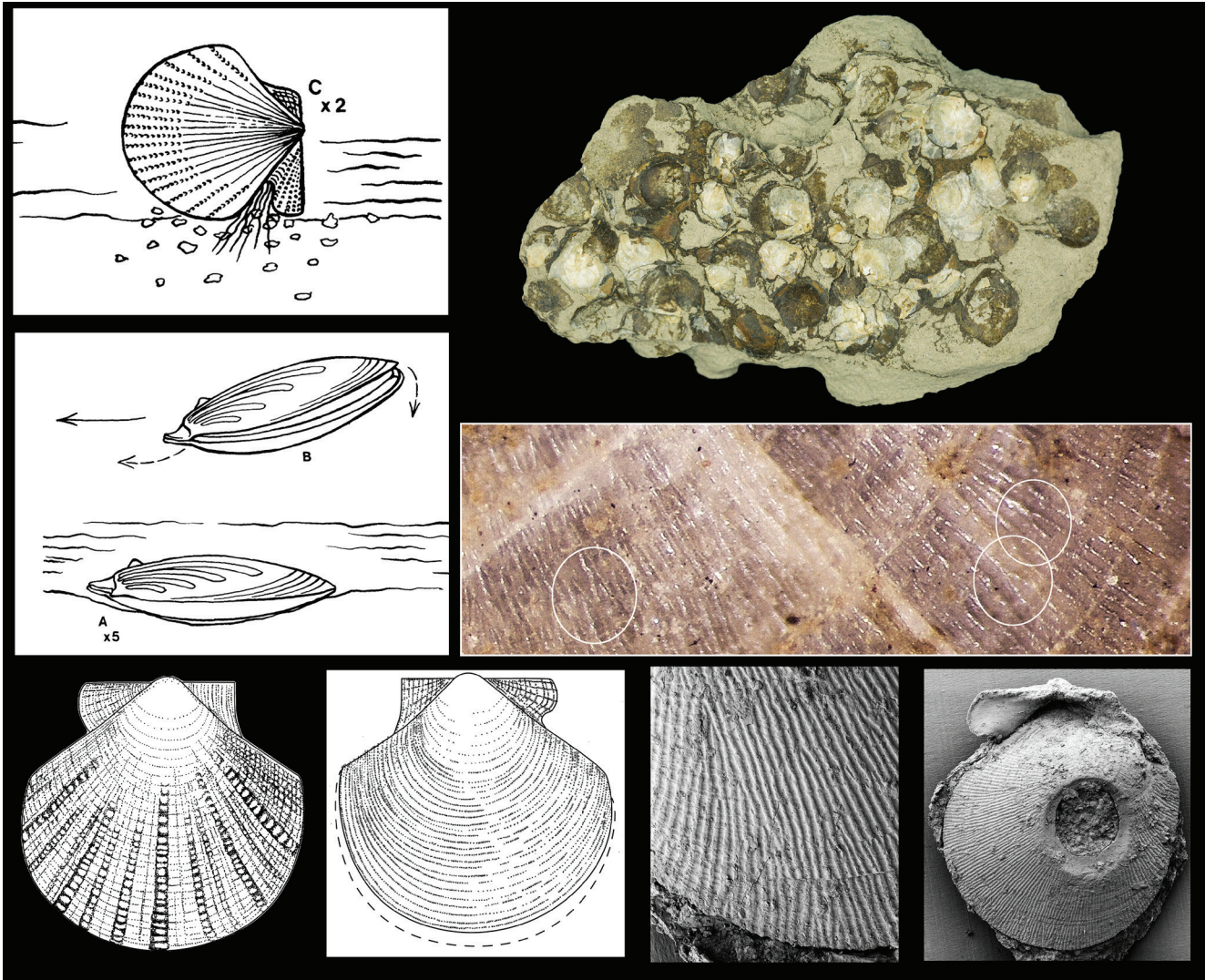


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Carole S. HICKMAN (2023). Paleogene marine bivalves of the deep-water Keasey Formation in Oregon, Part II: The pteriomorphs.

Cover: Byssally attached mud pectens and free-living glass scallops are abundant throughout the Keasey Formation, occurring in small clusters at many localities. Although they are seldom well preserved, microscopic sculpture of the thin, delicate shells is ornate and taxonomically diagnostic. Shells are sometimes partially articulated, and preserve drill holes of juvenile carnivorous naticid gastropods.

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Paleogene marine bivalves of the deep-water Keasey Formation in Oregon, Part II: The pteriomorphs

Carole S. Hickman

Department of Integrative Biology and Museum of Paleontology
University of California, Berkeley CA 94720-4780
caroleh@berkeley.edu

Systematic documentation of pteriomorph bivalves of the late Eocene–early Oligocene Keasey Formation in western Oregon follows previous monographic treatments of the anomalodesmatans and heteroconchs. It includes material from coeval Cascadia Margin strata in southwestern Washington in the context of major molluscan faunal turnover during the dramatic doublet climate transition from an ice-free tropical marine environment to the establishment of permanent polar ice caps and a cold temperate marine climate. The families represented are Crenellidae, Parallelodontidae, Glycymerididae, Limopsidae, Isognomonidae, Pectinidae, Propeamussiidae, and Limidae. New taxa include the genus *Bathysognomon* and five new species: *Limopsis squiresi*, *Bathysognomon smithwickensis*, *Delectopecten kieli*, *Delectopecten keaseyorum*, and *Propeamussium (Parvamussium) mistensis*. Small to minute mud pectens and glass scallops are among the most abundant and frequent taxa in the Keasey fauna, although they are poorly preserved and have been overlooked heretofore. Pteriomorphs are prominent elements of recurring associations of species in mudstone and fine-grained siltstone facies adjacent to three Keasey cold methane seeps. Previously described Keasey anomalodesmatans and heteroconchs in these seep-adjacent strata have living relatives adapted to dysoxia and toxic geochemistry. Because the unique macrofaunal associations in these settings are neither seep fauna nor part of the background fauna, this paper introduces and defines the concept of a transitional *peri-seep biotope*. Relationships, monophyly, systematic resolution within major pteriomorph groups, and global biogeographic distributions are reviewed in each systematic treatment. Recurring patterns include occurrences in active margin settings, inferred oscillatory deepening of the calcium carbonate compensation depth, late Eocene origin of two-layered oceans following establishment of the Antarctic Circumpolar Current, and biogeographic gateway changes that disrupted earlier Paleogene larval dispersal patterns.

Keywords: Eocene, bathyal, methane seep, peri-seep biotope, Cascadia Margin, doublet climate

INTRODUCTION

The following account of the pteriomorph bivalves of the Keasey Formation documents some of the rarest and least well-understood bivalve taxa in upper Eocene strata. The late Eocene was a time of global climate deterioration cooling and oceanographic change as well as dramatic tectonic reorganization of the Cascadia Margin of the Northeastern Pacific. Between 53 and 33.5 Ma the doublet interval of global cooling and climate instability (Hickman 2021) is characterized by rapidly oscillating deterioration from the tropical greenhouse state and thermal maximum of the Early Paleogene

through development of high latitude sea ice, culminating in permanent polar ice caps that define the Neogene and modern greenhouse climate state. The final and most pronounced Oi-1 cold temperature excursion, based on isotope proxies (Zachos et al. 1996), corresponds with dramatic molluscan faunal turnover in the Keasey Formation (Hickman 2003).

This systematic documentation of the Keasey pteriomorphs follows separate monographic treatments of the anomalodesmatan and heterodont bivalves (Hickman 2014, 2015) as well as the Keasey gastropods (Hickman 1976, 1980). It is based on field and laboratory studies

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conducted by the author, students, and colleagues over the course of 55 years, augmented by museum studies—notably material meticulously collected by the late Harold E. Vokes from localities and exposures that no longer exist.

During this research there have been many changes in bivalve nomenclature and classification as well as major revision of the chronostratigraphic and biostratigraphic framework for western Oregon, Washington, Vancouver Island, and increasingly detailed reconstruction of the history of the Cascadia convergent margin and subduction zone (e.g., Wells et al. 2014, Darin et al. 2022). The unique character of the Keasey molluscan fauna clearly reflects the inigimbrite flare-ups, tectonic extension, and voluminous input of volcanic ash into the initial forearc basin. Tectonic events coincide with the appearance of cold-seep carbonates within the massive tuffaceous siltstone and mudstone units exposed in road cuts, quarries, and river- and stream-bank exposures. The original account of three cold seeps in the Keasey Formation (Hickman 2015, pp. 2–5) includes discussion of faunal dependence on methane-rich fluids, tolerance of hypoxia and toxic geochemistry, and ecological opportunism. Some of the Keasey pteriomorph species are closely associated with seep carbonates and inferred diffusive methane seepage throughout the formation. Accordingly, this treatment includes illustration and discussion of living congeners in five of the eight Keasey pteriomorph families.

The final monograph in this series will document the protobranch bivalves, including 15 species in 13 genera and six families. The Keasey protobranchs are all deposit feeders with the exception of two obligately chemosymbiotic solemyids. Genus-group taxa with living oxygen minimum zone species and inferred association with chemosynthetic primary productivity in the sediment will be a continuing theme.

Unsatisfactory preservation of the Keasey pteriomorphs is largely responsible for their poor representation in museum collections. The thin-shelled mud pectens and glass scallops seldom retain original shell material and are represented primarily by exterior and interior casts. Shell fragments typically are not collected or included in museum collections, although illustrations provided here demonstrate useful and diagnostic information and encourage unconventional field methods. Impressions of delicate shell sculpture in exterior casts, remnants of ligament in a resilifer, and impressions of periostracum, when examined microscopically, are among the rewards of careful collection. These shell

features are easily captured and enhanced by modern photography and digital processing. Low voltage Scanning Electron Microscopy captures surface detail unavailable at standard high voltages in which secondary electrons pass through the extremely thin shells of mud pectens and glass scallops.

Some of the Keasey pteriomorph species are most abundant and frequent at cold-seep localities in clastic sediments adjacent to seep carbonates. Recurring Keasey bivalve associations in proximity to seeps are recognized here as elements of a distinctive “peri-seep biotope.” The term biotope, from the Greek *bios* (life) + *topos* (place), is used here to extend a seep seabed (a predominantly plan viewscape) downward to include its geologically longterm history. The biologist lacks access to a vertical sedimentary record below the plan viewscape of the seafloor at the same time that the paleontologist has no access to conditions in the overlying water column. Together these complementary sources of data offer the most broadly integrative approach to understanding methane seeps. The following brief account addresses questions of boundaries: sharp vs clinal gradients in fauna, substrate, hydrography, and associated physical and chemical factors.

THE KEASEY PERI-SEEP BIOTOPE

The peri-seep biotope is here characterized physically and chemically as a region of habitat adjacent to or surrounding a site of diffusive hydrocarbon expulsion associated with effusive seep carbonates. It is characterized paleobiologically by opportunistic megafaunal assemblages of taxa with adaptations for use of a locally abundant trophic resource—carbon fixed by chemosynthetic microbes. At the same time, the opportunistic taxa must have adaptations for tolerating sulfide and toxic geochemical conditions, including oxygen depletion. In the following systematic treatments fossil pteriomorphs are compared with living congeners. A high proportion of living counterparts of the Keasey pteriomorph and protobranch bivalves are oxygen minimum zone species, deposit-feeding taxa with enlarged hindguts, or suspension-feeding taxa with unique particle-capturing mechanisms that exploit enhanced chemosynthetic microbial productivity in the water column.

The peri-seep biotope can be visualized physically as a halo surrounding a cold seep or a transitional area adjacent to a seep. It is occupied by taxa that are neither part of the high-biomass core “seep fauna” nor what is conventionally regarded as “background fauna. As a transition zone it is similar in concept to the classical *ecotone*

of terrestrial community ecologists and landscape biologists studying shifting mosaics of vegetation on a geographic scale and successional time scale. Ecotones are now primarily of interest in resource management, environmental planning, and global change biology (see [Risser 1995](#)). The terrestrial ecotone has no formalized equivalent in the study of deep-sea biology and paleontology. However, recognition of transitional “realms of complex interaction” ([Levin 2005](#)) helps erase the sharp, artificial distinction between seep and background faunas.

Two distinct transitional concepts specific to both methane seeps and hydrothermal vents merit paleontological recognition. They are *sphere of influence* ([Levin et al. 2016](#)) and *chemotone* ([Ashford et al. 2021](#)). The original interest in methane seeps as oases on a barren deep-sea ocean floor has progressed far beyond the descriptive phase to include documentation of their transitional functions from local to global scales. Some of these transitions are subject to geological, geochemical, and paleontological quantification on an even longer time scale. The specific concept of a chemotone or geochemical transition zone in sediments surrounding a methane seep is especially amenable to multivariate geological study, including signals in the skeletal carbonates of mollusks and benthic foraminifera.

In the Keasey Formation, the peri-seep biotope is dominated by tuffaceous siliciclastic (muddy or silty) substrate adjacent to or surrounding a paleo-hydrocarbon seep site dominated by hard carbonate substrates that were available to epifaunal taxa. The hypothetical three-dimensional geometry is not visible as a “halo” in the face of an outcrop but is inferred from observations at multiple sites. Likewise, the recurring associations of peri-seep taxa are inferred from observations at multiple sites.

Of the six Keasey mollusk associations named and described by [Hickman \(1984\)](#) one is assigned to a seep biotope (*Thyasira-Lucinoma-Solemya*), and three to peri-seep biotopes (Protobranch, Mud Pecten, and *Acesta*). The recurring nature of these Keasey mollusk associations is reinforced by detailed sampling on a 600 m transect on Rock Creek in the lower part of the middle member of the formation ([Taylor et al. unpublished data](#)). Carbon and oxygen stable isotope analyses of rock samples from the main Rock Creek carbonate body and foraminiferal tests from muddy siltstone immediately peripheral to the core seep limestone have methane seep $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signatures. The main seep, two secondary seep sites and associated mudstone and siltstone outcrops on the Rock

Creek transect represent a continuum from effusive to diffusive fluid expulsion, open to more detailed future investigation ([Taylor et al. unpublished data](#)).

MATERIALS AND METHODS

Materials, methods, content and formatting conventions for systematic text and illustrations, institutional abbreviations, and geographic terminology in the following taxonomic section are the same as in preceding treatments of the Keasey anomalodesmatan and heteroconch bivalves ([Hickman 2014, 2015](#)).

SYSTEMATIC PALEONTOLOGY

The hybrid pteriomorph classification adopted here is based primarily on [Bouchet and Rocroi \(2010\)](#), [Carter and 50 others \(2011\)](#), and [Valentich-Scott et al. \(2020\)](#). Ranking differs among classifications and is also hybrid.

PTERIOMORPHIA [BEURLEN, 1944](#)

Five major groups of bivalves in the Keasey Formation (Mytilida, Arcida, Pteriida, Pectinida and Limida) are represented by taxa whose living species fall within a well-supported pteriomorph clade. Despite increasing support for monophyly from molecular data (e.g., [González et al. 2015](#), [Lemer et al. 2016, 2019](#)), these groups encompass major radiations of extinct families and genera. Any phylogenetic perspective based on living species is seriously limited and temporally shallow. At the same time pleasing topologies based on limited sampling of living taxa leave internal relationships in the five major groups highly unresolved, but with considerable promise for increasing use of shell microstructure in phylogenetic studies. The following taxonomic treatments emphasize geological, paleoecological, paleoenvironmental, and paleogeographic insights on pteriomorph history.

All five of the Keasey major pteriomorph groups have Paleozoic origins, with arcoids and pterioids appearing in the Ordovician and mytiloids, pectinoids and limoids dating from the Devonian or Carboniferous. Extinct family-groups and genus-groups must be included in evolutionary history along with studies of historical ecology and biogeography. As noted above, the Keasey pteriomorphs provide a remarkable window on history because they occur in deep water mudstone and siltstone lithofacies during the doubtouse interval of major global climate cooling as well as an interval coinciding with tectonic change and onset of arc volcanism and large volumes of tuffaceous sedimentary input on the Pacific Northwest margin. They thrived in environmentally challenging hydrocarbon seep and peri-seep environments.

They experienced the same dysoxic and geochemically toxic conditions previously noted for Keasey heteroconch and anomalodesmatan bivalves (Hickman 2014, 2015).

Stratigraphic range—Ordovician–Holocene.

MYTILOIDEA RAFINESQUE, 1815

CRENELLIDAE J.E. GRAY, 1840

This family-group of small to minute mussels (<10 mm) is represented in the Paleogene fossil record of the Northeastern Pacific by a single genus, *Crenella* T. Brown (1827). Following the proposal of Morton et al. (2016), the group is elevated here to family status. Five additional genera have been recognized in the living fauna of the Northeastern Pacific (Coan et al. 2000). They are represented by species that nestle or live infaunally in byssal nests, mucus-bound sedimentary crypts, or attached by byssal threads to shell fragments and larger particles in sandy mud. The shallow infaunal life habit at the sediment-water interface is associated with miniaturization and a departure from the more familiar epifaunal, hard-substrate mytiloid mode of life. Convergent reduction in shell size may be more common than currently suspected, confounding efforts to define natural groups.

In the North Pacific crenellids occur primarily in cold, deep-water settings at high latitudes. In the Southern Hemisphere crenellids are less diverse but also a predominantly high latitude faunal element.

Post-Paleogene diversification of crenellids in the tropical Eastern Pacific fauna (Coan and Valentich-Scott 2012) is recorded in the living fauna by additional genera, including species that bore in calcareous substrata and are not part of earlier Cenozoic infaunal lineages.

Fossil crenellid specimens are a minor element in faunas ranging from late Eocene to early Miocene in the Pacific Northwest and Alaska. Although never abundant, fragments of the thin shell have been recovered from numerous localities. These fragments are easily recognized by their peculiar opalescent luster as well as fine radial and concentric ornamentation and very finely crenulate shell margin.

Crenella is not present in the tropical Eocene fauna of the Northeastern Pacific. It appears after the onset of high-latitude global cooling in the late Eocene and early Oligocene in the deep-water (bathyal) transition faunas. In California the first records of the genus are Pliocene and Quaternary (Hertlein and Grant 1972, E.J. Moore 1983). In the Western Pacific it appears as a high latitude element in Neogene and Quaternary faunas of eastern Russia (predominantly Kamchatka and Sakhalin) (Kavanov et al. 2000, 2001).

Although the genus is absent from the tropical Paleogene faunas of the North Pacific, it apparently was present at much higher latitudes in cold water during the Late Cretaceous and earliest Paleogene. Marincovich (1993) described *Crenella kannoi* from Danian rocks of the Prince Creek Formation of northern Alaska, deposited in a detached and isolated Arctic Ocean. He suggested that the Danian Arctic Ocean acted as a refugium, subsequently giving rise to elements in the high latitude faunas of both the Pacific and Atlantic. Mesozoic history is even more obscure, with apparent Late Triassic origin of the family and a nestling mode of life that subsequently gave rise to epibyssate, hard-substrate forms as well as a variety of endobyssate and free-living forms in which life habit is not clearly reflected in shell morphology.

Crenellid evolutionary history is further complicated in the Northeastern Pacific by the presence in the living fauna of two larger-shelled species of similar ovate-elongate form that have been reassigned (Coan et al. 2012) to *Solamen* Iredale (1924), a genus based on a living Australian species. However, the earliest records of *Solamen* are in the Eocene Blanche Point Formation in South Australia and a silicified Eocene fauna in Western Australia (Darragh and Kendrick 1980). The tendency for crenellids to become more elongate as they increase in size was noted by Fleming (1959) and is noted below in discussion of the two Keasey species. Distinctions among crenellid genera and species are tenuous and remain subject to change with additional study of both fossil and living taxa.

The unsettled state of mytiloid systematics has been characterized more colorfully as a “taxonomic farrago” and as “nomenclatural chaos” (Morton et al. 2016). Convergent miniaturization of the shell associated with infaunal nestling (Harper and Skelton 1993) masks potentially significant anatomical differences. Although much-needed biological study is not likely to assist with systematics of fossil taxa, the shell ultrastructure underlying the distinctive luster of the shells of the two Keasey species is addressed in the treatment below.

Stratigraphic range—Upper Triassic–Holocene.

CRENELLA T. BROWN, 1827

Type species—By monotypy, *Mytilus decussatus* Montagu (1808). Holocene, northern Norway. Subsequently recognized in the Arctic Ocean and circum-boreal, extending to lower latitudes in both the Atlantic and Pacific.

The type species (Figs. 1, 2) is well represented in museum collections, although it is likely a species complex based on considerable variation observed by this

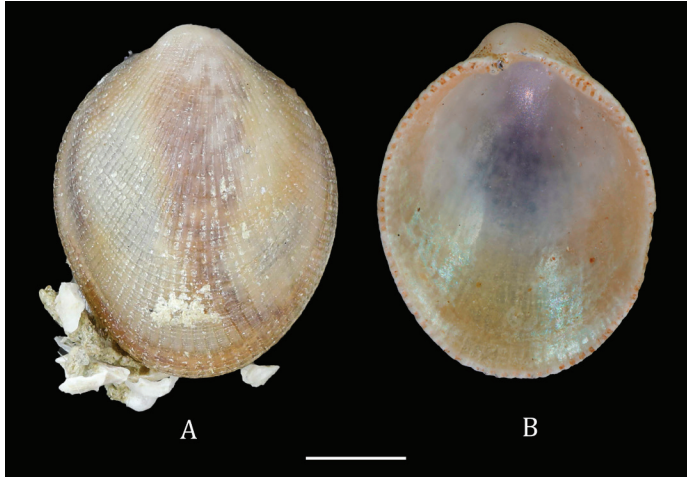


Figure 1. Type species of *Crenella*, *C. decussata* (Motagu, 1808). **A.** Left valve exterior of double-valved specimen with byssal threads cemented to shell fragments. **B.** Right valve interior. SBMNH 214640. Scale bar=1 mm.

author. This is consistent with a major difference in life habit between a North Atlantic population, described by Morton et al. (2016) as lacking a byssus and occupying crypts built of mucus-cemented sand grains, and the Northeastern Pacific forms that construct a network of fine byssal threads (Fig. 2A). These threads attach firmly to shell fragments and other particles within the sediment (Fig. 2B, C). Brooding and lack of a planktonic larval stage, also documented by Morton et al. (2016), are consistent with reduced dispersal and gene flow between isolated populations.

