Ferreira, 1979; Kaas & Van Belle, 1985).

Lepidochitona (*Spongioradsia*) *lioplax* (Berry, 1922:431-433, pl. 1, figs. 1-6) from the Sooke Formation on southern Vancouver Island, British Columbia, Canada, is the only other Paleogene chiton from the Pacific coast of North America that has been named and described. Moore & Addicott (1987) reported the age of the Sooke Formation to be late Oligocene to earliest Miocene.

Distribution: Late middle Eocene to late Eocene to early late Oligocene (Washington) to Recent (cosmopolitan). LATE MIDDLE EOCENE to LATE EOCENE: Humptulips Formation, Humptulips area, southern Olympic Peninsula, Washington. EARLY OLIGOCENE: Makah Formation, northern Olympic Peninsula, Washington. EARLIEST LATE OLIGOCENE: Upper part of Lincoln Creek Formation, Canyon River, southern Olympic Peninsula, Washington. RECENT: Cosmopolitan, in the Pacific, Atlantic, and Indian Oceans, and the Mediterranean Sea.

ACKNOWLEDGMENTS

The considerable help of Keith L. Kaler (Olympia, Washington) and Gail H. Goedert in collecting the specimens made this study possible. Roger N. Clark (Klamath Falls, Oregon) helped greatly in the identification, and shared his knowledge of chitons. William A. Newman (Scripps

Institution of Oceanography, La Jolla, California) provided identification help in the early phase of this study. James H. McLean (Natural History Museum of Los Angeles County, Malacology Section) allowed access to modern specimens of *Leptochiton* and to the Malacology Section library. The manuscript benefited from critical reading and insightful comments by Douglas J. Eernisse (Laboratory of Molecular Systematics, Smithsonian Institution) and an anonymous reviewer.

Some specimens used for this report were collected during fieldwork supported by a grant (4439-90) from the National Geographic Society to the Natural History Museum of Los Angeles County Foundation for fossil cetacean research on the Olympic Peninsula.

LOCALITIES CITED

LACM lot 49-309. At 311 m depth, sand and gravel, SW of St. Matthew Island, NW of Pribilof Islands, Bering Sea, Alaska (58°23'N, 174°56'W). Leg. Navy R/V *Epce* (R) 857. August, 1949.

LACM lot 66-85. At 3070 m depth, muddy bottom, abyssal Pacific, south of Callgo, Peru (15°34'S, 77°36'W). Anton Brunn, Cruise 17, by Agassiz Trawl. July, 1966.

LACMIP 12385. Limestone deposit cut by an abandoned meander on the East Fork of Humptulips River, latitude 47°15'17"N, longitude 123°49'00"W, in the NW part of sec. 4, T 20 N, R. 9 W, Quinault Lake U.S. Geological Survey quadrangle, 15-minute, 1955, Grays Harbor County, southern Olympic Peninsula, Washington. Humptulips Formation. Age: late middle Eocene to late Eocene. Collector: J. L. & G. H. Goedert, 1990.

LACMIP 15911. Limestone block within thin-bedded sandstone and siltstone deposits, accessible only at low tide, at Shipwreck Point, latitude 48°19'N, longitude 124°26'45"W, SE¼ of NE¼ of sec. 36, T 33 N, R. 14 W, Sekiu River U.S. Geological Survey quadrangle, 7.5-minute, provisional edition 1984, Clallam County, northern Olympic Peninsula, Washington. About 30 m stratigraphically above top of Jansen Creek Member of the Makah Formation. Age: early Oligocene. Collectors: J. L. & G. H. Goedert, 1991-1993.

LACMIP 16504. At elevation of 390 ft., limestone block within siltstone on the north side of a sharp bend in Canyon River, latitude 47°16'42"N, longitude 123°31'19"W, 600 m N and 290 m E of SW corner of sec. 25, T. 21 N, R. 7 W, Grisdale U.S. Geological Survey quadrangle, 7.5-minute, 1990 provisional edition, Grays Harbor County, southern Olympic Peninsula, Washington. Upper part of the Lincoln Creek Formation. Age: earliest late Oligocene. Collectors: J. L. & G. H. Goedert, & K. L. Kaler, 1993.