Recognition of the type species in the Northwestern Pacific is complicated by the introduction of additional names. Although this species has long been recognized in

the far northern seas of Russia and Japan, there are un-evaluated species names based on Japanese specimens, notably those proposed by A. Adams (1862) without illustration and no record of deposition in The Natural History Museum, London. These names along with discovery of the type species in a subtropical Korean fauna led Lutaenko (2014) to suggest a “regional complex” in need of much work.

In addition to the persistent problem of diagnosing the type species of *Crenella* and defining its distribution in the Northern Hemisphere, there are very similar small-shelled crenellids in the Subantarctic fauna. Melville and Standen (1912, p. 235) recorded the type species from the Burdwood Bank (an undersea plateau delimited by the 200 m isobath and situated approximately 200 km south of the Falkland Islands at 55° S). Linse (2002) subsequently described this form as *Crenella magellanica*, with excellent scanning electron micrographs and list of diagnostic features. A similar subantarctic species is *Crenella marionensis* (E.A. Smith, 1885) from the Marion and Prince Edward Islands in the sub-Antarctic Indian Ocean. The genus also is reported from the southern Atlantic coast of Argentina (Zelaya 2016). The identity and even the generic assignments of southern hemisphere crenellids remain unclear. A very brief review of some of the difficulties assessing genus-group names based on Australasian species is in order because some of these names are now used for species in the North Pacific.

In the Australian fauna, *Solamen* (type, by original designation, *Solamen rex* Iredale, 1924), was proposed with inadequate figures, although Iredale clearly stated that the hingeline was narrow and edentulous and that the ligament groove was semi-internal. Larger shell size

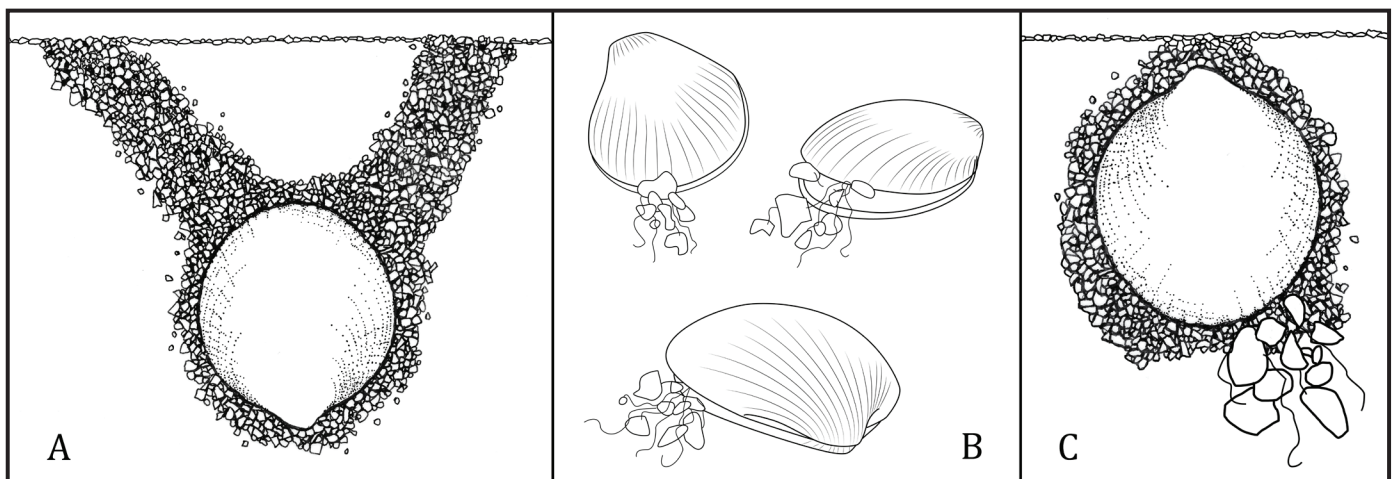


Figure 2. Alternative reconstructions of the life habit of *Crenella decussata*. **A.** Completely encased in crypt of cemented sedimentary grains, living below sediment-water interface in North Atlantic. **B, C.** Byssus attached to shell fragments, living at sediment-water interface in North Pacific.

(15–26 mm), relatively thinner shell, and greater inflation of the valves also are typical of living North Pacific species assigned to *Solamen*. *Megacrenella* Habe and Ito (1965) and *Exosiperna* Iredale (1929) have been treated as synonyms of *Solamen* (e.g., Coan et al. 2000, Coan and Valentich-Scott 2012). To complicate matters further, the type species of *Exosiperna* was described originally under *Arcoperna* Conrad (1865), a genus based on an Eocene fossil from Mississippi. Prasad (1932, p. 81) noted the strong similarity of Conrad's type species (*Arcoperna filosa*) to *Solamen*. It is therefore possible that *Solamen* is a synonym of *Arcoperna*.

In New Zealand *Crenella* is represented in the living fauna by *C. radians* Suter (1908), described from Hen Island off the east Coast of the North Island. Aside from a report of this species from the early late Pliocene of New Zealand (Beu and Maxwell 1990). The genus is absent from Cenozoic faunas. However, three small specimens from the Maastrichtian of the Chatham Islands, described and figured as *Crenella* n. sp. (Stillwell 1998) clearly establish its presence in the New Zealand fossil record. Stillwell noted its similarity to coeval species from Maastrichtian and Paleocene of North and South Dakota. Marinovich (1993) noted the presence of the genus in cool-water faunas of the Late Cretaceous of the Western Interior Seaway of North America as well as the earliest Paleogene (Danian) in Arctic Alaska. The Arctic Ocean was presumably geographically isolated from the North Pacific at this time (Marinovich et al. 1985, Marinovich 1993). Detailed study of the high latitude fossil crenellids may prove useful in reconstructing seaway connections during the Late Cretaceous and Early Paleogene.

Greater attention to the Neogene fossil record and names proposed for taxa in the North Pacific, especially Japan and Alaska, is essential to unraveling Cenozoic history of crenellids. Although it is tempting to introduce a new genus-group name for the two Paleogene species in the Keasey Formation, they are retained in *Crenella* in the treatment that follows.

Stratigraphic range—Cretaceous–Holocene.

CRENELLA PORTERENSIS WEAVER, 1912

FIGS. 3A–C, E; 4A

Crenella porterensis Weaver (1912). p. 15; pl. 14, fig. 115.

Crenella porterensis Weaver, Weaver (1916). pp. 36–37; figs. 41, 42.

Crenella porterensis Weaver, Weaver (1943). p. 115; figs. 3, 4.

Crenella porterensis Weaver, Durham (1944). p. 140.

(unfigured hypotype UCMP 35163).

Crenella porterensis Weaver, Vokes in Warren, Norbistrath and Grivetti (1945). (checklist)

Crenella porterensis Weaver, R.C. Moore and Vokes (1953). p. 119.

Crenella porterensis Weaver, Kanno (1971). p. 47. pl. 1, fig. 27.

Crenella porterensis Weaver, Armentrout (1973). pp. 387–389; pl. 8, fig. 23.

Crenella porterensis Weaver, E.J. Moore (1976). p. 45; pl. 12, fig. 12.

Solamen porterensis (Weaver), Addicott (1976b). p. 29; pl. 4, figs. 3, 11.

Crenella porterensis Weaver, Allison and Marinovich (1981). pp. 4, 8; pl. 1, figs. 5, 6.

?*Crenella* cf. *C. porterensis* Weaver, E.J. Moore (1963). p. 63; pl. 25, fig. 6.

?*Crenella* sp.? Hickman (1969). pp. 33–34.

?*Solamen snavelyi* Addicott (1976b). p. 29; pl. 4, figs. 6, 9. not *Crenella porterensis* Weaver, Tegland (1933). p. 112; pl. 6, fig. 2.

Discussion—*Crenella porterensis* is distinguished by its thin and strongly inflated shell, ovate-elongate shape, prominent prosogyrous umbones, external elongate posterior ligament groove, and sculpture of numerous (>100) very fine radial ribs with distinct narrow interspaces and weaker commarginal ribs. Ribs terminate at the ventral margin to produce fine interlocking crenulations. Increase in the number of radial ribs is primarily by intercalation (Fig. 4A, black arrows) of new ribs, although bifurcation also occurs (Fig. 4A, yellow arrow). Both modes of rib numerical increase may occur on a single specimen. Rib increase is most prominent late in growth on the medial portion of the shell. Shell growth is strongly allometric with an initially ovate shape increasing to elongate and clearly visible at growth checks on a single adult shell (Fig. 2A).

The finely decussate shell surface layer is translucent, and the thin underlying (middle) nacreous layer is visible as a pattern that is enhanced as light passes through fine interruptions of crossing radial and concentric elements of surface sculpture. A third non-nacreous layer is present interior to the middle nacreous layer in some of the Keasey shells. This is consistent with observations of complex crossed lamellar aragonite and other aragonitic microstructures in the interior layer of crenellids (Carter 1990). The interior of well-preserved dry shells of living *Crenella decussata* (Hickman, personal observation) suggests a patchy, discontinuous distribution of mineralogy and microstructure that includes some nacre.

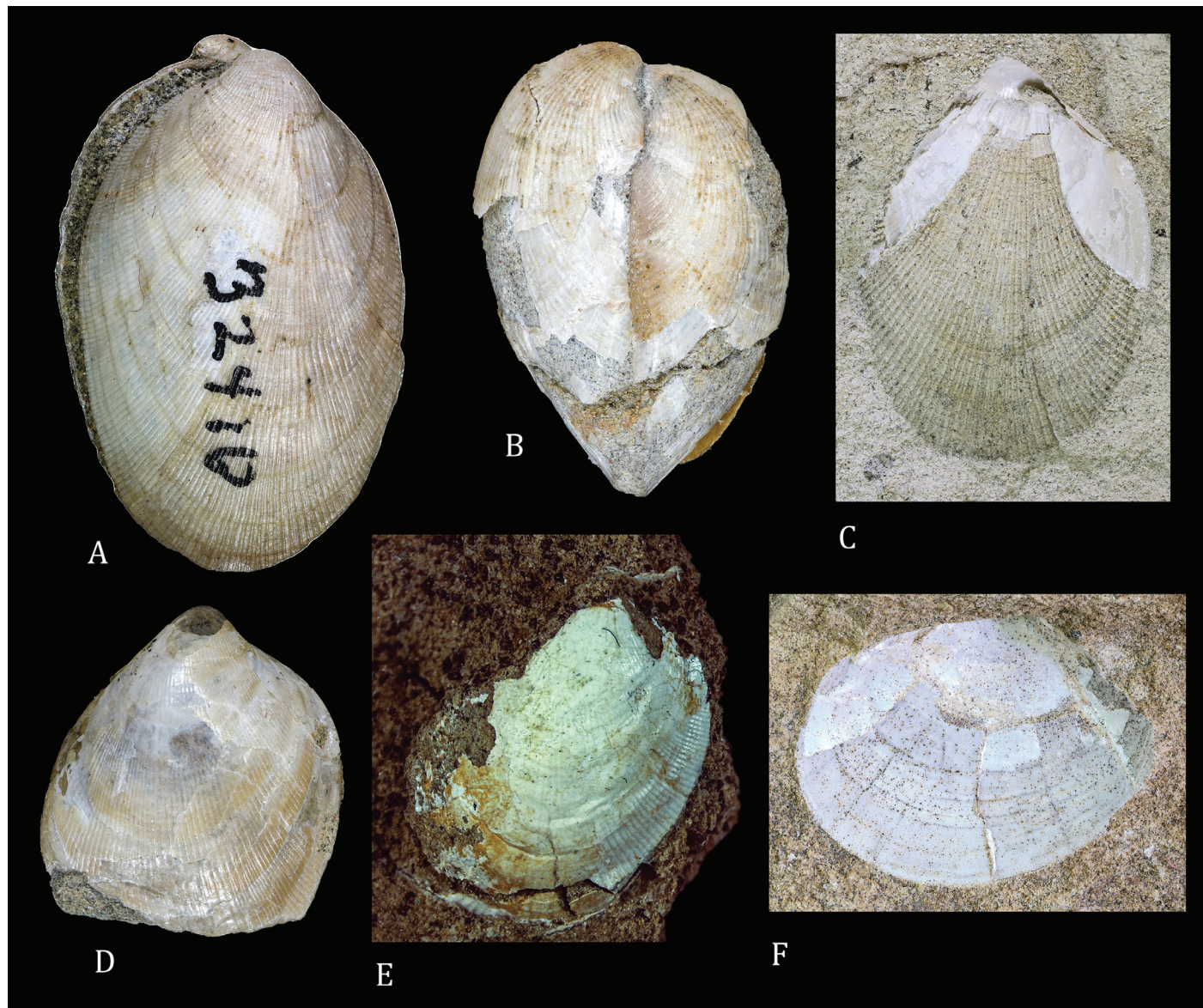


Figure 3. *Crenella porterensis* Weaver (1912) (A–C, E) and *C. washingtonensis* Weaver (1916) (D, F). **A.** Articulated, left valve, hypotype UCMP 32410, Lincoln Creek Formation, height 18.2 mm. **B.** articulated, hypotype USNM 561803, Keasey Formation, height 13.5 mm. **C.** Exterior mold in matrix, hypotype UCMP 110725, Keasey Formation, height 10.8 mm. **D.** Right valve, hypotype UCMP 32250, Blakeley Formation, height 12.5 mm. **E.** Partial shell exterior in matrix, hypotype UCMP 110726, Keasey Formation, height 10.3 mm. **F.** Partial shell exterior in matrix, hypotype 110727, Keasey Formation, height 5.4 mm.

Although none of the specimens examined are sufficiently well preserved for excavation of the hinge, offset of the valves below the beaks reveals part of a thickened denticulate plate (Fig. 3A). A denticulate hinge plate is characteristic of type *Crenella*, distinguishing it from edentulous living species assigned to the genus *Solamen*. This is probably a long-ranging species complex that includes the Miocene crenellid described by Addicott (1976b) as *Solamen snavelyi*. Armentrout (1973) reported it from six molluscan zones extending from the late Eocene into the early Miocene. The Miocene specimen

from the Astoria Formation, illustrated by E.J. Moore (1963, pl. 25, fig. 6) has a denticulate hinge, and the mode of duplication of radial sculpture is consistent with the two modes documented here in *Crenella porterensis*.

Geographically, this is a high-latitude, cool-water species complex, occurring from the Keasey Formation in Oregon to the Poul Creek and Narrow Cape Formations in the Gulf of Alaska (Kanno 1971, Allison and Marinovich 1981). The fauna of the Narrow Cape Formation is noted for its mixture of Asiatic, North American, and endemic high-latitude North Pacific taxa (Allison and

Marincovich 1981).

The Danian *Crenella kannoi* Marincovich (1993) from the Prince Creek Formation on the Arctic coastal plain of Alaska is strikingly similar in size and ovate-elongate shape to *C. porterensis*, but differs in a distinctive pattern of concentric undulations and wavy radial threads. As noted above, Arctic and Northeastern Pacific faunas were not connected at this time.

Material examined—13 specimens.

Figured Keasey hypotypes—UCMP 110725 (in matrix), length 7.9 mm, height 10.8 mm, Loc. UCMP IP7984 (=USGS 25031); UCMP 110726 (in matrix), length 7.9 mm, height 9.8 mm, Loc. UCMP IP2286 (=USGS 15265); USNM 561803, length 8.9 mm, height 9.5 mm. Loc. USGS 15282.

Figured Lincoln Creek hypotypes—UCMP 32410, length 10.18 mm, height 18.2 mm, Loc. UCMP A9 (=UW 256, Weaver's type locality); UCMP 35163, length 11.7 mm, height 18.0 mm, Loc. UCMP A1811.

Keasey Formation localities—Lower member: UCMP IP2286, USGS 15265. Middle member: UCMP IP7984, USGS 15282, 15276, 15277, 15279, 15525. Upper member: USGS 13515, 15518.

Other occurrences—In Oregon this species also occurs stratigraphically higher in the overlying Pittsburg Bluff Formation and Miocene Astoria Formation. In

Washington it occurs in the Eo-Oligocene Lincoln Creek Formation, Quimper Sandstone, and Blakeley Formation.

CRENELLA WASHINGTONENSIS WEAVER, 1916

FIGS. 3D, F; 4B

Crenella washingtonensis Weaver (1916). p. 37; pl. 3, fig. 40.

Crenella washingtonensis Weaver, Weaver (1943). p. 116; pl. 25, fig. 4

Crenella porterensis Weaver, Tegland (1933). p. 112; pl. 6, fig. 2.

Crenella washingtonensis Weaver, Durham (1944). p. 140, unfigured hypotype UCMP 35164.

Discussion—*Crenella washingtonensis* was described from the Lincoln Creek Formation after description of *Crenella porterensis porterensis* and from a different type locality in the Lincoln Creek. It is distinguished by its smaller shell, ovate outline, and inconspicuous sculpture. It is recognized here from a single, distinctly ovate specimen from a locality in the upper part of the middle member of the Keasey Formation. The shell is a left valve with the exterior surface imbedded in matrix (Fig. 3F). The shell is considerably thinner and more fragile than that of *C. porterensis*. Portions of the opalescent interior layer remain intact, and thin exterior layer is sufficiently translucent that exceedingly fine radial

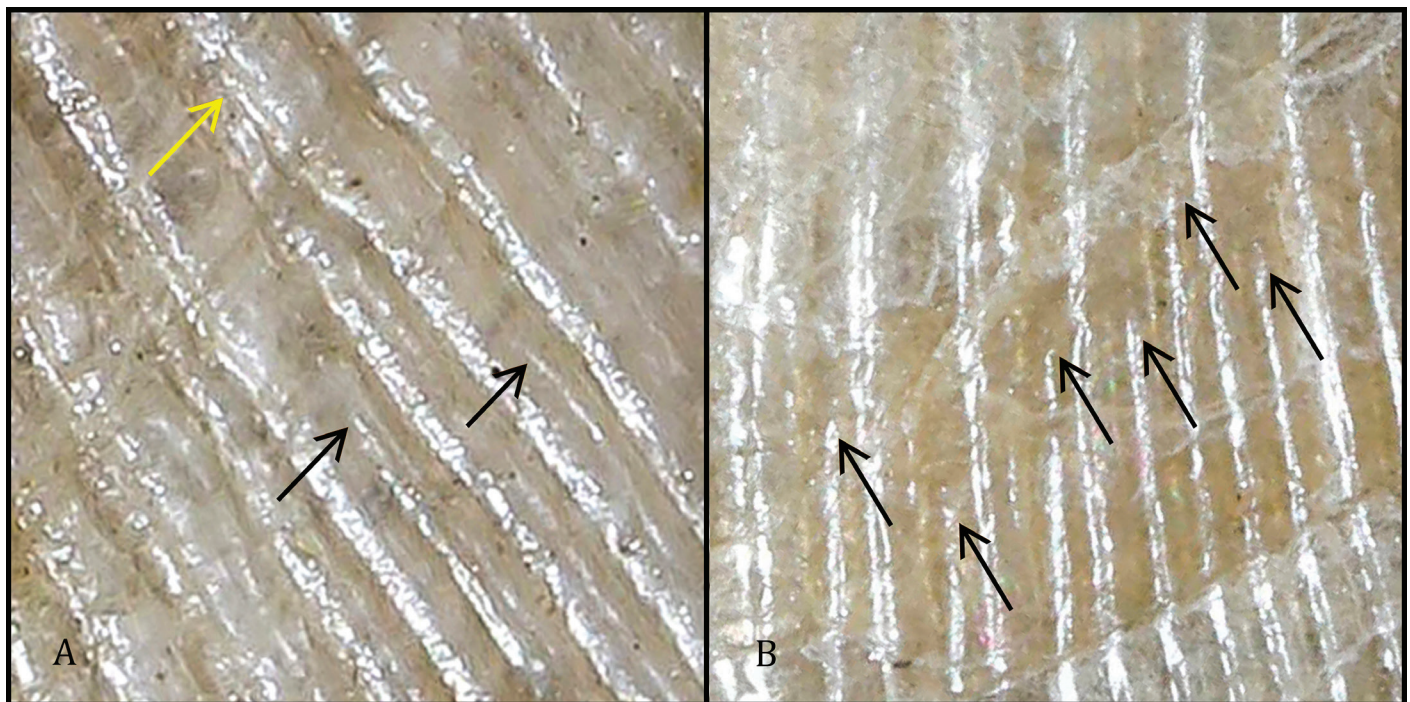


Figure 4. A. *Crenella porterensis* detail of coarser ribs and rib increase by splitting (yellow arrow) and by intercalation (black arrows) (enlarged from Fig. 3A). B. *Crenella washingtonensis* detail of finer ribs and rib increase by intercalation (black arrows) (comparable enlargement from Fig. 3D).

sculpture is visible with a microscope under oblique lighting. The hinge plate is missing and probably was not well developed. The ovate shape may be primarily a correlate of smaller size, although the thin fragile shell and fine ornamentation serve to differentiate it from its more elongate, robust-shelled congener.

The stratigraphic range of this rarer species is unclear. It appears to extend into younger Oligocene strata. Close examination of Tegland's (1933) hypotype of *C. porterensis* from the Oligocene type locality of Blakeley Formation at Restoration Point, Washington reveals an ovate shape and finer radial sculpture (Fig. 3D). It is here re-assigned to *C. washingtonensis*. In addition to finer and more numerous radial ribs, the Tegland specimen also shows numerous insertions of new ribs by intercalation (Fig. 3B).

Figured Keasey hypotype—UCMP 110727 (in matrix), approximate length 7.4 mm, approximate height 5.4 mm, Loc. UCMP IP7984.

ARCIDA J.E. GRAY, 1854

ARCOIDEA LAMARCK, 1809

PARALLELODONTIDAE DALL, 1898

GRAMMATODONTINAE STEPHENSON, 1941

Triassic and Jurassic arcoid taxa assigned to the presumed extinct Parallelodontidae Dall (1898) and Grammatodontinae Stephenson (1941) have received considerable attention from paleontologists although taxonomic distinctions vary among authors. Despite treatment by Arkell (1930a, b) of the genus *Parallelodon* Meek and Worthen (1866), as a subgenus of *Grammatodon* Meek and Haydn (1858), followed by a nomenclaturally misguided attempt to change Dall's family group name to Grammatodontidae (Branson, 1942), the name Parallelodontidae persists. Stephenson's Grammatodontinae stands as a morphologically justified family group name (ICZN Article 24.1) with priority over subsequently-proposed family group names for extinct Mesozoic and Cenozoic taxa that share differences in the form and orientation of anterior and posterior hinge teeth.

On the Pacific Coast of North America most fossil arcoids were described under *Arca* Linnaeus (1758) or *Barbatia* J.E. Gray (1842) in the Arcidae Lamarck (1809). Detailed comparative studies and revision of Cretaceous and Tertiary Arcidae (Schenck and Reinhart 1938, Reinhart 1943) identified very few taxa that required removal and reallocation to the more basal arcoid families. Basal arcoids underwent a dramatic Cretaceous and Cenozoic decline and regional extinction in western North

America. Especially notable is the Cenozoic disappearance of the cucullaeid bivalves that thrived during the Cretaceous in the interior seaway. Following a different pattern from that of the parallelodontids, cucullaeid history is marked by progressive biogeographic contraction into a present-day Indo-Pacific species complex (Buick 2009). The pattern of decline in parallelodontids is more complicated, with relict taxa surviving only in deep water in the Paleogene on the active margin of North America while persisting on shallow carbonate platforms of the epicontinental seas of eastern Europe (Hickman 2021).

The occurrence of a relict parallelodontid in the Keasey Formation is remarkable not only in its narrowly restricted temporal stratigraphic and geographic distribution but also in its occurrence in coeval bathyal assemblages of the Lincoln Creek and Gries Ranch formations of southwestern Washington. These unusual assemblages are part of a transitional "recovery fauna" following local extinction of the "tropical Eocene fauna" and prior to establishment of the "temperate modern fauna" (Hickman 2003). The local extinction and recovery coincide with major tectonic realignment of plates on the Cascadia Margin. The transitional recovery fauna also marks the close of the doubt-house interval (*sensu* Hickman 2021) of global cooling prior to establishment of permanent ice sheets at high latitudes.

Although parallelodontids continue to be treated as extinct (Bouchet and Rocroi 2010), there is at least one confirmed living species and new genus *Kamenevus* Valentich-Scott, Coan, and Zelaya (2020). Other deep-water arcoids, including species assigned to *Bathyarca* Kobelt (1891) and *Bentharca* Verrill and Bush (1898) bear close reexamination as relict parallelodontids or potentially close allies.

Additional genus group names based on small (mostly <20 mm length), thin-shelled species with posterior teeth subparallel with dorsal shell margin and a central edentulous gap are documented with excellent figures and descriptions by Kamenev (2007a, b). These include *Asperarca* Sacco (1898); *Deltaodon* Barnard (1962); *Pseudoporterius* Kamenev (2007a), and *Samacar* Iredale (1936). These taxa also live at offshore depths, frequently >200 m.

Oliver and Holmes (2006) recognized that the evolutionary radiation of modern arcoids mimics that of Paleozoic and Mesozoic parallelodontids. It is therefore possible that some living deep-water forms with subparallel hinge teeth may be parallelodontids while others "may simply display a secondary appearance

of this character associated with the thin nature of the hinge plate” (p. 240–241). It is also a possible result of heterochronic change in miniaturized arcoids.

Stratigraphic range—Lower Ordovician–Holocene.

PORTERIUS CLARK, 1925

Type species—By original designation, *Barbatia andersoni* Van Winkle (1918). Upper Eocene Lincoln Creek Formation, Washington (= *Barbatia gabbi* Dickerson (1917), Gries Ranch Formation).

Pseudogrammatodon Arkell (1930a). p. 307. Type species: *Arca adversidenta* Deshayes (1860), Eocene, Paris Basin.

?*Notogrammatodon* Maxwell (1966). p. 439–441. Type species: *Pseudogrammatodon (Notogrammatodon) inexpectatus*. Eocene, New Zealand.

?*Siptionella* Berezovsky (2014). p. 451–452. Type species: *Siptionella prompta* (Berezovsky, 2002, as *Porterius promptus*), upper Eocene, Ukraine.

Differential Diagnosis—*Porterius* is uniquely characterized by a combination of derived arcid shell shape and sculpture typical of species of *Barbatia* and parallelodontid hinge features that include elongate posterior hinge teeth parallel to the hinge line and separated by an edentulous gap from a series of short, diagonal anterior teeth. The edentulous gap widens during ontogeny as the ligament overgrows the hingeline. The posterior-most teeth in the series are short and chevron shaped and the anteriormost tooth is longer and subparallel to the hingeline. Anterior and posterior teeth are finely striate as in *Barbatia*.

Discussion—When Clark (1925) originally proposed *Porterius* as a subgenus of *Parallelodon* Meek and Worthen (1866), he had limited material and believed that the hinge was “almost if not quite identical” with that of species of the Ordovician to Jurassic parallelodontids, but distinct in having the shell form of younger arcids of the genus *Barbatia*. Clark’s original description and illustrations were an inadequate basis for evaluating the name, and its subsequently contorted history reflects a combination of factors. Most importantly, more than 18 authors who have speculated on the allocation and relationships of *Porterius* have done so based on an inadequate description and without examining fossil specimens. Full review of this confused literature on arcoid relationships is beyond the scope of this treatment, but a few examples follow.

Stewart (1930, p. 68) stated that *Porterius* “is related to *Cucullaria*” Deshayes (1829). Reinhart (1935,

p. 7) suggested that “careful comparison may show that *Pseudogrammatodon* is to be considered a synonym of *Porterius*.” Glibert and van de Poel (1965, p. 48) questioned the validity of *Porterius* because it seemed closely similar to the type of the Paris Basin *Cucullaria* Conrad (1869). Heinberg (1979, p. 116) expressed similar doubt about validity. Maxwell (1966) proposed the name *Notogrammatodon* as a subgenus of *Pseudogrammatodon*, allocating both to Arcidae (?). He stated that “the position of *Porterius* and *Pseudogrammatodon* is in doubt”, but he noted that his knowledge of *Porterius* was based exclusively on Clark’s description and figures. *Notogrammatodon* is treated here as a questionable synonym of *Porterius*.

Berezovsky (2014) described the new genus *Siptionella* to accommodate a species previously described under *Porterius*. However alleged differences in the hinge based exclusively on Clark’s original description are difficult to evaluate and it is here questionably treated as a synonym. Although Berezovsky’s (2015) generic assignments of Paris Basin Eocene arcoid species were based on examination of “well-preserved valves” provided by a colleague in the Netherlands, the possibility for error is always present in material that has not been compared directly with primary types. This same potential for error exists in the Cloez Collection in the Museum of Paleontology at Berkeley, although misidentifications are minimized by indications that “identifications of many or all of the species in the collection were either made by or checked by Cossmann” (Peck 1957). For differences between the hinge plates and teeth of *Porterius* and *Cucullaria* see treatments and illustrations in Hickman (2021).

The possibility of living deep-sea parallelodontids persisting in disguise as arcoids has been expressed by Morton (1982, p. 280), who noted the retention of three elongate posterior teeth parallel to the hinge in the living genus *Bathyarca* Kobelt (1891). As noted above, *Bathyarca* and *Bentharca* Verrill and Bush (1898) are candidates for scrutiny as living parallelodontid derivatives.

Stratigraphic Range—lower–upper Eocene; Holocene?

Geographic occurrences—Washington, Oregon, California, Paris Basin, ?Ukraine, ?New Zealand.

PORTERIUS GABBI (DICKERSON, 1917)

FIGS. 5A–H, 6A–G

Barbatia gabbi Dickerson (1917). p. 167; pl. 29, fig. 4.

Barbatia andersoni Van Winkle (1918). pp. 81–82; pl. 6, fig. 2.

Parallelodon (*Porterius*) *andersoni* (Van Winkle), Clark (1925). pp. 79–80; pl. 8, fig. 33; pl. 9, figs. 1, 6.

“Barbatia” andersoni Van Winkle, Reinhart (1935). p. 7.

Porterius gabbi (Dickerson), Schenck (1936). p. 7.

Cucullaria (*Porterius*) *gabbi* (Dickerson), Effinger (1938). p. 366; pl. 46, fig. 6.

Porterius gabbi (Dickerson), Weaver (1943). pp. 53–54;

pl. 9, figs. 7, 10, 11, 14; pl. 11, fig. 3.

Porterius gabbi (Dickerson), Vokes in Warren, Norbistrath and Grivetti (1945) (checklist).

Porterius gabbi (Dickerson), Warren and Norbistrath (1946). p. 227.

Porterius gabbi (Dickerson), R.C. Moore and Vokes (1953). pp. 115, 118, 119.

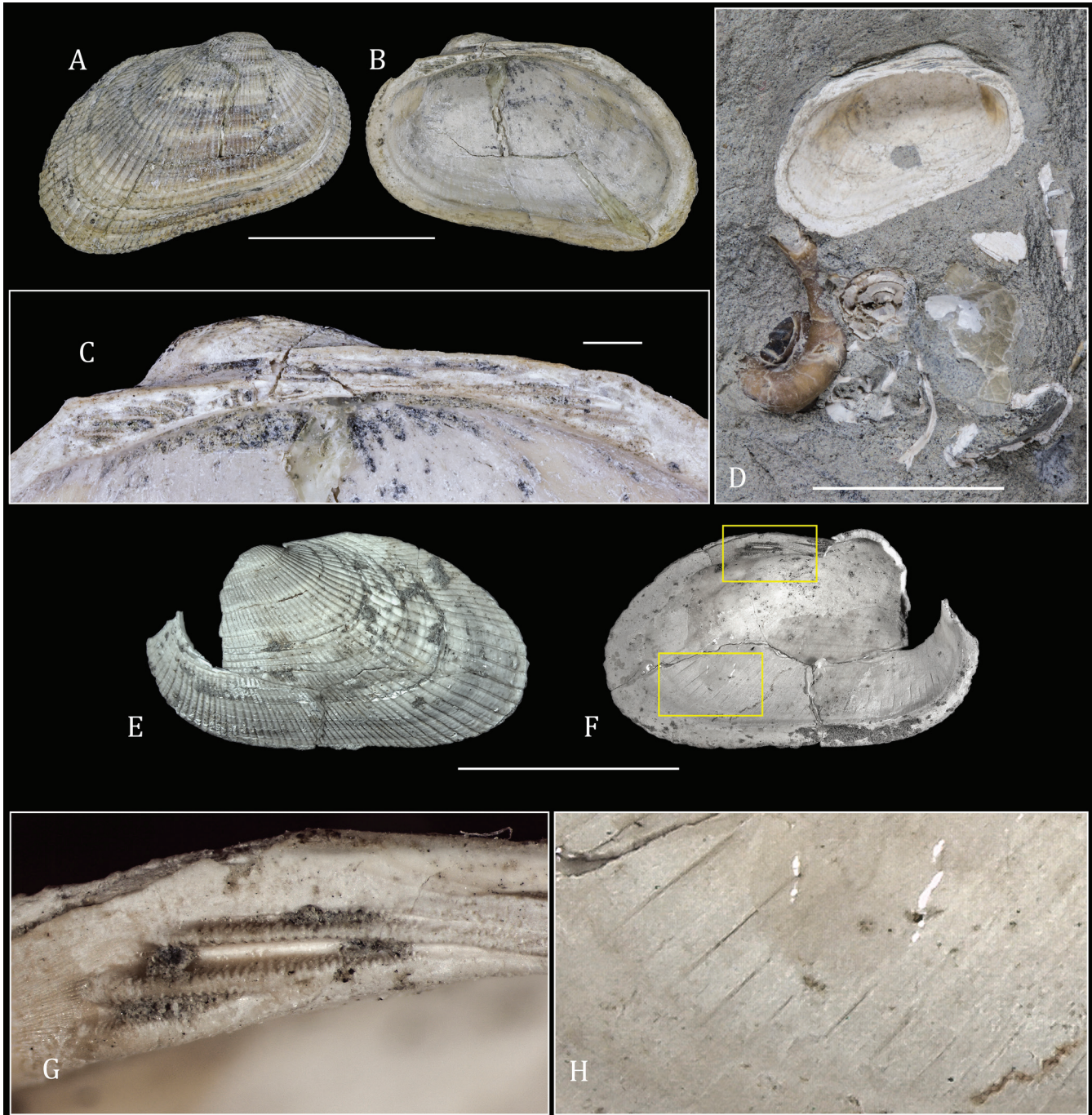


Figure 5. *Porterius gabbi* (Dickerson, 1917), Keasey Formation. **A, B.** Exterior and Interior of right valve, hypotype USNM 561838, scale bar=1 cm. **C.** Detail of cardinal area and hinge plate of **B**, scale bar=1 mm. **D.** Interior of left valve interior in matrix, hypotype UCMP 110736, scale bar=1 cm. **E-H.** Interior and exterior of left valve, hypotype UCMP 110737, with detail views of hinge tooth striations (**G**) and interior shell lines (**H**), scale bar=1 cm.

Porterius gabbi (Dickerson), Hickman (1984), pp. 1223, 1226; fig. 7c.

Amended description—Shell small (length <20 mm), thin; shape ovate-elongate, moderately inflated, strongly inequilateral, with small prosogyrous umbones far anterior to midline; anterior margin rounded and narrow relative to obliquely expanded posterior margin; dorsal margin straight, ventral margin with faint byssal flexure but no indication of gape; exterior sculpture of well-developed radial ribs separated by deep narrow grooves;

posterior ribs becoming broader and flat-topped during growth, anterior ribs remaining narrow and increasing in number, either by splitting or intercalation; comarginal sculpture absent except for irregular growth checks; shell interior with well-developed adductor scars and simple pallial line; inner shell surface with slightly-upraised radial threads of subequal prominence, most distinct where they terminate at pallial line; hinge plate slightly arched, divided into anterior and posterior sets of teeth interrupted by edentulous central gap resulting

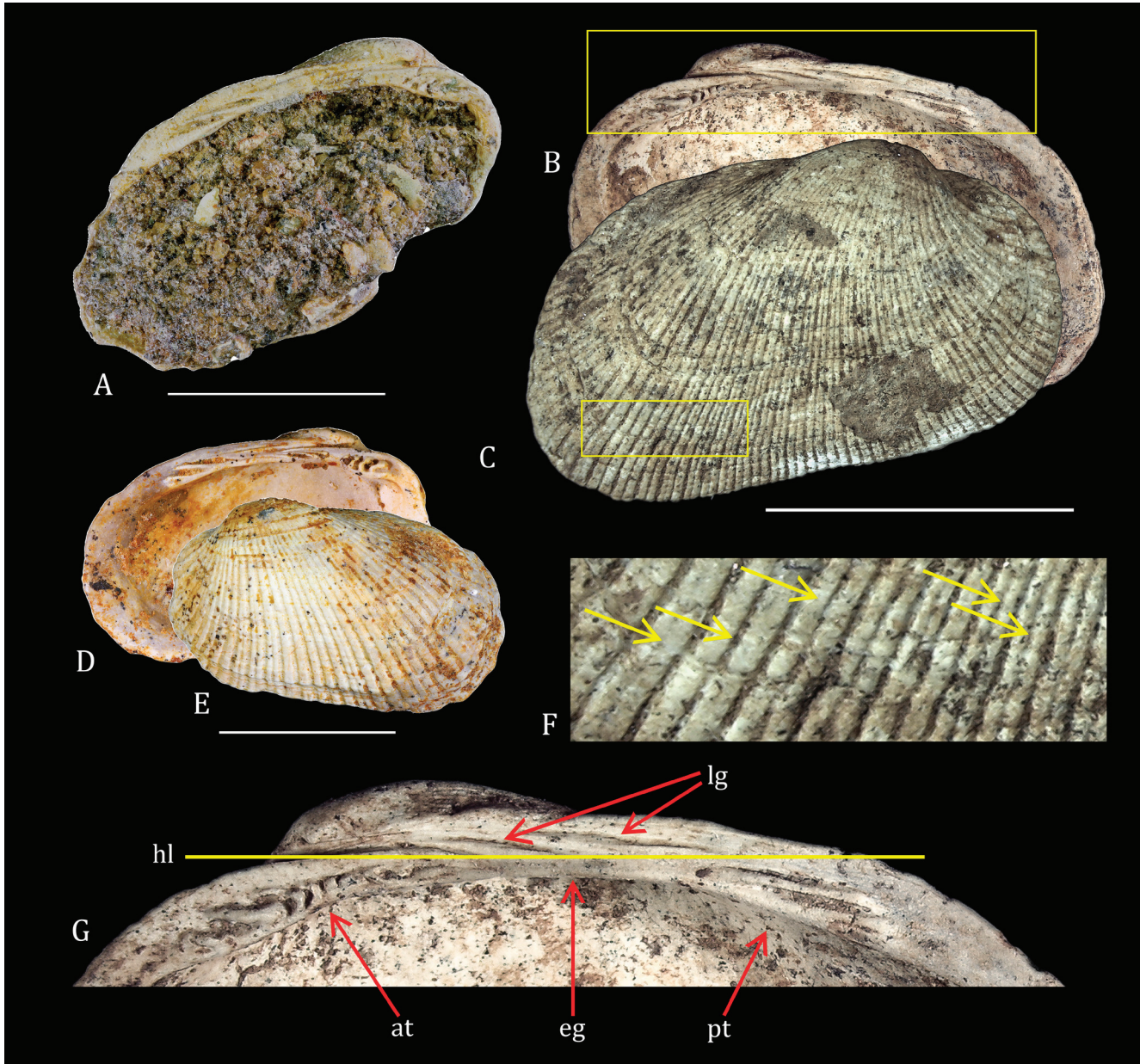


Figure 6. *Porterius gabbi* (Dickerson, 1917), Gries Ranch Formation. **A.** left valve interior of Effinger (1938) hypotype UCMP 32429, scale bar=5 mm. **B, C.** Interior and exterior of adult right valve, hypotype UCMP 110738, scale bar=1 cm. **D, E.** Interior and exterior of juvenile left valve, hypotype UCMP 110739, scale bar=5 mm. **F.** Detail of rib increase by splitting from **C.** **G.** Detail of cardinal area and hinge plate from **B:** **hl**=hinge line, **lg**=ligament grooves on cardinal area, **at**=anterior hinge teeth, **eg**=edentulous gap, **pt**=posterior hinge teeth.

from overgrowth of duplivincular ligament; two or three well-developed posterior teeth, elongate and distinctly parallel to hinge; variable number of small anterior teeth, crowded and chevron shaped with short, vertical posterior segment and longer anterior segment subparallel to hinge; both sets of hinge teeth finely striate.

Discussion—The elongate posterior hinge teeth parallel to the hinge plate (Figs. 5B–D, F, G; 6B, D, G) separated by a broad edentulous central gap (Figs. 5B, C; 6B, G) from the complex of small anterior teeth with anterior segments subparallel to the hinge (Figs. 5B, C) distinguish *Porterius*. Asymmetric growth of the ligament increasingly displaces the anterior and posterior cardinal margins and is less evident in juvenile shells (Fig. 6D). The edentulous gap becomes increasingly large during ontogeny. The faint flexure in the ventral margin of the valves (Figs. 5A, B; 6C) suggests that a weak complex of fine byssal threads provided semi-infaunal attachment, in contrast to the byssal gape characteristic of epifaunally attached arcoids. The ovate-elongate shell shape, lack of a posterior umbonal carina, fine exterior radial sculpture, and fine micro-striation of the hinge teeth provide a superficial similarity to Paris Basin Eocene species of *Barbatia* (Hickman 2021, Figs. 5, 6)

Porterius gabbi is part of the *Acesta* Community of Hickman (1984), where it occurs in patchy epifaunal assemblages in association with giant limids, a terebratulid brachiopod, a vermetid gastropod, basal root tufts of hexactinellid sponges, and occasionally with hexactinellid spicules and fragments of spicular meshworks.

Reliance on poor literature illustrations of fossil material, coupled with failure to examine actual specimens of this species as the type of *Porterius*, has led to questionable allocation of species that extend its geographic range to Europe and the Western Pacific and its temporal range from Eocene to Holocene. Unfortunately, systematic treatment of paralleodontids in the Treatise on Invertebrate Paleontology (Newell 1969) illustrates the hinge of *Porterius* with a drawing of an Eocene arcoid from the Paris Basin. The clarification presented here and by Hickman (2021) is therefore followed by treatment of an older Paleocene–middle Eocene species of *Porterius* from California.

Material examined—18 specimens.

Figured Keasey hypotypes—USNM 561838 (right valve), length 22.6 mm, height 10.5 mm, Loc. USGS 15518; UCMP 110736 (left valve in matrix), length 13.0 mm, height 9.0 mm, Loc. UCMP IP2549; UCMP 110737 (left valve), length 17.3 mm, height 10.6 mm, Loc. UCMP 2540.

Figured Gries Ranch hypotypes—UCMP 32429 (left

valve), length 11.1 mm, height 7.2 mm, Loc. UCMP 3607; UCMP 110738 (right valve, adult), length 22.9 mm, height 11.0 mm), Loc. UCMP IP2289; UCMP 110739 (left valve, juvenile), length 10.0 mm, height 6.5 mm, Loc. UCMP IP2289.