LITERATURE CITED

ASHBY, E. 1925. Monograph on Australian fossil Polyplacophora (chitons). Proceedings of the Royal Society of Victoria, new series, 37(pt. 2):170-205, pls. 18-22.

BERNARD, F. R. 1983. Catalogue of the living Bivalvia of the eastern Pacific Ocean: Bering Strait to Cape Horn. Canadian Special Publication of Fisheries and Aquatic Sciences 61:1-102.

BERRY, S. S. 1922. Fossil chitons of western North America. Proceedings of the California Academy of Sciences, Fourth series, 11(18):399-526, pls. 1-16.

CLARK, R. N. 1994. Review of the genus *Placiphorella*. The Veliger 37(3):290-311.

COAN, E. V. 1990. The Recent eastern Pacific species of the bivalve family Traciidae. The Veliger 33(1):20-55.

DALL, W. H. 1878. Descriptions of new forms of mollusks from Alaska contained in the collections of the National Museum. Proceedings of the United States National Museum 1:1-3.

DALL, W. H. 1889. Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78) and in the Caribbean Sea (1879-80), by the U.S. coast survey steamer "Blake." 29, Report on the Mollusca. 2, Gastropoda and Scaphopoda. Bulletin of the Museum of Comparative Zoology, Harvard University 18:1-492, pls. 10-40.

FERREIRA, A. J. 1979. The family Lepidopleuridae (Mollusca: Polyplacophora) in the eastern Pacific. The Veliger 22(2): 145-165.

FERREIRA, A. J. 1980. A new speices of *Lepidopleurus* Risso, 1826 (Mollusca: Polyplacophora) in the deep waters of the eastern Pacific. The Veliger 23(1):55-61, pl. 1.

GOEDERT, J. L. & K. A. CAMPBELL. 1995. An early Oligocene chemosynthethic community from the Makah Formation, northwestern Olympic Peninsula, Washington. The Veliger 38(1):22-29.

GOEDERT, J. L. & R. L. SQUIRES. 1990. Eocene deep-sea communities in localized limestones formed by subduction-related methane seeps, southwestern Washington. Geology 18:1182-1185.

GRAY, J. E. 1847. Additional observations on chitones. Proceedings of the Zoological Society of London 15:126-127.

KAAS, P. 1981. Scandinavian species of *Leptochiton* Gray, 1947 (Mollusca, Polyplacophora). Sarsia 66:217-229.

KAAS, P. & R. A. VAN BELLE. 1985. Monograph of Living Chitons (Mollusca: Polyplacophora). Vol. 1. Order Neoloricata: Lepidopleurina. E. J. Brill/W. Backhuys: Leiden. 240 pp.

KAAS, P. & R. A. VAN BELLE. 1987. Monograph of Living Chitons (Mollusca: Polyplacophora). Vol. 3. Suborder Ischnochitonina Ischnochitonidae: Chaetopleurinae, & Ischnochitoninae (pars). Additions to Vols. 1 & 2. E. J. Brill/W. Backhuys: Leiden. 302 pp.

KULM, L. D. & E. SUESS. 1990. Relationship between carbonate deposits and fluid venting: Oregon accretionary prism. Journal of Geophysical Research 95(B6):8899-8915.

LINDBERG, D. R. & R. L. SQUIRES. 1990. Patellogastropods (Mollusca) from the Eocene Tejon Formation of southern California. Journal of Paleontology 64(4):578-587.

LOVÉN, S. L. 1846. Index molluscorum litora Scandinaviae occidentalia habitantium. Kungliga Vetenskaps-Akademien Förhandlingar Stockholm 3:134-160.

MARINCOVICH, L., JR. 1977. Cenozoic Naticidae (Mollusca: Gastropoda) of the northeastern Pacific. Bulletins of American Paleontology 70(294):169-494, pls. 17-42.

MONTAGU, G. 1803. Testacea Britannica or Natural History of British Shells. 2 Vols. London. 606 pp., 16 pls.

MOORE, E. J. & W. O. ADDICOTT. 1987. The Miocene Pillarian and Newportian (Molluscan) Stages of Washington and Oregon and their usefulness in correlations from Alaska