Localities—Keasey Formation: Upper Member: UCMP IP2540, 2549; UGSG 15269, 15315, 15518, 15581, 15601. Gries Ranch Formation: CAS 181 (Dickerson's holotype); UCMP 3607 (Effinger's hypotype), UCMP IP2289. Lincoln Creek Formation: UW 126 (old log dam on Porter Creek).

Stratigraphic range and age—This species is narrowly restricted to upper member of the Keasey Formation, Gries Ranch Formation, and coeval beds in the Lincoln Creek Formation. The age of these beds has been treated alternatively as late Eocene or early Oligocene. The peculiar community assemblages of this “turnover fauna” (Hickman 2003) postdate a dramatic regional extinction of the “tropical Eocene Fauna” and predate establishment of the Oligocene recovery fauna that subsequently led to the temperate “modern fauna.” The transitional turnover assemblages are correlated with the dramatic Oi-1 climate cooling and glaciation at 33.5 MA.

PORTERIUS WOODFORDI (M.A. HANNA, 1927)

FIG. 7A, B

Barbatia woodfordi M.A. Hanna (1927). p. 273; pl. 27, figs. 1, 6, 8, 10.

Porterius woodfordi (Hanna), Reinhart (1937). pp. 176–178.

Porterius woodfordi (Hanna), Vokes (1939). p. 45; pl. 1, fig. 13.

Porterius woodfordi (Hanna), Keen and Bentson (1944), pp. 31, 103.

Porterius woodfordi (Hanna), Givens (1974), p. 41.

Porterius woodfordi (Hanna), E.J. Moore (1983), pp. 46–47; pl. 10, figs. 3, 4.

Discussion—A second Paleogene species of *Porterius*, described from middle Eocene rocks of the Ardath Shale in California, differs from the type species in having finer and more numerous radial ribs with narrower interspaces. The shells of the three specimens in the type lot are relatively thinner, more fragile, as illustrated here (Fig. 7A) by a paratype (UCMP 31063) that was not clearly illustrated by Hanna. Although the types are less well preserved than those of *P. gabbi* it is fortunate that the hinge two of the primary types preserve the elongate posterior teeth that are parallel to the hingeline, confirming that it is, indeed, a paralleodontid. Only the hinge of

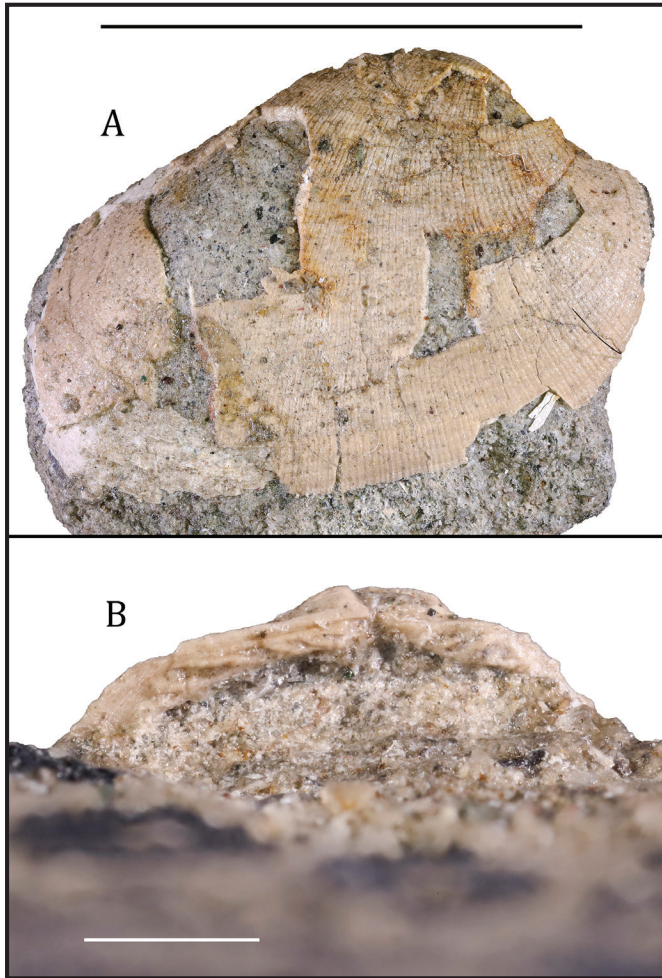


Figure 7. *Porterius woodfordi* (Hanna, 1927), Ardath Shale, paratype UCMP 31063. **A.** Exterior of with numerous very fine radial ribs, scale bar=1 cm **B.** previously unfigured cardinal area and hingeplate, scale bar=1 mm.

the holotype was figured by Hanna, and the hinge of the less well-preserved paratype (UCMP 31063) is illustrated here (Fig. 7B).

Givens (1974) documentation of the geology and molluscan biostratigraphy provides the clearest evidence that the early Eocene occurrence of *P. woodfordi* is in a mudstone facies in a large tropical marine deltaic complex, in a mudstone facies that “was deposited below wave base in a calm outer sublittoral or bathyal environment” (Givens 1974, p. 33). This is potentially a warmer deep setting, rare in the Eocene prior to the onset of the global cooling recorded subsequently in the Keasey fauna.

The Eocene geologic setting in southern California is of special interest here because regional tectonic and paleobathymetric interpretations are independent of the molluscan fauna. The Ardath Shale is part of a

genetically-related complex of intergrading stratigraphic units that record major Eocene coastal submergence (Kennedy and G.W. Moore 1971). The succession also includes graded beds, submarine slides and benthic foraminifera indicative of outer shelf and slope depths.

Refigured paratype—UCMP 31063.

Locality—UCMP 5062.

Stratigraphic range and age—Paleocene (Cerros Shale member of the Lodo Formation) to lower middle Eocene (Ardath Shale). It is also present in the lower Eocene Juncal Formation.

PORTERIUS? COWLITZENSIS
(WEAVER AND PALMER, 1922)

Arca (Barbatia) cowlitzensis Weaver and Palmer (1922), p. 9; pl. 8, fig. 9.

Arca (Barbatia) cowlitzensis Weaver and Palmer; Weaver (1943). pp. 67–68; pl. 12, fig. 13.

Porterius cowlitzensis (Weaver and Palmer), Reinhart (1943). pp. 85–86; pl. 2, fig. 5)

Discussion—A poorly-known species, based on a single specimen from the middle Eocene Cowlitz Formation in Washington, is similar in shape to *Porterius gabbi* but clearly distinguished by very fine radial sculpture. The Cowlitz is a middle Eocene tropical marine deltaic complex (Nesbitt, 1995) intermediate in age between the Ardath Shale and the Keasey Formation. Reinhart (1943) noted the similarity of the Cowlitz shell to *P. woodfordi* and assigned the species to *Porterius* although the hinge plate is not exposed. Because it is impossible to distinguish some species of *Barbatia* from those of *Porterius* without knowledge of the hinge teeth, the generic assignment of the Cowlitz species remains in doubt. The holotype is larger than any of the known specimens of *P. woodfordi*, but it is possible that it represents the same species or is part a Paleogene species complex.

GLYCYMERIDIDAE DALL, 1908

The thick, subcircular shells of glycymeridids are generally considered to reflect life in shallow high-energy environments and poorly sorted coarse sediments. In contrast to arcids, they are free living burrowers, able to plough through sediment with a well-developed axe-shaped foot and capable of reestablishing themselves beneath the sediment-water interface when disturbed (Stanley 1970, Thomas 1970). They are remarkably conservative (Thomas 1975), probably derived from cucullaeid arcoids (Nicol, 1950) and first appearing in the Early Cretaceous (Valenianin). Their evolutionary conservatism has been attributed to specialized

environmental demands, leading Thomas (1975) to characterize the glycymeridid as “a much compromised organism.” In the absence of clear diagnoses of supraspecific groups, there is precedence for treating both living and fossil species under a single genus.

It should not be surprising that glycymeridids were well represented and locally abundant in the tropical Eocene fauna of the Pacific Northwest and that they disappeared with the onset of late Eocene global cooling. They are absent from the post-extinction transition fauna of the Keasey Formation in Oregon (Hickman 1984, 2003) as well as in the recovery fauna (*sensu* Hickman 2003) of the overlying Pittsburg Bluff Formation (E.J. Moore 1976) and coeval Eugene Formation (Hickman 1969). The two glycymeridid species treated here are part of an enigmatic transition faunal assemblage in the Gries Ranch Formation in southwestern Washington. The geographically isolated Gries Ranch beds are here considered coeval with the upper member of the Keasey Formation, based in part on the restricted occurrence of the parallelodontid arcoid *Porterius gabbi*. Although the Gries Ranch mollusks have been interpreted in the past as a free-living shallow-water fauna (e.g., Effinger 1938, E.J. Moore 1976), the assemblage also contains a deep-water giant limid and the thin-shelled *P. gabbi*, both taxa that form byssal attachments. The anomalous presence of the limid and the parallelodontid suggest a dramatic depositional mass movement that displaced shallow-water fauna into a near-shore deep slope setting to form an allochthonous jumbled shellbed (*sensu* Donovan et al. 2013). The glycymeridids are part of the displaced shallow-water component in the conglomeratic facies of the Gries Ranch Formation.

Stratigraphic range—Lower Cretaceous–Holocene.

GLYCYMERIS DA COSTA, 1778

Type species—By tautonymy, *Arca orbicularis* Da Costa (1778) (= *Arca glycymeris* Linnaeus, 1758). Living, Mediterranean.

The relatively thick glycymeridid shell is easily recognized by its nearly equilateral, subcircular shape; typically, with broad flat-topped radial ribs separated by narrow interspaces. The strongly-crenulate interior valve margins are interlocking. The triangular ligament area and alternating ridges and grooves serve as attachment for the duplivincular ligament. The curved hinge plate is typically robust, with interlocking taxodont teeth of nearly equal number anterior and posterior to the beak. Worn shells are frequently chalky, and shell alteration dramatically accentuates radial sculpture that may be

only faintly expressed on pristine specimens.

The two Keasey-equivalent glycymeridids treated below, combine with the Keasey parallelodontid and limosid to provide a snapshot of persistence of the ancient Arcida at a time of marine climate change and geologic change coinciding with tectonic reorganization on the Cascadia margin. These species are restricted to the transition fauna and are absent from the late Eocene tropical faunas of the underlying Cowlitz Formation. Glycymeridids subsequently disappear and are not represented in the recovery faunas of the Pittsburg Bluff and Eugene formations.

Stratigraphic Range—Lower Cretaceous–Holocene.

GLYCYMERIS ANDERSONI DICKERSON, 1917

FIGS. 8A–E, 9A, B

Glycymeris andersoni Dickerson (1917). pp. 166–167; pl. 27, figs. 3a–c.

Glycymeris andersoni Dickerson, Effinger (1938). p. 366.

Glycymeris andersoni Dickerson, Weaver (1943). p. 59; pl. 10, figs. 5, 11.

Discussion—*Glycymeris andersoni* is easily recognized by its ovate, moderately inflated, nearly equilateral shell with broad flat-topped radial ribs and narrow interspaces accentuated by chalky preservation (Fig. 8B, D). The commissural margin is strongly crenulate (Fig. 8D) and the interlocking of the valves is further reinforced by interior crenulation (Fig. 8A, C). Maximum shell size is large (length and height >25 mm) relative to species in the older tropical Eocene faunas of the Pacific Northwest and California. It is abundant in the Gries Ranch Formation and represented by both juvenile and adult specimens of equal linear dimension, consistent with isometric growth. The dorsal slope angle does not differ between large and small shells (Fig. 9A, B), indicating isometric growth.

A second Gries Ranch glycymeridid species, described subsequently by Effinger (1938), is treated below, and figured for comparison.

Material examined—39 specimens from Loc. UCMP IP2289.

Type information—Figured hypotypes, all from Loc. UCMP IP2289: UCMP 110729, length 19.5 mm, height 19.2 mm; UCMP 110730, length 22.1 mm, height 21.6 mm; UCMP 110731, length 29.0 mm, height 27.7 mm; UCMP 110732, length 19.0 mm, height 17.1 mm; UCMP 110733, length 8.2 mm, height 7.6 mm.

Stratigraphic occurrence—This species is known only from the Gries Ranch Formation. It is not present in

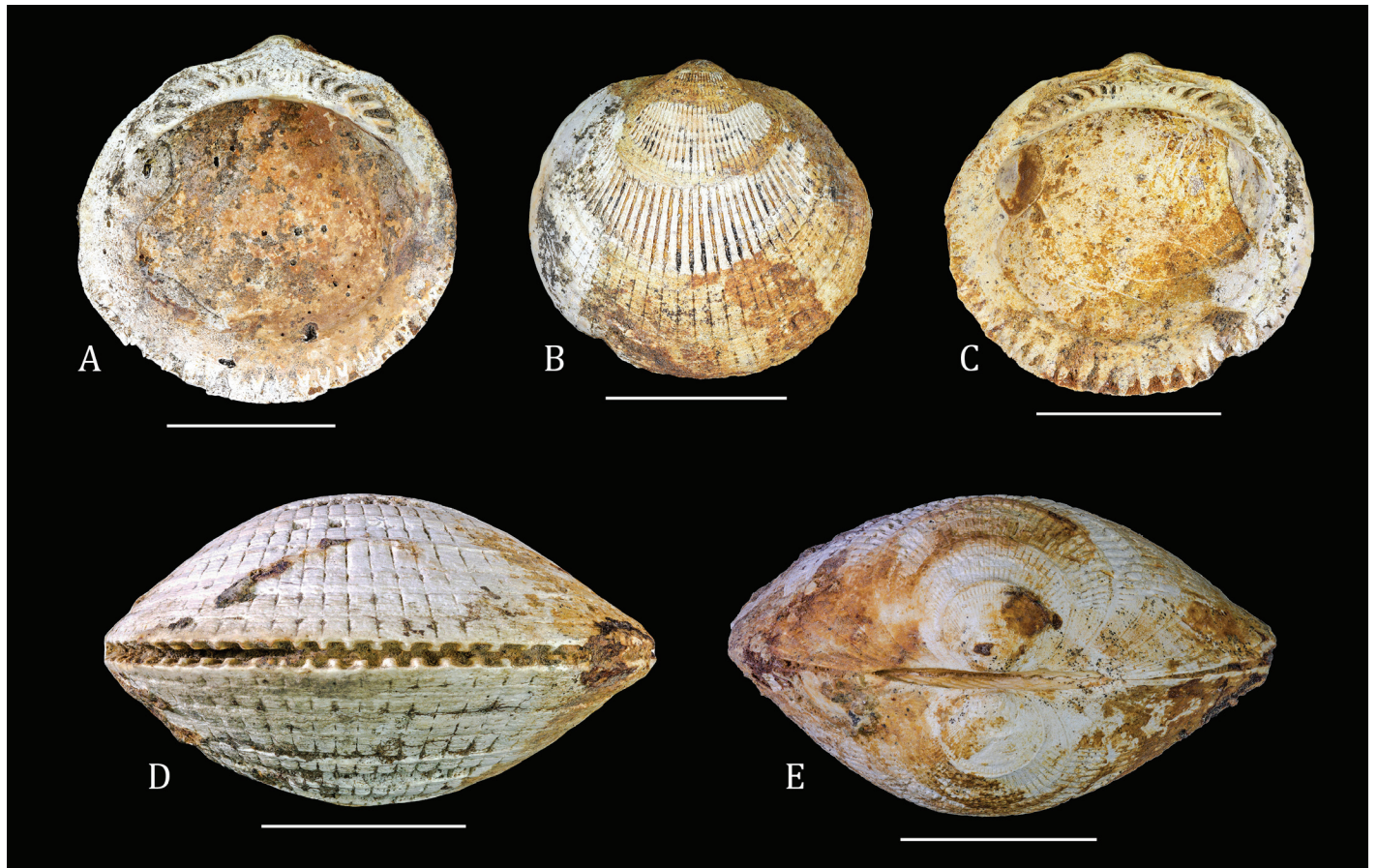


Figure 8. *Glycymeris andersoni* Dickerson (1917), Gries Ranch Formation. **A.** Interior of right valve, hypotype UCMP 110730. **B, C.** Exterior and interior of right valve, hypotype UCMP 110729. **D, E.** Ventral and dorsal of articulated valves, hypotype UCMP 110731. Scale bars=1 cm.

the tropical Eocene fauna of the underlying Cowlitz Formation or in the recovery fauna of the overlying Pittsburg Bluff and Eugene Formations.

GLYCYMERIS WINLOCKENSIS EFFINGER, 1938

FIG. 9C, D

Glycymeris winlockensis Effinger (1938). pp. 366–367; pl. 45, figs. 2, 5.

Glycymeris winlockensis Effinger, Weaver (1943). p. 61; figs. 6, 13.

Discussion—*Glycymeris winlockensis* differs from the more common *Glycymeris andersoni* in its subtrigonal outline, with more prominent beaks and sloping rather than rounded dorsal hinge margin. Although radial ribs typically are not preserved on the shell exterior, they are sometimes visible where corrosion has not removed the thin exterior layer (Fig. 9C). All known specimens are smaller than the largest shells of the more common *G. andersoni*, and differences in dorsal slope angle in the available specimens suggest allometric decrease in the

angle (Fig. 9C, D). More specimens are required for an accurate assessment.

Although the two species co-occur in the jumbled shellbeds at locality UCMP IP2289 and 2548, it is hypothesized that in life they occupied different habitats and depths, co-occurring allochthonously only because of the short-distance downslope transport event suggested above.

Material examined—two specimens from Loc. UCMP IP2289.

Type information—Figured hypotypes, both from Loc. UCMP IP2289: UCMP 110734, length 18.8 mm, height 18.2 mm; UCMP 110735, length 10.0 mm, height 9.9 mm.

Stratigraphic occurrence—This species is known only from the Gries Ranch Formation. It is not present in the tropical Eocene fauna of the underlying Cowlitz Formation. Glycymeridids are absent from the younger recovery faunas of the Pittsburg Bluff and Eugene Formations of the Pacific Northwest.

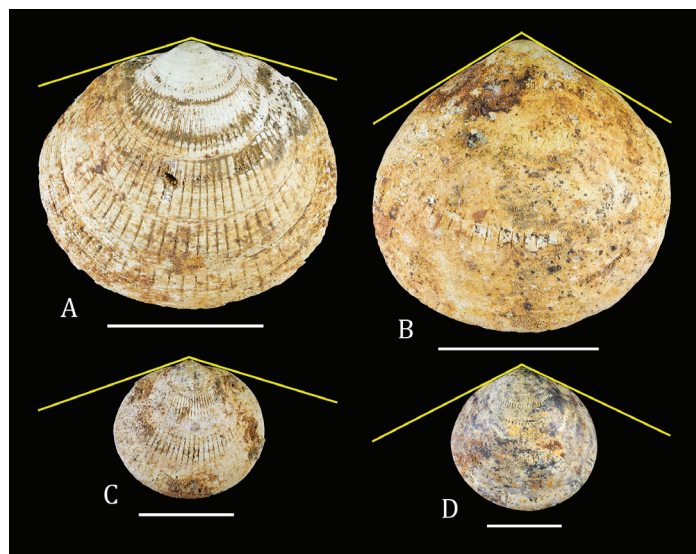


Figure 9. Comparison of dorsal slope angles in Juvenile and adult shells of *Glycymeris andersoni* Dickerson (1917) and *Glycymeris winlockensis* Effinger (1938), Gries Ranch Formation. **A.** Adult *G. andersoni* hypotype UCMP 110732, scale bar=1 cm. **B.** Adult *G. winlockensis* hypotype UCMP 110734, scale bar=1 cm. **C.** Juvenile *G. andersoni* hypotype UCMP 110733, scale bar=5 mm. **D.** Juvenile *G. winlockensis* hypotype UCMP 110735, scale bar=5 mm.

LIMOPSOIDEA DALL, 1895

LIMOPSIDAE DALL, 1895

Thin shells of small to minute limopsid bivalves are rare in Cenozoic faunas of the Northeastern Pacific, occurring primarily in deep-water assemblages. Limopsids appear in the Jurassic (Bathonian), with a probable deeper arcidan ancestry in either the Grammatodontidae or Cucullaeidae. There was a minor limopsid radiation in the Cretaceous followed by subsequent decline as siphonate burrowing bivalves replaced taxa constrained by a nestling, byssate, semi-infaunal life habit. Although the thin aragonitic shells do not preserve well, the typical obliquely ovate shape of the shell, crenulate interior margin, compressed valves, straight hingeline, taxodont dentition, and finely-tessellated sculpture aid in recognition. The alivincular ligament in a central triangular resilifer, when preserved, is an aid in recognizing fossil limopsids. The dense covering of flat-lying, thatched periostracal bristles may aid in the initial preservation of buried shells and is sometimes expressed in external molds in fine-grained siltstone and mudstone.

Although this is a relatively small family group with living diversity concentrated in the Antarctic, high southern latitudes, and deep sea, it has attracted considerable interest for subtle distinctions in shell shape, ligament, and anatomical features considered key to understanding

arcidan evolution (Oliver 1981). The limopsoid ligament has figured in defining constraints on evolutionary diversification in arcidan bivalves as recorded in the fossil record (Thomas 1976). Considerable taxonomic confusion among living species has been resolved through detailed studies of anatomy, shell morphology, and life habits and the designation of thirteen morphological classes in three functional groups (Oliver 1981). Experimental studies demonstrate behavioral flexibility and life positions that vary with substrate type (Oliver and Allen 1980).

Lack of evolutionary diversification is popularly attributed to morphological constraints, and groups that fail to diversify are often viewed as *unsuccessful* or *evolutionary dead ends*. An alternative suggested here is that limopsids are highly successful in their geologically persistent ability to colonize and maintain semi-infaunal populations at the sediment-water interface, between the opportunistic epifaunal exploration of hard substrate diversity and the infaunal partitioning explored by siphonate burrowing bivalves.

Some of the disagreement over the use of available genus-group names and unresolved phylogenetic relationships has been attributed to lack of knowledge of early ontogenetic features (Malchus and Warén 2005). Early ontogeny in Jurassic arcidans suggests heterochronic evolutionary change (Malchus 2004). Deep ancestral relationships are fundamentally a paleontological problem awaiting more detailed study. As a sister group to Arcoidea, deeper Paleozoic origins for the Limopsoidea are possible.

The low-energy fine-grained sedimentary habitat of many limopsids at slope depths is in marked contrast to that of glycymeridids, a similarly conservative low-diversity family group occupying high-energy, poorly-sorted sands and gravels at shelf depths. The deep-water Keasey limopsid described here is consistent with this ecological distinction.

Stratigraphic range—Middle Jurassic–Holocene.

LIMOPSIS SASSI, 1827

Type species—By monotypy, *Arca auritica* Brocchi, 1814. Miocene and Pliocene, Italy. Subsequently recognized living in the Mediterranean and Northeastern Atlantic.

There is no critical review of available genus-group names for limopsids. Tevesz (1977) recognized 17 available names based on species that are insufficiently well characterized to bear critical scrutiny. Beu (2006) documented 20 available names, in chronological order of their proposal, including seven proposed by Tom

Iredale for living Australian species. Shells of the Iredale species are illustrated by Lamprell and Healey (1998). Anatomical and molecular data may require reassignment of some of these taxa to Crenellidae, Philobryidae, or Glycymerididae.

Although the type species is based on a Neogene fossil, it is widely recognized as a significant element in the living fauna of the Mediterranean and Northeastern Atlantic as far north as Norway and possibly the Arctic Ocean at depths ranging from 20 m to >1000 m. Oliver and Allen (1980) provide detailed characterization of the anatomy and shell, ontogenetic variation in shell form, and observations of behavior and variation in shell orientation in different sediment types.

The geographic range of the type species is further extended by (dubious?) live reports from Antarctic, Subantarctic and Arctic faunas. The stratigraphic range of the type species was extended more than a century ago to Paleogene formations in Australia (Victoria and Tasmania) (Tate 1866). There is at least one additional fossil limopsid genus based on a species from the late Eocene of Australia (*Limarca* Tate, 1886). Available genus-group names based on Cretaceous and Paleogene species are seldom used, but well-preserved shallow-marine Cretaceous limopsid shells are locally abundant and available for study in museum collections (Squires 2012).

Taxonomic uncertainty provides strong justification for following the detailed treatment of Oliver (1981), who defined and classified the entire range of limopsid morphological and functional variation using *Limopsis sesu lato*. Conservative recognition of a single genus is increasingly appropriate and prevalent in modern treatments of the diversity of fossil species in the high-latitude southern hemisphere (e.g., Beu 2006, Wittle et al. 2011).

Stratigraphic range—Middle Jurassic–Holocene.

LIMOPSIS SQUIRESI N. SP.

FIG. 10C, E

ZooBank LSID—urn:lsid:zoobank.org:act:8D7171A4-268E-4C19-AA5F-7264CDAF1E94

Diagnosis—Shell small (<10 mm), ovate, nearly equilateral, thin, somewhat compressed, with impressions in matrix of numerous (>40) fine radial ribs and thatched periostracum. Hinge line straight, with central trapezoidal amphidetic alivincular ligament and resilifer. Remnant of fibrous ligament preserved but beaks and hinge teeth missing. Inner aragonitic layer glossy; altered outer layer preserving radial ribs, but lacking fine detail preserved in external mold.

Discussion—Description of a new species based on a

single specimen is seldom justified unless it is extraordinarily well preserved. The specimen described and figured here is remarkable because it does preserve evidence of the characteristic dense exterior periostracum, the ligament pit with altered remnant ligament, and features of both outer and inner shell layers (Fig. 10 C, E). The only previously described *Limopsis* species from the Cenozoic of the Pacific Northwest are based on type specimens that are less well preserved. The primary justification for proposing a new name here is to provide a search image for collectors who are eager to include the potentially valuable specimens and fragments that typically are left behind in the field.

The shell is larger, more compressed, and more obliquely ovate than *Limopsis marysvillensis* Dickerson (1913) (Fig. 10D) from the Paleocene and early Eocene Meganos and Capay Stages (Merriam and Turner 1937) of northern and southern California (E.J. Moore 1983). Dickerson's species is based on a minute (ht. 5 mm, wd. 5 mm) shell from a tropical Eocene fauna in northern California and was subsequently recognized by Givens (1974) from coeval strata in southern California. The species was described originally under *Glycymeris* da Costa (1778) with two line drawings. The holotype was damaged and ineptly glued together but is illustrated photographically here in hinge view (Fig. 10D) because it shows the hinge teeth and trapezoidal ligament and is more informative than Dickerson's drawings. *Limopsis nitens* (Conrad, 1849) from a bathyal methane seep horizon in the uppermost Lincoln Creek Formation (early Oligocene) also has a smaller, thicker, and more inflated shell that is distinctly crenulate on the inner margin. It is abundant at the type locality (Knappton, Washington) and well documented by E.J. Moore (1963) and Kiel (2010). *Limopsis carmanahensis* Clark (1925) from the upper Oligocene Sooke Formation on Vancouver Island, was described from a single specimen. Because it lacks a straight dorsal margin and exposed hinge it cannot be confirmed as a limopsid. *Limopsis phrear* Woodring (1938), known only from lower Pliocene well cores in the Los Angeles Basin, is more obliquely ovate and more closely allied with living Eastern Pacific deep-water limopsids. A specimen of the living *L. panamensis* Dall, 1902 from 1,719 m (reported as 940 fms.) is illustrated here (Fig. 10A, B). Epibenthic dissolved oxygen concentrations associated with live-collected individuals indicate that it lives under moderately to severe hypoxic conditions (Suárez-Mozo et al. 2019).

Limopsid history in the Northeastern Pacific has four distinct phases: (1) Late Cretaceous diversification and

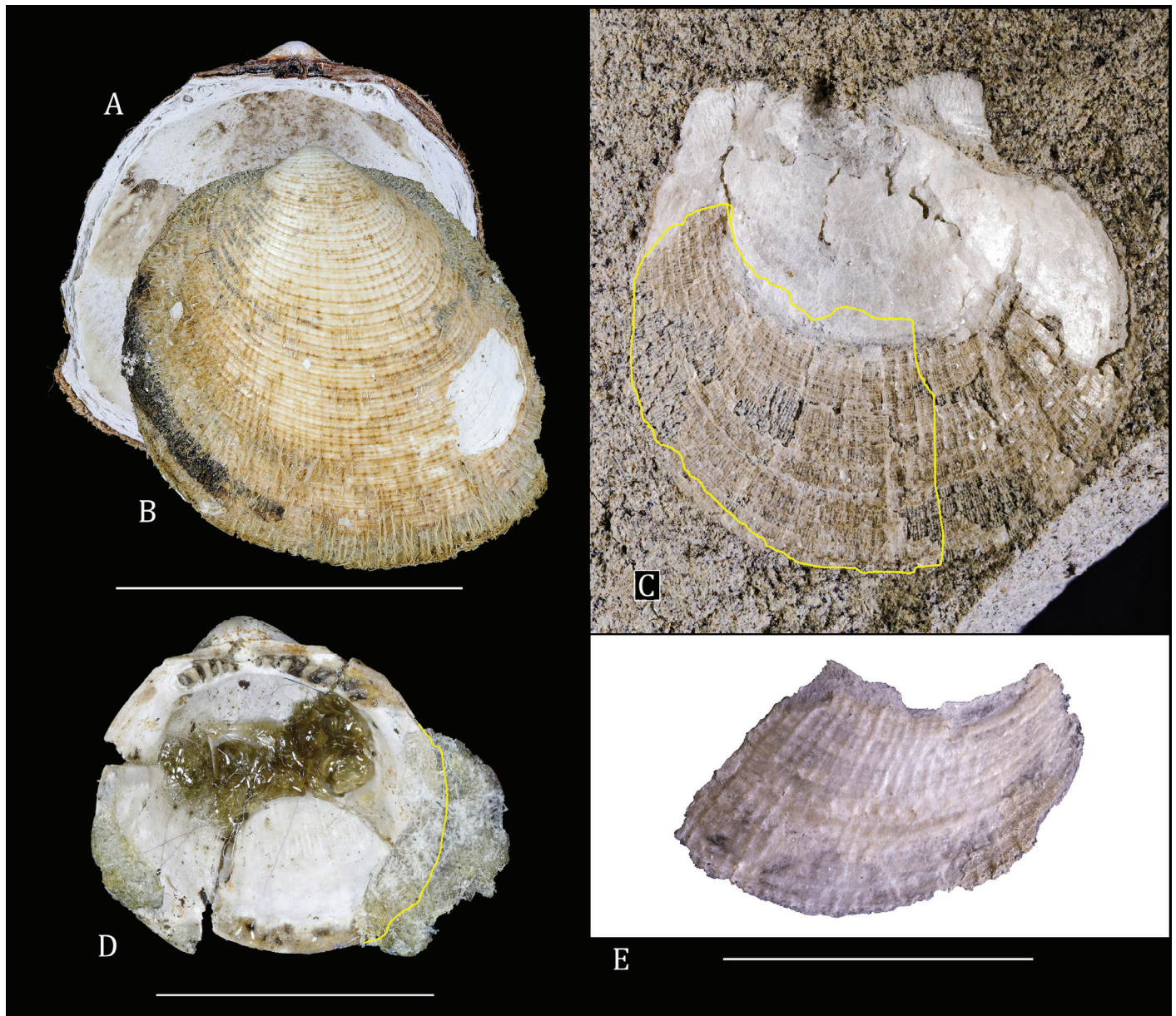


Figure 10. Living and fossil limopsids. **A, B.** Exterior and interior of left valve, *Limopsis panamensis* Dall (1902), SBMNH 474078, scale bar=1 cm. **C, E.** *Limopsis squiresi* n. sp., Keasey Formation holotype, UCMP 110728. **C.** Left valve shell interior and resilifer preserved dorsally in matrix, with remnant periostracum and exterior shell of right valve preserved ventrally. **E.** Fragment of right valve exterior outlined in yellow on **C**, removed and inverted. Scale bar=5 mm. **(D).** *Limopsis marysvillensis* (Dickerson, 1913), Capay formation holotype, UCMP 11766.

prominent representation in shallow-water communities (Squires 2012) followed by (2) Paleogene decline in diversity, shell size, and abundance in the tropical Eocene fauna, (3) Eo-Oligocene disappearance from shallow water at the onset of global cooling, and (4) appearance in deep-water turnover communities (Hickman 2003) in association with chemosymbiotic bivalves. Prominence in deep- and cold-water environments in the Northeastern Pacific persists in the modern fauna.

Limopsid history in the southern hemisphere is characterized by a similar Cenozoic transition at the onset of global cooling. The event corresponds with the isolation of Antarctica and establishment of the circum-Antarctic Current and resulted in an evolutionary radiation of cold-water limopsids (Whittle et al. 2011).

Etymology—Named for Richard L. Squires in recognition of his many contributions to systematic paleontology of Paleogene mollusks of the Northeastern Pacific and

his documentation of Late Cretaceous shallow-water limopsids.

Material examined—one specimen. The new name is proposed following focused examination of fossil and living limopsids in an effort to encourage more careful attention to poorly preserved and fragmental material in Paleogene bathyal facies, including unique detail in external molds in fine-grained rocks.

Holotype—UCMP 110728, length 9 mm, height 9.5 mm (a nearly complete disarticulated left valve).

Type locality—UCMP IP1600 (=USGS 15315). Upper member, Keasey Formation. The specimen was collected and donated by Casey Burns. The fauna at the type locality includes basal root tufts of hexactinellid sponges and a unique assemblage of bivalves suggestive of methane seepage, hypoxic conditions, and chemosynthetically fixed carbon.

Comparative figured material—*Limopsis marysvillensis*, holotype, UCMP 11766 and *Limopsis panamensis*, hypotype, SBMNH 474078.

PTERIIDA NEWELL, 1965

PTERIOIDEA J.E. GRAY, 1847

ISOGNOMONIDAE WOODRING, 1925

Isognomonids are an ancient cosmopolitan group of shallow water, epifaunal and semi-infaunal, byssally attached bivalves that first appear in the Permian. Shells are edentulous, with an internal multivincular ligament. Shell shape varies from rounded to narrowly elongated. Taxonomy and phylogenetic relationships are poorly resolved and contentious because isognomonids are only one of five pteriid families with multivincular ligaments, variation in shell shape, and variation in inferred life habit. Fossils in these families are often poorly preserved. Independent origins of the multivincular ligament have been proposed by many authors (e.g., Cox 1954, Kauffman and Runnegar 1975, Fischer-Piëtté 1976, Crampton 1988, Knight and Morris 2009). A brief comparative summary of each family follows.

Isognomonidae and Pulvinitidae Stephenson (1941) are the only two families with living representatives and known anatomy and are the most easily distinguished. Living and fossil Pulvinitids are distinguished by few, closely spaced ligament grooves with narrow interspaces and a circular foramen in the right valve. The byssus emerges from the foramen in the deep-water monotypic genus *Foramolina* Hedley (1914). The life habit is epibyssate and acline, closely attached with valves horizontal to the hard substrate. Pulvinitids are the most easily distinguished from the other duplivincular families by the

byssal foramen in the functionally ventral valve. Brooding has been documented in living *Foramolina*, (Tëmkin 2006) although planktotrophic development is inferred Isognomonids and other pteriods.

Pulvinitids appeared in the Late Jurassic and have a highly discontinuous fossil record and biogeographic distribution. However, two species described by Zinsmeister (1978) from the Paleogene of southern California along with a new species from the Cretaceous of the Antarctic Peninsula demonstrate survival across the K-Pg boundary. A Paleocene species subsequently described from the Atlantic Coastal Plain of North America (Ward and Waller 1988) further demonstrates survival, although there is a significant gap between the shallow-water Paleocene species and the living deep-water Australian species.

Isognomonidae and Inoceramidae Giebel (1852) are less easily distinguished. Cox (1954) saw no reason to recognize them as separate, although he subsequently did so in the Treatise on Invertebrate Paleontology (Cox 1969a, b). Other authors have noted differences that include shell microstructure and attachment of the ligament to the interior, aragonitic nacreous layer in isognomonids and to the exterior prismatic calcitic layer in inoceramids. However, ultrastructural evidence suggests that architectural reorganization of hingeplate mineralogy from aragonitic to calcitic occurred within inoceramids between the Jurassic and Cretaceous (Knight and Morris 2009). Additional distinguishing features of the inoceramid ligament area include more numerous ligament pits and wider interspaces between pits. Crampton (1988) provides a detailed and well-illustrated comparison of diagnostic and differential characters of the two families, including a table with literature references and page numbers. Both families include a variety of shell shapes and both epibyssate and endobyssate species.

Isognomonidae and Retroceramidae Koschelkina (1971): Triassic and Jurassic retroceramids have been separated more recently from placement in Isognomonidae. As in isognomonids the ligament area is attached to an inner aragonitic hingeplate, but Crampton (1988, p. 972) notes that some Late Triassic and Early Jurassic species are difficult to assign to either family, an observation consistent with difficulties reconstructing evolutionary divergences in the Early Mesozoic.

Isognomonidae and Bakevillidae King (1850): Cox (1954) resuscitated Bakevillidae as a family-group name for another group of multivincular taxa from the Permian of England with distinctive obliquely-elongate shells with a prominent posterior wing. Irregular spacing of the ligament pits is a distinctive apomorphic feature

of bakevillids (Waller 1998). Isognomonids may have arisen from bakevillids in the Triassic, but this is another Early Mesozoic evolutionary scenario that lacks strong support.

Stratigraphic range—Permian–Holocene.

ISOGNOMON LIGHTFOOT, 1786 EX SOLANDER MS.

Type species—By tautonymy, *Ostrea isognomum* Linnaeus, 1758. Holocene, Indo-Pacific.

ISOGNOMON? SP.

FIG. 11

Discussion—A nacreous shell fragment from the upper member of the Keasey Formation preserves a portion of the ligament area of an isognomonid that clearly shows four narrow ligament pits and five broad, shallowly concave interspaces. The specimen preserves features that cannot be compared with *Isognomon clarki*, originally described as *Pedalion clarki* by Effinger (1938) from the coeval Gries Ranch Formation, or with the slightly older new genus and species described below from the middle member of the Keasey Formation. However, it is noteworthy in showing details of the ligament area that are not clearly preserved on any Paleogene isognomonid specimens from the Eastern Pacific margin of North America. The ligament area is clearly attached to nacreous aragonitic shell layers, and ontogenetically the width of the pits expands while the broad, concave interspaces contract in width.

Figured specimen—USNM 561801, length of fragment is 32 mm.

Keasey Formation Locality—USGS 15581. Upper member, Keasey Formation.

BATHYISOGNOMON N. GEN

Type species: *Bathysisognomon smithwickensis*. Upper Eocene, middle member, Keasey Formation, northwestern Oregon.

ZooBank LSID—urn:lsid:zoobank.org:act:A072890E-4645-4A24-AB91-1527878B3076

Diagnosis—Shell mytiliform, inflated and equivalve; edentulous; ligament area narrow, with few widely-spaced ligament pits and broad interspaces; ligament attached to interior nacreous shell layer; beaks small, prosogyrous, forming sharply acute angle at anterior end of hingeplate; lacking byssal gape, but with distinct byssal concavity immediately anterior to beaks; posterior margin of hinge line merging gradually with posterior shell margin.

Discussion—The shell shape, thick inflated valves,



Figure 11. *Isognomon?* sp. Fragment of nacreous isognomonid ligament area with narrow ligament pits and five shallowly concave interspaces. USNM 561801. Scale bar=1 cm.

and details of the ligament area are in marked contrast to the thin, compressed, elongate shells of typical shallow-water isognomonids and indicate an endobyssate, semi-infaunal mode of life. This mode of life is consistent with the fine-grained tuffaceous siltstone in which it occurs, in marked contrast to the epibyssate mode of other isognomonids, which occur on or nestling in hard substrata in shallow water.

This contrast in mode of life and shell form also occurs in Mesozoic inoceramid bivalves, which include both endobyssate and epibyssate taxa (as well as some forms that are free-living), although the inoceramids are clearly distinguished by numerous closely-spaced ligament pits and ligament area that is attached to the outer prismatic calcitic shell layer. The outer shell layer is not preserved on any of the specimens of the new genus and species, which appears to be a result of exfoliation of outer shell as well as some of the interior nacreous layers. The exfoliation is attributed to post-exposure weathering. Available specimens were not collected *in situ*, although they are double valved and indicate lack of exposure and transport prior to burial.

Etymology—bathy (from the Greek *bathos*, deep water), + *Isognomon*.

Stratigraphic range—upper Eocene, known only from massive siltstone beds of the upper part of the middle member of the Keasey Formation.

BATHYISOGNOMON SMITHWICKENSIS N. SP.

FIGS. 12A–F, 13A–C

Isognomon clarki (Effinger, 1938) Squires (1989), in part, p. 279.

ZooBank LSID—urn:lsid:zoobank.org:act:3E81A342-9A89-4CBD-8A0B-B84164CA2CB0

Diagnosis—Same as diagnosis of the genus, which

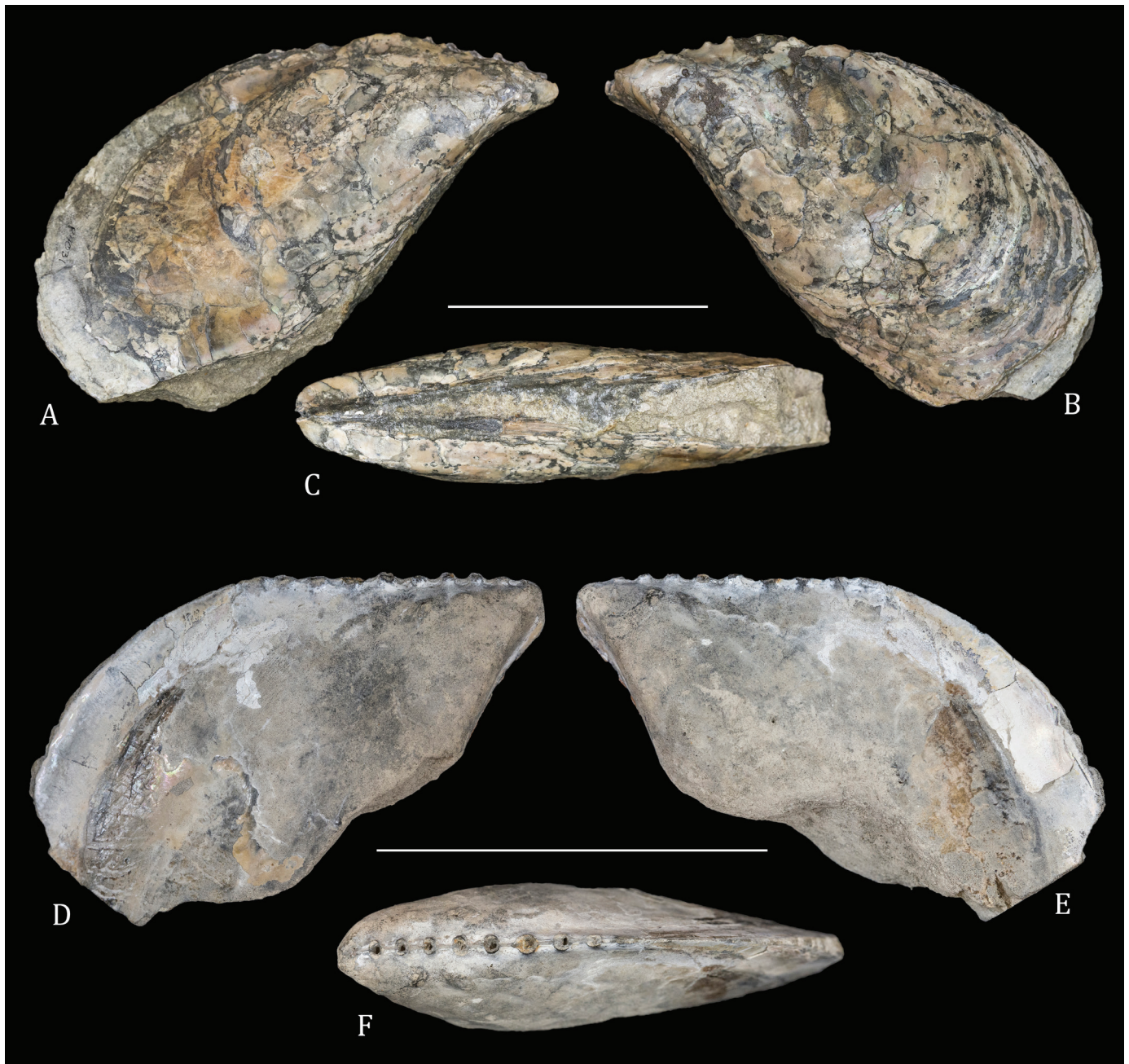


Figure 12. *Bathysisognomon smithwickensis* n. sp. **A–C.** Right valve exterior, left valve exterior, and exterior view of ligament pits, double-valved holotype, UCMP 110744. **D–F.** Right valve exterior, left valve exterior, and exterior view of ligament pits, double-valved paratype, UCMP 110745. Scale bars=5 cm.

is monotypic.

Description—The hinge line is slightly arcuate and there is no distinct posterior wing or auricle. The beaks are produced, forming a narrowly acute angle (40–50°). There is a sharp anterior byssal indentation beneath the beaks followed by a nearly straight anterior shell margin. The posterior and ventral margins are evenly rounded posterior to the hinge line. The ratio of height to length=0.7.

Discussion—The description of this species is necessarily broad and subject to qualification based on additional specimens and better preservation of the outer calcitic shell and ornamentation that are not present in the type material. The thickness of the interior aragonitic shell is unknown due to exfoliation of individual layers, which is common in fossil isognomonids with disintegration of the organic layers separating successive thin nacreous increments. This phenomenon is illustrated here

(Fig. 14A–C) in a set of stacked layers of isognomonid nacre (UCMP B-5162) from Miocene strata of the Calvert Cliffs, Chesapeake Bay, Maryland.

Squires (1989) conservatively assigned all isognomonid specimens from the Eocene of California, Oregon, and Washington to *Isognomon clarki*, considering it a single highly variable species with preservation inadequate for morphological separation. Specimens described as *Isognomon* n. sp.? by Givens (1974) from older Eocene strata of the Juncal Formation in California (Loc. UCR 4752) have a similar mytiliform shape but are proportionally wider and less long than the new Keasey species and come from a calcareous sandy conglomerate lens in a shallower depositional facies. Word-of-mouth references to Keasey specimens in private collections from the Smithwick Quarry could not be confirmed, and access to the abandoned site is now prohibited.

Etymology—The name refers to the now abandoned Smithwick Concrete Products Haydite Quarry, commercial source for manufacture of lite-rock, a mid-20th century strong, lightweight aggregate material used in dam and bridge construction. Large quantities of volcanic ash in the massive tuffaceous siltstone beds at the Smithwick and Empire Quarries produced a composite of exceptional quality.

Material examined—The description is based on the two double-valved type specimens (Figs. 12A–F) and a tentatively-assigned large, double-valved partial specimen (Fig. 13A–C) from the upper middle member of the Keasey Formation.

Holotype—UCMP 110744, length 10.2 mm, height 8.6

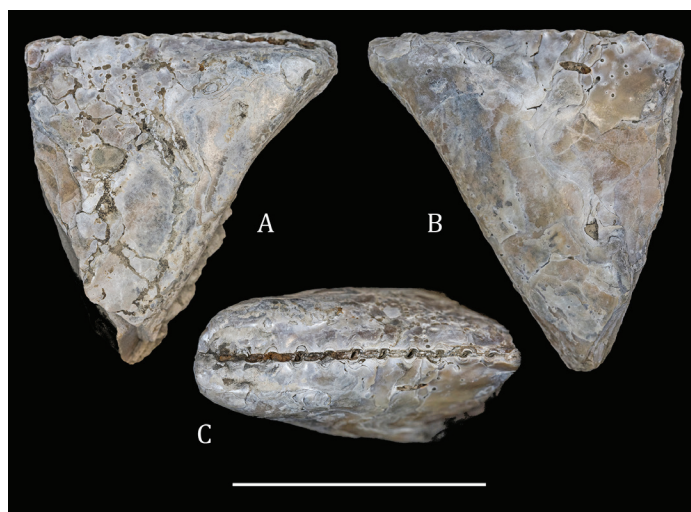


Figure 13. *Bathysisognomon smithwickensis*? Right valve exterior, left valve exterior, and exterior view of ligament pits on large, incomplete specimen from Loc. LACM IP5806. Scale bar=5 cm.

mm. Loc. UCMP IP7984.

Paratype—UCMP 110745, length 7.1 mm, height 5.0 mm. Loc. UCMP IP7984.

Tentatively-assigned—Loc. LACMIP 5806, length (incomplete) 6.5 mm, height (incomplete) 7.5 mm.

Type locality—UCMP IP7984. Upper middle member.

PECTINIDA J.E. GRAY, 1854

PECTINOIDEA RAFINESQUE, 1815

The ancient order Pectinoidea originated in the Carboniferous. Two of the major clades recognized by Waller (1978, 1991, 2006) are represented in the Keasey Formation. Both appeared in the Middle Triassic. The pectinids are here recognized as having a ctenolium (Fig. 16C), a feature that is absent in propeamussiids. However, the ctenolium is variable in its morphological expression and may have arisen multiple times as a series very fine denticles along the ventral margin of byssal notch, serving functionally to separate fine byssal threads and increase attachment stability. Pectinoidean family-group relationships remain unresolved, and molecular data further suggest that propeamussiids are not monophyletic (Smedley et al. 2019). While supraspecific allocation of

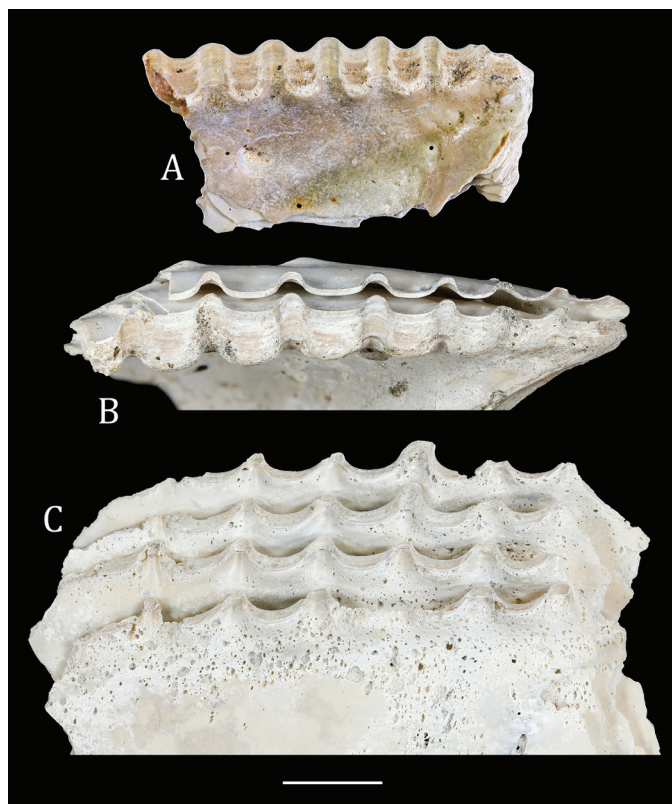


Figure 14. Unidentified isognomonid shell with successive nested nacreous layers separated by diagenetic loss of organic shell layers, unidentified species, Miocene of Maryland, Loc. UCMP B-5162. Scale bar=1 cm.

the Keasey taxa is necessarily provisional, intensive collecting has yielded well-preserved specimens that are morphologically distinct and assignable to family-group shell morphotypes and ecotypes.

Stratigraphic range—Carboniferous–Holocene.

PECTINIDAE RAFINESQUE, 1815

Pectinids are the best known of the pteriomorph bivalves. Commonly known as scallops, the family includes many living and fossil species in cosmopolitan genera. Shell microstructure and mineralogy and the prismatic or foliated calcite of exterior microsculpture are often exceptionally well preserved in fossil pectinids, and the abundance and short stratigraphic ranges of many species have made them especially important in Cenozoic biostratigraphic zonation and correlation. The fossil record of Northeastern Pacific pectinids is predominantly a shallow water record. Less well known are the small-shelled deep-water (>200 m) pectinids and propeamusoids (mud pectens and glass scallops). They are the most

abundant bivalves in the Keasey fauna. However, they are seldom collected and poorly represented in museum collections because the thin translucent shells are fragile and often crushed. They often occur in dense but highly localized aggregations (Fig. 15A–D). Shells in some of these assemblages are peculiarly associated with large numbers of small echinoid spines (Fig. 15C) or amber-colored fragments of fish scales (Fig. 15D). Preservation is usually inadequate for generic and species recognition, and even when delicate ornamentation is well preserved it is difficult to photograph. Low angle illumination required for photography often produces optical illusions in which negative features appear positive. Scanning Electron Microscopy contributes significantly to characterizing microsculpture of the new species described below.

Stratigraphic range—Lower Triassic–Holocene.

CAMPTONECTINAE HABE, 1977

DELECTOPECTEN STEWART, 1930

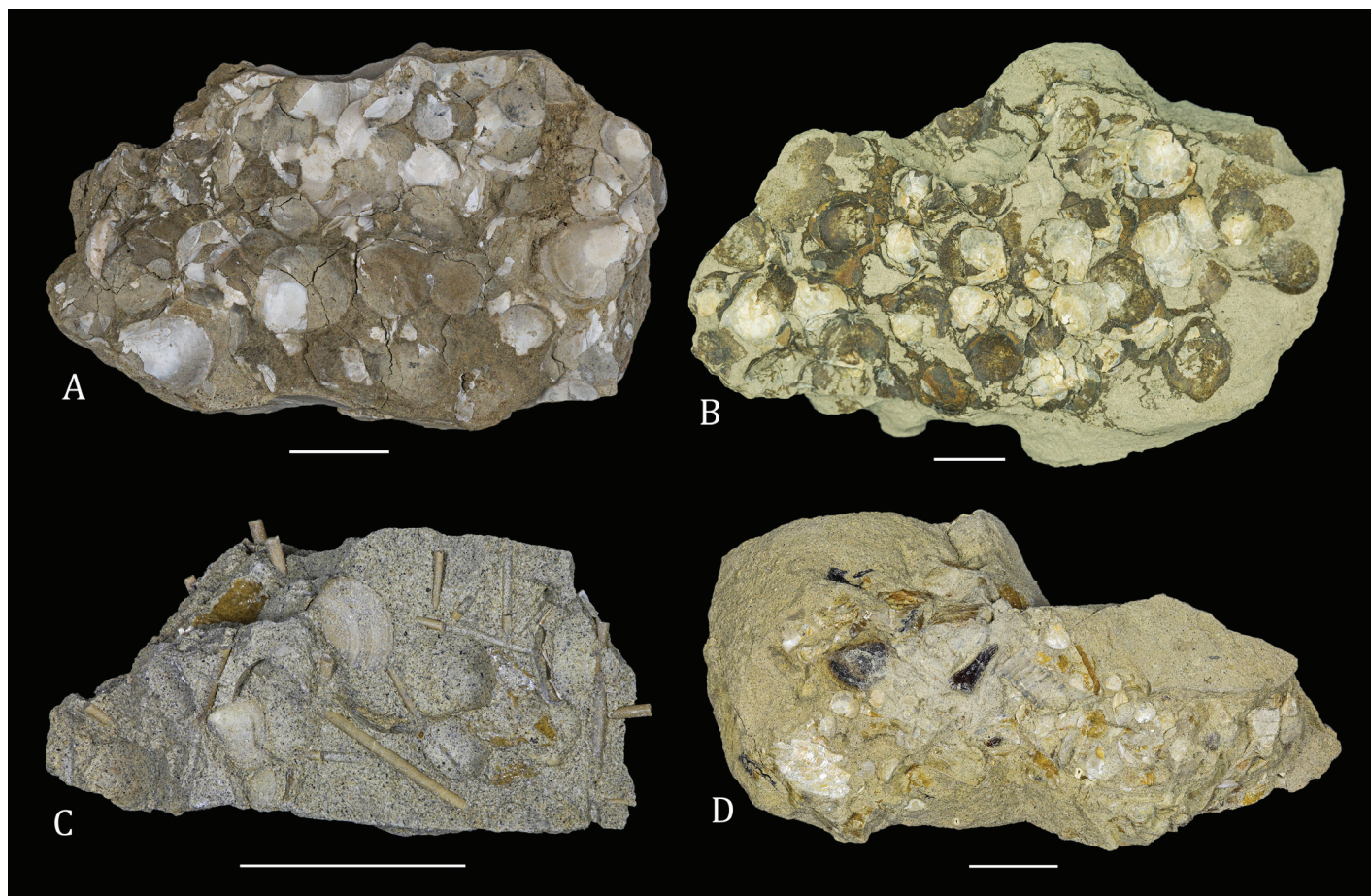


Figure 15. Dense concentrations of mud pectens in matrix. **A.** *Delectopecten keaseyorum* n. sp. in silty mudstone, middle member. **B.** *Delectopecten keaseyorum* in tuffaceous siltstone. **C.** *Delectopecten kieli* n. sp. in silty mudstone with echinoid spines. **D.** *Delectopecten kieli* in silty mudstone with fish scales and bone. Scale bars= 1cm.

Type species—by original designation, *Pecten* (*Pseudamussium*) *vancouverensis* Whiteaves (1793). Holocene, North Pacific. Pliocene of California.

A peculiar form of surface ornamentation, defined by Waller (1972b) as camptonectes microsculpture, covers the surface exterior of both valves in geometrically regular patterns of very fine foliated calcite striae (Waller 1972a, b). The striae are oblique or antimarginal, forming a variety of net-like patterns in which elements are neither radial (continuously produced) nor commarginal (periodically produced and conformable with the shell margin). Classifications of antimarginal sculpture are supported by computer simulations (e.g., Hayami and Okamoto 1986) and theoretical morphospaces including camptonectes patterns (Ubukata 2005). Other forms of divergent sculpture occur on the exterior surface of bivalve shells, although their taxonomic significance is less clear than their microstructural expression and potential functional roles. However, the microscopic, foliated calcite striae, also referred to by some authors as “diverging scratches,” “radial scratches,” or “antimarginal striae” (e.g., Dijkstra 1991), are treated as a clade within Pectinidae (e.g., Habe 1977, Waller and Marinovich 1992, Dijkstra and Kastoro 1997, Dijkstra and Gofas 2004, Bouchet and Rocroi 2010, Carter et al. 2011, Coan and Valentich-Scott 2012).

The North Pacific living and fossil *Delectopecten vancouverensis*, type species of the genus, has microscopic camptonectes sculpture on both valves (Fig. 16A, B) that is comparable to that of the new species in the Keasey Formation described below. The type species also has a prominent anterior auricle (Fig. 16B), deep byssal notch

with ctenolium (Fig. 16C), and poorly delineated posterior auricle that is continuous with the posterior margin of the disc (Fig. 16A). *Delectopecten vancouverensis* is especially pertinent to interpretation of Pacific coast fossil *Delectopecten* because of its tolerance to severe hypoxic conditions (0.0–0.2 ml/l O₂) (Suarez-Mozo et al. 2019). It occurs in assemblages that include chemosymbiotic solemyid and lucinid bivalves as well as other oxygen minimum zone taxa capable of tolerating hypoxia (Levin 2003).

Delectopecten is cosmopolitan in distribution and has been considered a descendant of the Jurassic–Cretaceous *Camptonectes* Agassiz in Meek (1864) (Waller 1972a, b). Although the Cenozoic fossil record of *Delectopecten* is best documented taxonomically in strata of the west coast of North America (MacNeil 1967, E.J. Moore 1984b), it is well represented and often abundant in Japanese deep-water facies. However, Paleocene occurrences in Australia (Darragh 1997) and Argentina (del Rio et al. 2008) as well as Late Cretaceous pectinids with camptonectes sculpture from New Zealand and the Chatham Islands (Crampton 1988) are consistent with hypothesized long cosmopolitan history.

Stratigraphic range—Lower Paleocene (Danian)–Holocene.

DELECTOPECTEN KIELI n. sp.

FIGS. 17A–E, 18A–L

Delectopecten n. sp. Vokes in Warren, Norbistrath and Grivetti (1945) (checklist).

Delectopecten n. sp. R.C. Moore and Vokes (1953). pp. 115, 119.

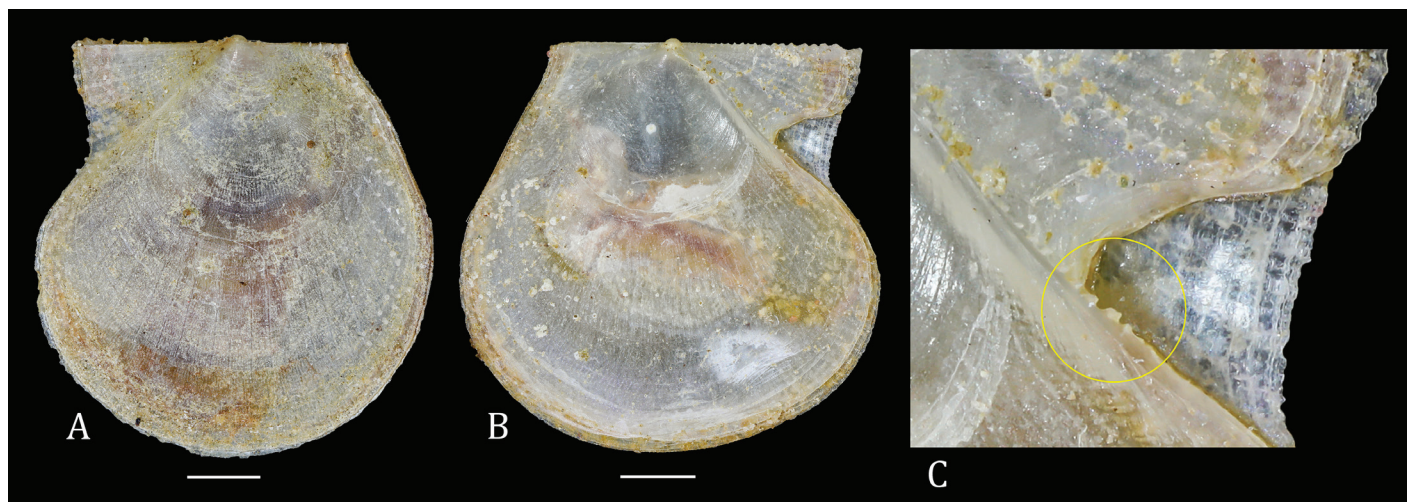


Figure 16. *Delectopecten vancouverensis* (Whiteaves, 1893), North Pacific live-collected, articulated representative of the type species of *Delectopecten*. SBMNH 130085. **A.** Left valve. **B.** Right valve. **C.** Enlargement of byssal notch with ctenolium (yellow circle). Scale bars=1 mm.

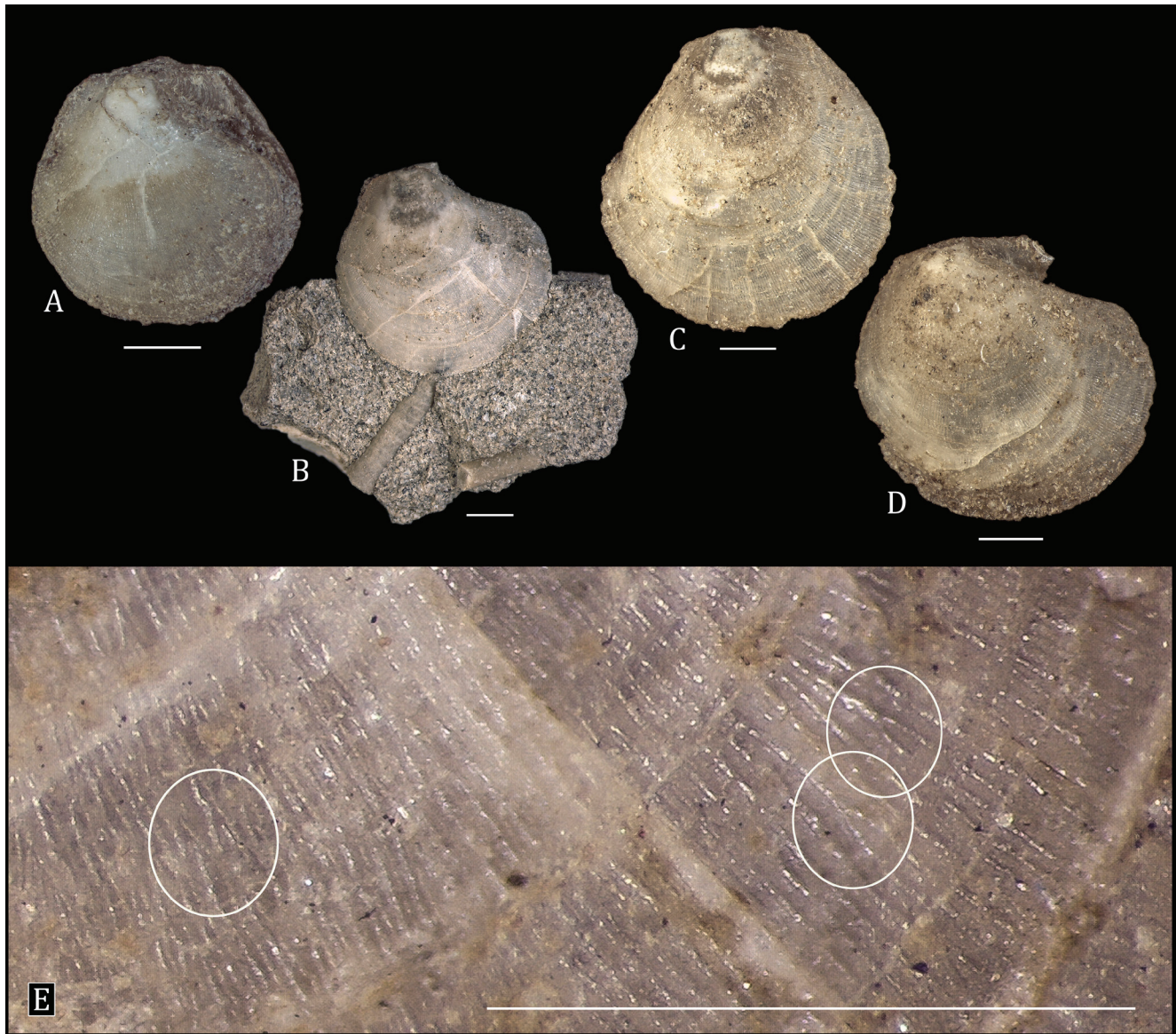


Figure 17. *Delectopecten kieli* n. sp. **A.** Right valve exterior, Holotype, UCMP 110746. **B.** Right valve exterior, Paratype, UCMP 110747. **C.** Left valve exterior, Paratype, UCMP 110748. **D.** Right valve exterior, Paratype UCMP 110749. Scale bars=1 mm. **E.** Detail of camptonectes sculpture on **B**, with reticulations and splitting of fine radial ribs (white circles). Scale bar=0.5 mm.

Delectopecten sp. Hickman (1984). p. 1221; fig. 5D.

?*Delectopecten* sp. Kiel (2006). p. 133; figs. 3.4, 3.5.

ZooBank LSID—urn:lsid:zoobank.org:act:165BAA17-9286-4E98-B4FF-616439C176CF

Diagnosis—Shell small, subcircular in outline, equi-valve, length equal to or slightly greater than height; anterior auricle large, with deep byssal notch and imperceptible to weakly-developed ctenolium in right valve; posterior auricle small, weakly-developed, merging indistinctly with posterior shell margin; very fine camptonectes sculpture well-developed, similar on both right and left valves but variable between specimens; early

portion of disc smooth, with finely beaded and slightly antimarginal striae becoming increasingly well developed; commarginal striae imperceptible and irregularly developed, most prominent as periodic growth pauses interrupting antimarginal striae; shell interior with prominent fold defining right anterior ear byssal notch; small triangular resilifer distinct in many specimens; anterior and posterior adductor scars not preserved.

Discussion—The anterior auricle is shorter and more rounded than in the *Delectopecten vancouverensis* and the shell shape (height \approx length) differs from that of the type species (height $>$ length). The most important feature of

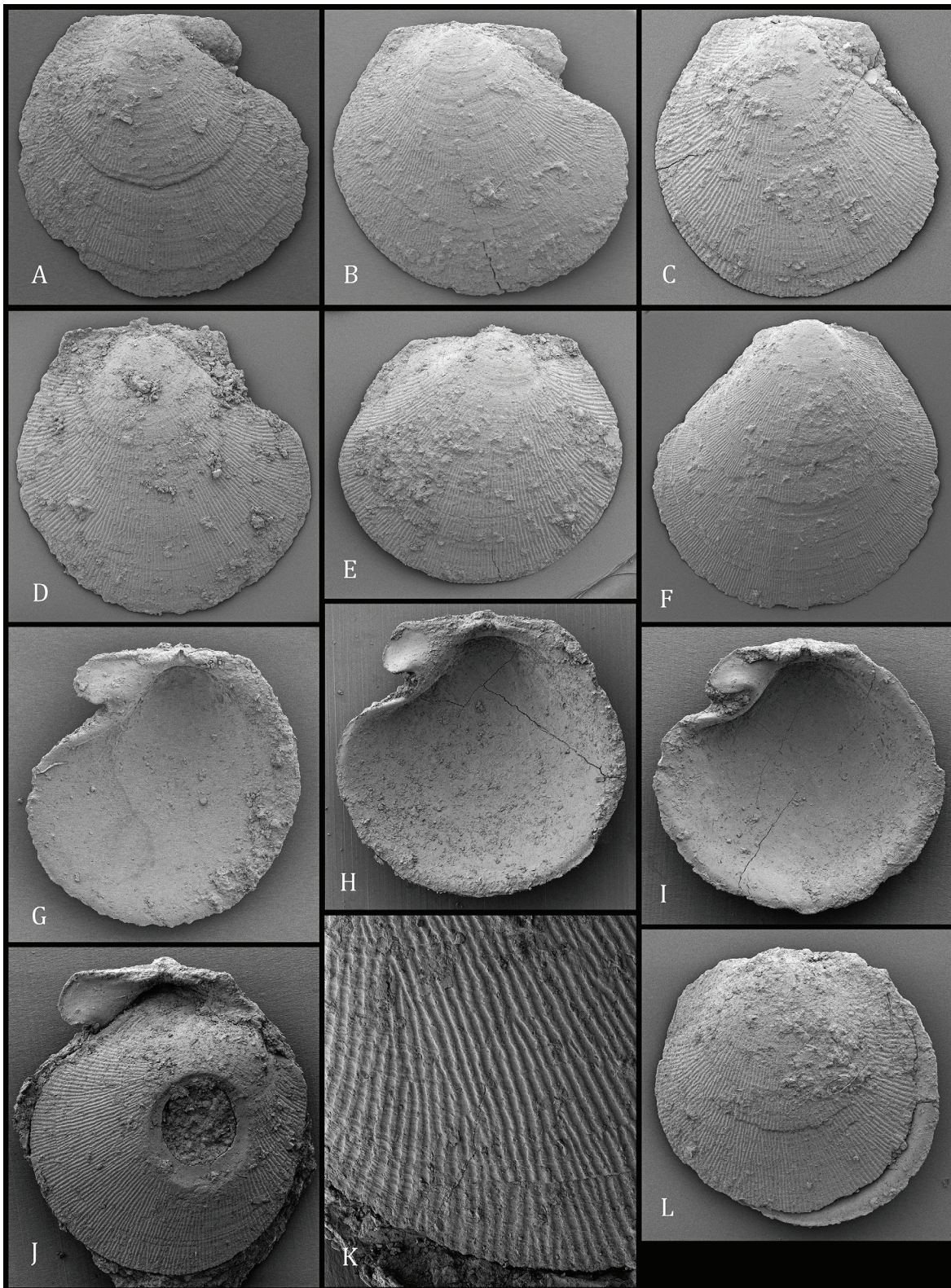


Figure 18. *Delectopecten kieli* n. sp. Low voltage scanning Electron Micrographs. **A.** Right valve exterior, Paratype, UCMP 110750. **B.** Right valve exterior, Paratype, UCMP 110751. **C.** Right valve exterior UMMP 110752. **D.** Right valve exterior, Paratype UCMP 110753. **E.** Left valve exterior, Paratype, UCMP 110754. **F.** Left valve exterior, Paratype UCMP 110755. **G.** Right valve interior, Paratype UCMP 110756. **H.** Right valve interior, Holotype, UCMP 110746. **I.** Right valve interior, Paratype UCMP 110757. **J.** Articulated, left valve exterior rotated within right valve interior, Paratype UCMP 110758. **K.** Detail of sculpture on **J.** **L.** Articulated, left valve exterior displaced on top of right valve interior, Paratype UCMP 110759. Range of shell lengths: 2.2–3.2 mm.

the shell exterior is the distinctive reticulate pattern of camptonectes microsculpture (Figs. 17E, 18A–E, J–L). The most important features of the shell interior are the well-preserved resilifer and the prominent fold bordering the anterior ear and byssal notch of the right valve (Fig. 18G–J).

Occurrences range from individual internal and external molds to concentrations of highly altered disarticulated valves and concentrations of well-preserved and occasionally articulated valves. Some localized concentrations are monospecific (Fig. 15A, B) while others include echinoid spines (Fig. 15C) and fish scales (Fig. 15D). The tooth of a demersal angelshark in one of these concentrations suggests that it may be a regurgitate of undigested material.

It is remarkable that this species had not been collected prior to its discovery in such great abundance at the type locality and a closely-adjacent small outcrop in the lower member of the Keasey. The type lot includes >100 specimens recovered from disaggregated matrix. Additional shells remain in hand samples. Discovery of the fresh outcrops on a new logging road was fortuitous. A diverse fauna of rarer gastropods is associated with the pectinid concentrations. This is the type locality for *Conus weltoni* Hickman (1980), *Svelltella? keaseyensis* Hickman (1980), and *Turrinosyrinx nodifera* Hickman (1976). These three species also are restricted to the lower member. It is also the type locality of a minute (<3 mm) marginellid gastropod *Granula profudorum* Hickman (1980), also known from two localities in the middle member.

Comparisons—This species is easily distinguished from other pectinids and propeamussiids in the Keasey Formation by its distinctive camptonectes sculpture, strongly developed anterior ear and byssal notch, weakly developed posterior ear, and shell proportions. It is similar to two Paleogene species from California, notably many of the specimens that have been assigned various authors to *Pecten peckhami* Gabb (1869). The lack of a clearly designated type is reviewed by Stewart (1930), and the assignment of California Eocene and Oligocene forms assigned to Gabb's species are reviewed by E.J. Moore (1963, 1984) as belonging to *D. peckhami* of Arnold (1906). The difficulty of comparison resides primarily in poor preservation, especially lack of the diagnostic microsculpture.

The closest comparison to the Keasey species is *Delectopecten* sp. Kiel (2006) from the Lincoln Creek Formation in Washington. It is known from a single small (4 mm) incomplete left valve. However, the camptonectes

microsculpture on the posterior portion of the shell and auricle in Kiel's micrograph (his Figure 15.5) is indistinguishable from the unique microsculpture of *D. kieli*. It is also notable that the Lincoln Creek specimen is from a cold seep carbonate, consistent with seep associations of the Keasey pectinids and propeamussiids. As noted above, the living type species of *Delectopecten* is an oxygen minimum zone species, occurring in association with chemosymbiotic bivalves and mollusks that tolerate severe hypoxic conditions.

Etymology—Named for Steffen Kiel for his insightful contributions to molluscan paleontology of hydrocarbon seeps in Cenozoic forearc strata of the Cascadia Margin.

Material examined—more than 200 entire valves (some articulated) and shell fragments from the main outcrop at type locality and a closely adjacent small outcrop on a logging road in the lower member.

Direct measurements from delicate specimens are not possible, and values for size derived from scale bars in photographs and SEM images are approximate.

Holotype—UCMP 110746, length 3.4 mm, height 3.4 mm. Loc. UCMP IP7983 (formerly USGS 25026).

Figured Paratypes—UCMP 110747, length 4.5 mm, height 4.5 mm. UCMP 110748, length 5 mm, height 5 mm. UCMP 110749, length 4.3 mm, height 4.4 mm. UCMP 110750, length 3 mm, height 3 mm. UCMP 110751, length 3 mm, height 3 mm. UCMP 110752, length 3 mm, height 3 mm. UCMP 110753, length 3 mm, height 3 mm. UCMP 110754, length 2 mm, height 2 mm. UCMP 110755, length 4 mm, height 4 mm. UCMP 110756, length 3 mm, height 3 mm. UCMP 110757, length 3 mm, height 3 mm. UCMP 110758, length 3 mm, height 3 mm. UCMP 110759, length 2 mm, height 2 mm.

All from Loc. UCMP IP7983 (formerly USGS 25026).

Type locality—UCMP IP7983 and closely adjacent UCMP IP2536 (formerly USGS 25026 and 52025), lower member.

DELECTOPECTEN KEASEYORUM N. SP.
FIGS. 15A, B; FIG 19A–E

Delectopecten n. sp. Vokes in Warren, Norbistrath and Grivetti (1945) (checklist).

Delectopecten n. sp. R.C. Moore and Vokes (1953), pp. 115, 119.

Delectopecten sp. Hickman (1984), p. 1221; fig. 5D.

ZooBank LSID—urn:lsid:zoobank.org:act:8B64E474-0E4C-4152-B5FE-8EB1F2F2AC5A

Diagnosis—Shell small (average length=1 cm), equivalved, with strongly compressed valves of equal length and width; shell material extremely thin, typically



Figure 19. *Delectopecten keaseyorum* n. sp. Holotype and two paratypes in matrix. **A.** Partial left valve exterior over nested right valve fragments, Holotype UCMP 110760. **B.** Right valve of paratype exterior partially overlapping holotype, UCMP 110761. **C.** Right valve exterior partially overlapping adjacent paratype, UCMP 110762. Scale bar for A–C=5 mm. **D.** Detail of fine camptonectes sculpture on holotype. **E.** Right valve exterior of paratype in matrix preserving ctenolium denticles in byssal notch (yellow arrow), UCMP 110763. Scale bar=1 mm.

preserved with distinctive hyaline or glassy appearance; valves compressed, with slightly raised, sharply pointed umbones; posterior auricles not clearly delimited from disc, flat with fine camptonectes surface sculpture; anterior auricles large, strongly set off from disc; posterior auricles flat, not clearly delimited; right anterior auricle with deep byssal notch and sculpture of 10 to 12 fine radial riblets crossed by fine growth lines; left anterior auricle sharply delimited from disc, flat, with fine camptonectes surface sculpture; disk surfaces of both valves

covered with extremely fine camptonectes sculpture, weak commarginal undulations sometimes developed beneath umbones on early portion of disc.

Discussion—Assignment to Pectinidae is based on the presence of the same pattern of camptonectes microsculpture on right and left valves (Fig. 19A–D) and the presence of a ctenolium along the ventral margin of the byssal notch (Fig. 19E).

This is undoubtedly the most abundant bivalve species in the Keasey Formation. It was collected from many

localities and in all three members of the formation during geologic mapping and noted in the checklist of Warren et al. (1945) as *Delectopecten* sp. Harold Vokes had intended to describe it, and his material and prospective types were examined in the present study. However, better material collected subsequently by the author is the basis of the new name. Lack of representation of this species in collections is attributable to the relative rarity of isolated concretions and crushing of the delicate shells. Less frequent and abundant species traditionally attract collectors with a search image for the rare, single, entire, and well preserved Keasey gastropod and bivalve taxa. Collectors skilled in the preparation of delicate fossils may be rewarded by working with this species.

A preservational peculiarity of this species, especially in the massive tuffaceous siltstone of the upper part of middle member, its occurrence in small, dense concentrations or concretionary masses, isolated from other mollusks at any given locality (Fig. 15 A, B). Within these concentrations shells have no predominant orientation and are stacked on top of one another. Although valves are entire, they have been fragmented by compression or distorted by pressure from adjoining individuals (e.g., Fig. 15A, B; Fig. 19). Articulated specimens are present in these concentrations indicating lack of significant pre-burial transport or exposure.

Etymology—Named for members of the Keasey Family of Vernonia, Oregon for their longstanding interest in the fossil fauna and encouragement of its collection and study, including access to outcrops on their property.

Comparisons—*Delectopecten keaseyorum* is clearly distinguished from *Delectopecten kielii* by its larger and thinner shell, hyaline surface, and finer, submicroscopic camptonectes sculpture (Fig. 19A–E). The sculpture is visible with a light microscope only at higher magnification and with strongly oblique illumination. As noted above, meaningful comparison with the ill-defined *D. peckhami* is confounded by Gabb's generalized original description, persistent lack of a clearly designated type, and inadequate illustration. The broad stratigraphic range (Eocene–Miocene) of specimens assigned to *D. peckhami* is consistent with the suggestion that it is a complex of deep-water species in need of detailed study and revision. In the experience of this author, the most similar material to *D. keaseyorum* is from the Paleogene Kreyenhagen Formation of the Coalinga district in California, removed from *D. peckhami* and described as *D. lil-lisi* Hertlein (1934). E.J. Moore (1963, 1984b) provides a detailed history of the treatment of these small mud peccens and helpful illustration of relatively well-preserved

Eocene to Holocene specimens.

Material examined—More than 500 entire valves (some articulated) and recognizable and shell fragments, including material from numerous USGS localities originally collected by Vokes, Warren, Norbistrath, and Grivetti.

Holotype—UCMP 110760, incomplete left valve in matrix, exposed length 8 mm, exposed height 9.5 mm, Loc. UCMP IP2543.

Figured Paratypes—UCMP 110761, incomplete right valve in matrix, partially overlapping holotype, UCMP Loc. IP2543; UCMP 110762, incomplete right valve partially overlapping paratype 110761, Loc. UCMP IP2543; UCMP 110763, partial right valve with byssal notch and ctenolium, Loc. UCMP IP16620.

Type locality—UCMP IP2543 (Empire Lite-Rock Quarry) (formerly USGS 25036) (Coll. C. Hickman and Undergraduate Invertebrate Paleontology Class field trip; 1967, C. and J. Hickman, 1970).

Other localities—USGS 15263, 15265, 15306, 15307, 15308, 15309, 15584 (lower member). UCMP IP16620; USGS 15267, 15268, 15274, 15276, 15279, 15280, 15281, 15282, 15283, 15217, 15313, 15314, 15316, 15318, 15509, 15525, 15582, 15602 (middle member). USGS 15315, 15318 (upper member).

DELECTOPECTEN n. spp.

Fragmental specimens from two localities in the Keasey formation have forms of ornamentation that differ dramatically from the two species described above as well as from one another. The inferred maximum length and height of the specimens at hand is <1 cm. In both species the sculpture changes abruptly during ontogeny. The first is from the classic Mist locality (USGS 15318) and is represented by an external mold (USNM 561848) in which radial and concentric ribs of equal strength on the dorsal half of the disc cross one another to form a scaly pattern that changes abruptly to a very fine radial camptonectes pattern that continues to the ventral shell margin. The second species is from a locality in the upper member (USGS 15315) and is represented by an external mold with a different discrepant sculpture pattern. On this specimen the subumbonal portion of the disc is smooth, with an increasingly well-developed concentric sculpture on the dorsal portion changing abruptly to a relatively coarse cancellate pattern that continues to the ventral margin. Descriptions were never published, although Harold Vokes obtained the prospective USNM type numbers and intended to propose a new name for the upper Keasey specimens and to treat the Mist specimen in open nomenclature. The material is

here considered inadequate for proposing new names. However, the distinctive sculptural patterns in these fragmental specimens call attention to the diversity in the Keasey mud pecten fauna. It is perhaps significant that the Mist specimen occurs at one of the three methane seep localities in the formation, co-occurring with the abundant propeamussiid species described below.

PROPEAMUSSIIDAE ABBOTT, 1954

A second family group of small-shelled, fragile deep-water pectinoideans also appeared during the Triassic. The ancient propeamussiids (glass scallops) have a long fossil record independent of the pectinid mud pectens. Propeamussiids have been recognized, described, and treated under *Propeamussium* de Gregorio (1854) from numerous Paleogene formations on the Northeastern Pacific margin for more than 100 years, distinguished primarily by the presence of slat-like interior radial ribs of lathic calcite imbedded in the inner aragonitic layer. The ribs have been interpreted as an adaptation strengthening the fragile shells for efficient swimming and a free-living mode of life. Experimental study of valve design identifies an airfoil system of complex features that increase the lift required for level swimming (e.g., Hayami 1991). For more than 50 years some propeamussiids have been recognized as carnivorous, feeding on small epibenthic and planktic protists and invertebrates (e.g., Knudsen 1967, Tëmkin and Strong 2013). Fossil propeamussiids also have been recognized as microcarnivores, and sometimes abundant in bathyal mudstone faunas (e.g., Maxwell 1988).

The concept of the family has been refined substantially by detailed studies of both hard and soft parts, including details of shell microstructure (Waller 1971, 1972b, 1976, 2006). Although all propeamussiids are apparently capable of swimming (Waller 2006), byssal attachment is characteristic in some species, and interior radial ribs are not diagnostic of the entire family. An important feature of the most efficient swimming propeamussiids is the lateral gape in the margin of both valves, creating fluid jets during rapid valve adduction (Morton and Thurston 1989).

Examples of living Northeastern Pacific species in three genera are illustrated here (Fig. 20A–F). The most reliable features distinguishing Cenozoic fossil propeamussiids from the Northeastern Pacific are lack of a ctenolium in the byssal notch (if present) of the right valve and size difference of right and left valves in the taxa with prominent internal radial ribs. Most of the nominal species are easily distinguished from *Delectopecten* by

discrepant sculpture of right and left valves and the lack of camptonectes microsculpture. Interior radial ribs are present in most of the Paleogene species examined, and species are commonly distinguished by rib number, point of origin, and extent.

Refined morphological data bearing on pectinoidean family relationships, paleontological data, and molecular analyses do not agree, and homoplasy in shell features exacerbates the problem by increasing the number of evolutionary hypotheses. The concept of Propeamussiidae is especially unstable in terms of molecular analyses suggesting non-monophyly (Smedley et al. 2019). If more comprehensive sampling supports non-monophyly, major revision of the family will be required.

Propeamussiids are treated here as monophyletic and recognized as an important element in a cosmopolitan post-Cretaceous radiation in deep water. Because shells are small, thin, and often poorly preserved they are difficult to distinguish from the similarly fragile pectinids. Their significance in the Keasey is the abundance and remarkable preservation of shell morphology in exterior and interior molds at the famous Mist crinoid locality where they are part of a diverse macrofauna at one of the three methane seeps in the formation.

Stratigraphic range—Middle Triassic–Holocene.

PROPEAMUSSIUM DE GREGORIO, 1884

Type species—by monotypy, *Pecten (Propeamussium) ceciliae* de Gregorio (1884). Miocene, Sicily.

There are many available genus-group names for the fossil glass scallops. Although *Propeamussium* itself is based on a Miocene fossil, shell morphology is distinctive. The free-living *P. jeffreysii* (E.A. Smith, 1885) (Fig. 20A, B) illustrates the difference between the functionally dorsal right valve (A) with its uncalcified flexible prismatic apron, which is adpressed against the rigid interior margin of the fully calcified (functionally ventral) left valve (B) when the valves are closed. Although swimming has never been observed in live specimens, Morton and Thurston (1989) inferred rapid valve adduction and strong swimming capability by combining shell morphology with detailed study of adductor muscle components and insertions on the shell. Their reconstruction is presented in an elegant series of illustrations (Morton and Thurston 1989 figs. 3; 4a, b; and 5a, b) of the airfoil shape, opening and closure of the shell, and flexure of the apron during valve adduction.

An early functional reconstruction of the Keasey propeamussiid (Hickman 1984, Fig. 8A, B), recognized the design of jet propulsion system, swimming in an edge

upward orientation but without evidence of the lateral gape that is more evident in *Propeamussium* s.s. Potential multiple functions of the gape during valve opening and adduction in swimming and carnivorous feeding (swimming jets, intake of meiobenthonic prey, and cleansing of the mantle cavity) have not been explored, and theory requires additional anatomical data and testing in live animals. There is strong evidence of sex-selective predation on meiobenthonic copepods (Hicks and Marshall 1985), although hypothesized mechanisms are yet to be tested.

Propeamussiids are the only pectinoideans in which the right valve is functionally dorsal or uppermost. If they do not comprise a monophyletic group, it is even more remarkable that an uppermost right valve and discrepant shell size and surface sculpture have evolved multiple times.

The well-developed slat-like ribs of lathic calcite, which act as buttresses in both valves, are partially imbedded in the shell interior layer of crossed lamellar aragonite.

Interior ribs are often visible externally through the thin translucent shells (Fig. 20A, B). All species are apparently capable of swimming even if normally attached by a weak byssus (Waller 2006), and all available evidence suggests that propeamussiids are living “relicts of the past” (Waller 1971), surviving extinctions at the close of the Paleozoic and Mesozoic to persist and radiate at bathyal and abyssal depths during the Cenozoic.

Stratigraphic range—Jurassic–Holocene.

PARVAMUSSIUM SACCO, 1897

Type species—By original designation, *Pecten duodecimlamellatus* Bronn (1832). Upper Miocene, northern Italy.

Parvamussium is treated here as a subgenus of *Propeamussium*, accommodating small, rounded shells, with interior shell slats developing later in ontogeny and coinciding with the inception of distinctive scabrous exterior sculpture on the initially smooth disc of the left valve. Discrepant sculpture on the right and

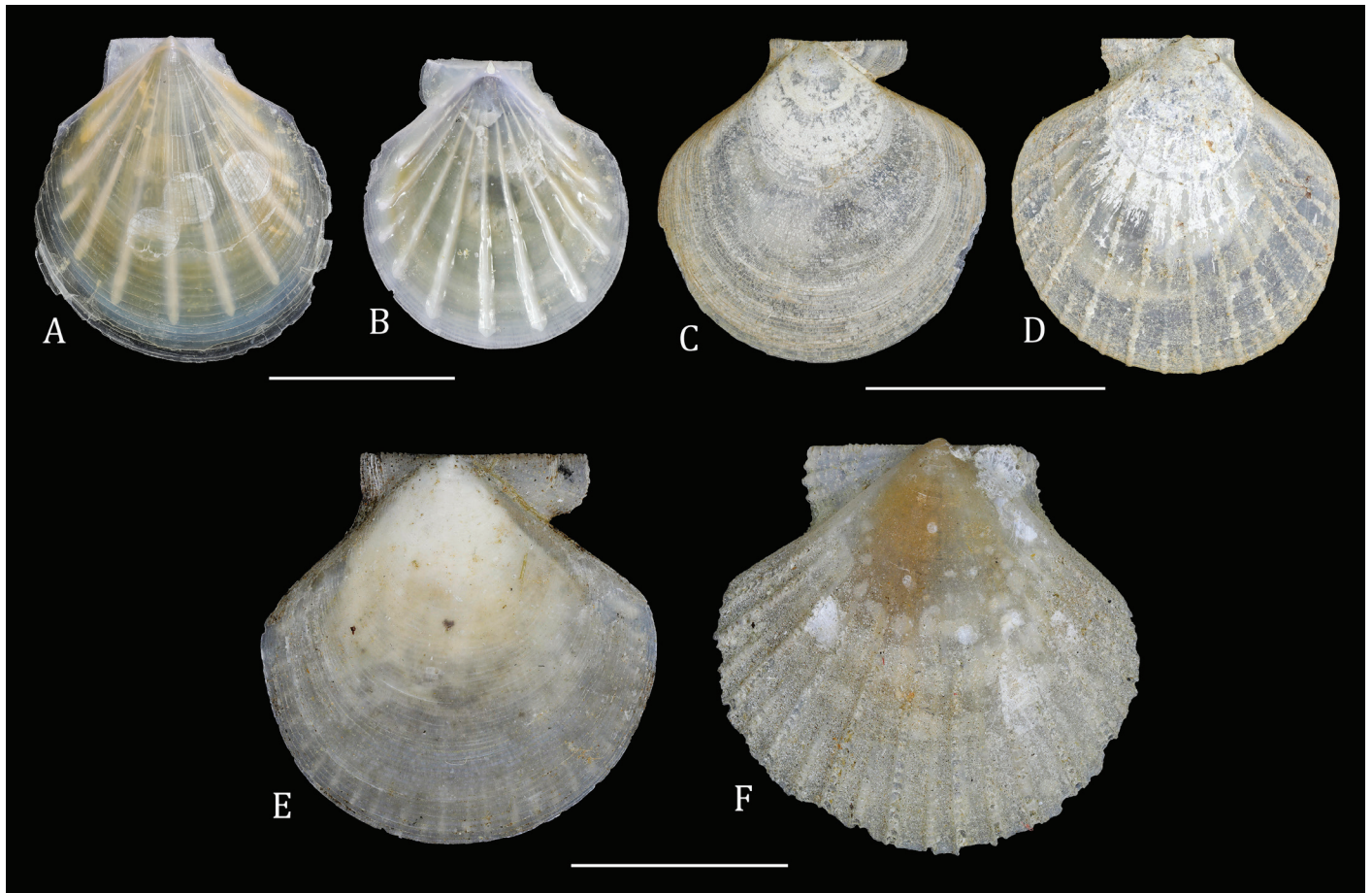


Figure 20. Variation in shell morphology in living North Pacific Propeamussiidae. **A, B.** Right and left valves of *Propeamussium jeffreysi* (E.A. Smith, 1885), SBMNH 126833. **C, D.** Right and left valves of *Cyclopecten davidsoni* (Dall, 1898), SBMNH 123955. **E, F.** Right and left valves of *Parvamussium alaskense* (Dall, 1871), SBMNH 103661. Scale bars=1 cm.

left valves is illustrated here in the living *Parvamussium alaskense* (Dall, 1871), a typically sedentary form with a well-developed byssal notch in the anterior auricle of the right valve (Fig. 20E). Both auricles are clearly demarcated from the disc, and both are ornamented with radial and commarginal striae. The scabrous pattern of intersecting radial and commarginal striae on the left valve (Fig. 20F) is in marked contrast to the subdued ornamentation of the right valve with commarginal striae only (Fig. 20E). Small size, scabrous sculpture of the left valve, and presence of a byssal notch do not constitute a strong argument for monophyly. However, the lack of a ctenolium in the byssal notch, discrepant valve size and sculpture, and interior slat-like ribs do exclude it from the Pectinidae and clearly distinguish it from the two new Keasey *Delectopecten* species.

Mesozoic species that can be assigned to either *Parvamussium* or *Propeamussium* s.s. first diversified during the Cretaceous, surviving the end Cretaceous extinction to begin a second and continuing radiation in the deep sea (Waller 2006). *Parvamussium* achieved cosmopolitan distribution by the Eocene, with records as early as Danian in Patagonia (del Rio et al. 2008). Paleocene and Eocene records in the southern Hemisphere from both Australia (e.g., Darragh 1994, 1997, Stilwell 2003, 2005) and New Zealand (e.g., Beu and Maxwell 1990, Maxwell 1992). Del Rio et al. (2008) provide additional references to Paleogene records from Europe and the Gulf Coast of North America but suggest that the Paleogene taxa inhabited shallow-water facies at this time. In the Northwestern Pacific, however, *Parvamussium* is well documented in Japan from Upper Cretaceous forearc slope mudstones along the subduction zone on Kyushu (e.g., Komatsu et al. 2008) and Hokkaido (e.g., Tsujino and Maeda 2007). These Late Cretaceous forearc sequences also include methane seeps (e.g., Takahashi et al. 2007). The *Parvamussium* bivalve associations are remarkably like those in the Keasey and indicative of an even earlier shift of the minute squamose glass scallops to low energy, oxygen depleted conditions associated with methane seeps.

The major difficulty assessing monophyly and relationships of the squamose glass scallops is the large number of genus group names that have been placed in synonymy under *Parvamussium*. For example, Dijkstra (2013) lists five names based on extant species, including *Squamamussium* Oyama (1944). Harold Vokes (pers. comm. 1981) intended to assign the new Keasey species to *Squamamussium* and obtained USNM type numbers for the specimens described and figured here under *Parvamussium*.

Stratigraphic range—Upper Jurassic?–Holocene. Cosmopolitan, bathyal and abyssal depths (modern), shallower in Mesozoic and Early Paleogene.

PROPEAMUSSIUM (PARVAMUSSIUM) MISTENSIS N. SP.
FIGS. 21A–E, 22A–C, 23A–D

Propeamussium n. sp. R.C. Moore and Vokes (1953). p. 119.

Propeamussium sp. Hickman (1984). p. 1224.

ZooBank LSID—urn:lsid:zoobank.org:act:3BEBE80B-2C47-4694-A13C-DB5A3B9FAB0D

Diagnosis—Shell small (<5 mm), thin, outline circular, equilateral with length slightly greater than or equal to height; inequivalve: larger, right valve with smaller calcified portion and missing uncalcified maginal flexible apron (not preserved) that fits adpressed to the ventral margin of larger left valve; hingeline narrow with small auricles distinctly set off from disc, right anterior auricle with byssal notch but no ctenolium; exterior surface sculpture discrepant; right valve with numerous sharply defined commarginal riblets and no radial riblets, left valve scabrous, with prominent primary, secondary and tertiary radial riblets crossed by weaker commarginal lirae with semi-erect spines or nodules forming at intersections; interior of both valves smooth with prominent radial slats of lathic calcite imbedded in crossed-lamellar aragonite.

Description—The squamose or cancellate surface texture of the larger left valves is well-preserved in exterior molds (Fig. 21A, B). Although the surface of the smaller right valves is more subdued in the absence of radial riblets, the commarginal riblets are well defined in exterior molds (Fig. 21C, D). Radial riblets are absent in the umbonal region of the left valve, with inception occurring at approximately 1/3 of the distance from the umbones and continuing to the ventral margin of the disc. Secondary and tertiary riblets are added by intercalation. The total number of riblets is variable, with 55 on the holotype. The total number of commarginal riblets on the right valve is approximately 25–30. Sculpture of the anterior and posterior auricles of the right valve includes both radial and commarginal sculpture while those of the left valve are predominantly concentric on the posterior ear, with strongly developed radials on the anterior ear. Interior molds preserve deep impressions of 12 to 14 narrow slat-like ribs.

An incomplete interior mold of a valve from Mist (UCMP 110764) lacks auricles (it may be either a right or a left valve), but the disc preserves deep impressions

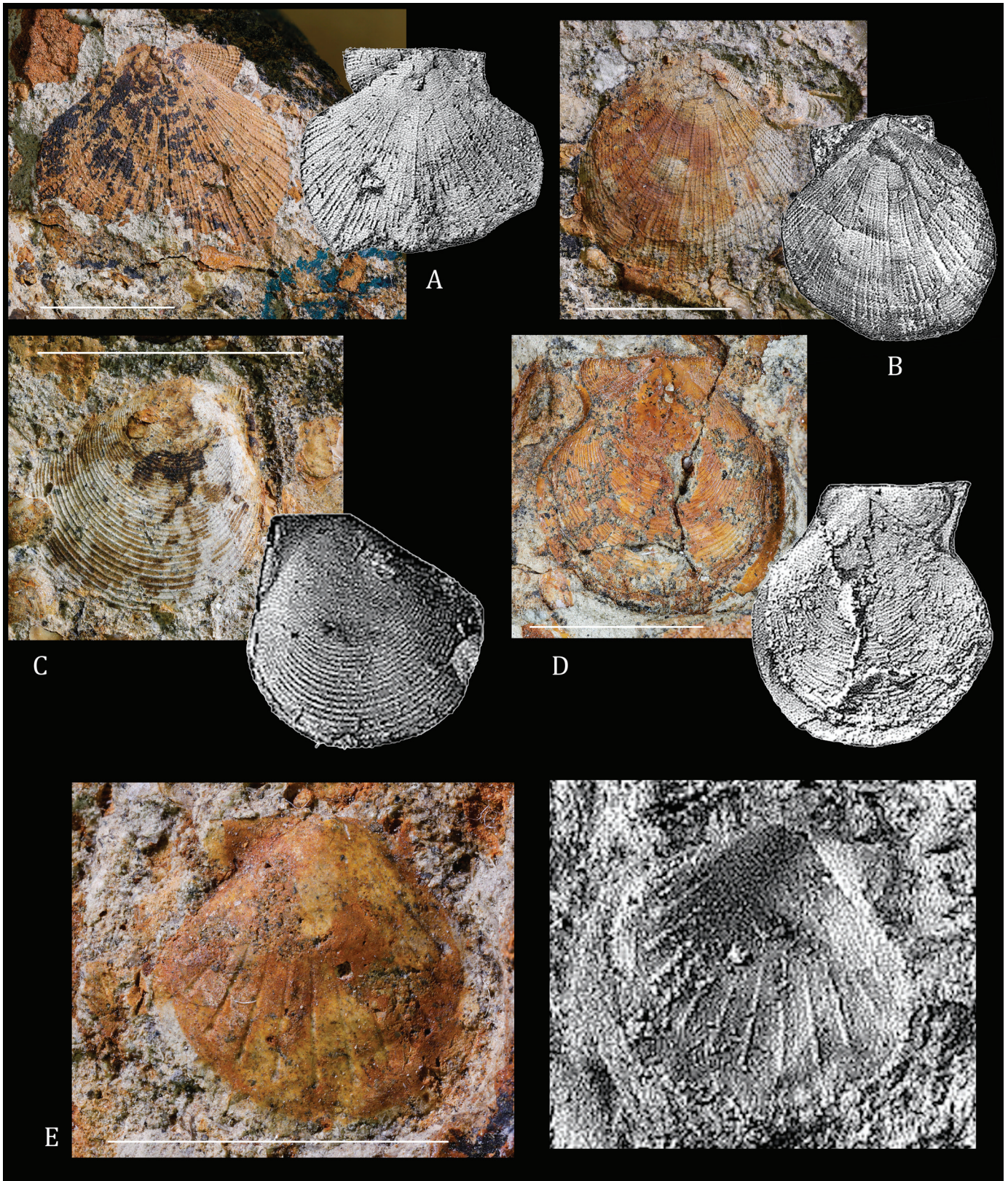


Figure 21. *Propeamusium* (*Parvamusium*) *mistensis* n. sp., paired color images of molds in matrix and corresponding ammonium chloride-coated casts. **A.** Left valve exterior, holotype USNM 561849, length 8 mm. **B.** Left valve exterior, paratype USNM 561856, length 8.1 mm. **C.** Right valve exterior, paratype USNM 561850, length 5 mm. **D.** Right valve exterior on top of left valve, paratype USNM 561854, length 7 mm. **E.** Left valve interior, Paratype USNM 561852, length 6 mm.

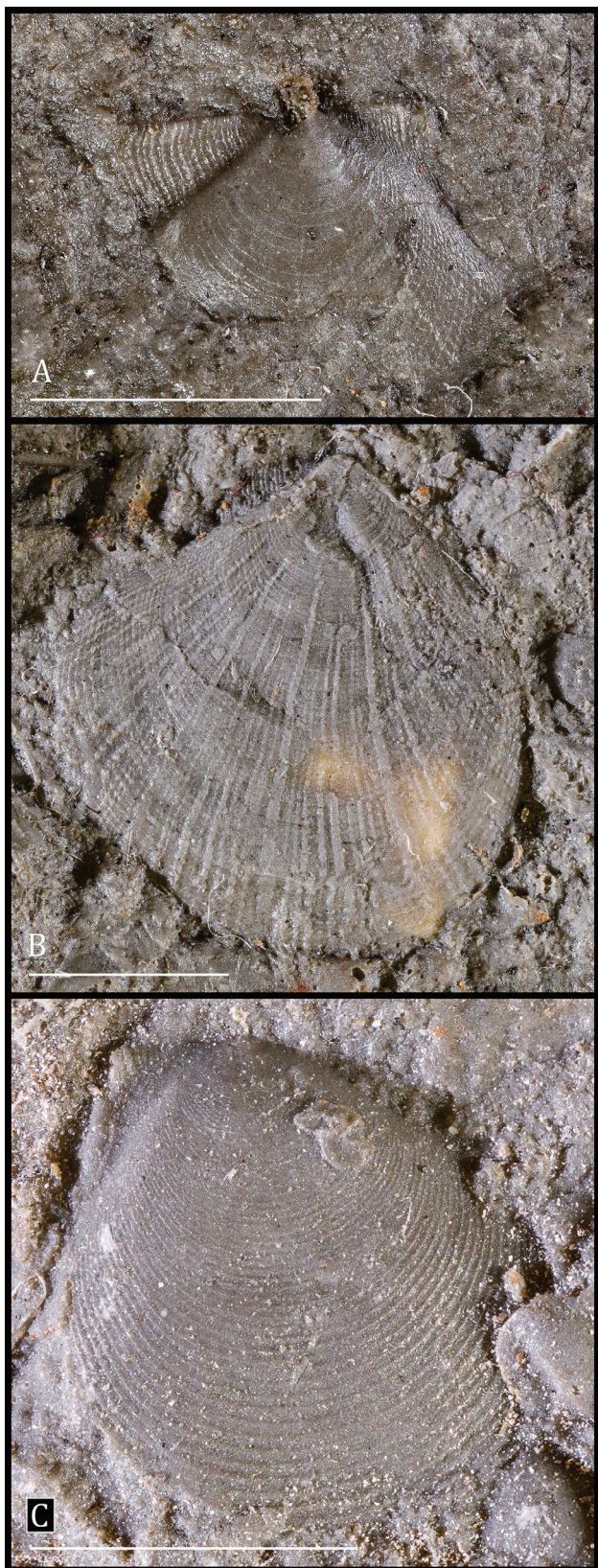


Figure 22. *Propeamussium* (*Parvamussium*) *mistensis* n. sp., uncoated latex casts of three paratypes. **A.** Left valve exterior, USNM 561853. **B.** Left valve exterior, USNM 561856. Right valve exterior, USNM 561850. Scale bars=3 mm.

of 14 ribs that extend to the ventral margin of the valve. A small fragment of adhering shell, removed from the mold, preserves portions of five of the imbedded slat-like ribs.

Discussion—This is the first population of an unequivocal propeamussiid named and described from the Paleogene of the Cascadia Margin. It is also the earliest documentation of Eastern Pacific propeamussiids from a methane seep hardground. However, Kiel (2006) extracted a suspect propeamussiid shell with well-preserved foliated calcite microstructure from an Oligocene limestone float block in Washington State yielding $\delta^{13}\text{C}$ values indicating methane seep origin, describing it in open nomenclature as *Catillopecten* sp.

Byssally-attached “living fossil” propeamussiids were discovered earlier on the periphery of hydrothermal vent systems at 13° and 9° N on the East Pacific Rise (Schein-Fatton 1985). Described as a new genus and species, *Bathypecten vulcani* Schein-Fatton (1988), it is now assigned to *Catillopecten* Iredale (1939). Detailed anatomical study of this peri-hydrothermal vent species (Beninger et al. 2003, LePennec et al. 2003) reveals a unique and putatively archaic particle processing mechanism. This reinforces previous evidence for a peripheral zone of seep mollusks uniquely adapted to hypoxic and chemically hostile environments as well as opportunistic suspension feeding on an unconventional carbon source—in this instance chemosynthetic microbes in the water column.

The new Keasey propeamussiid is easily distinguished from all previously described Eastern Pacific species. Details of the discrepant sculpture on the discs and auricles of the right and left valves, delayed ontogenetic appearance of the slat-like internal ribs, the presence of a byssal notch, and squamose sculpture on the right valve support its assignment to *Parvamussium* rather than *Propeamussium* s.s.

Although Paleogene propeamussiids have a long history of recognition in California, most of the material is preserved in mudstone facies as poorly-preserved interior casts recognized primarily by sharply-incised impressions of the radial ribs. *Propeamussium interradiatus* (Gabb, 1869) has been used for much of this material, and difficulties with the typification and hand-drawn illustrations of Gabb’s species have been discussed by many authors (e.g., Stewart 1930, Grant and Gale 1931, Addicott 1971). Five California Paleogene species of *Parvamussium* are recognized and illustrated by E.J. Moore (1984b). Propeamussiids in Alaska (Scholl et al. 1970), in rocks originally considered Paleozoic, were identified, and described by Addicott (1971) along with

Eocene Foraminifera, extending the distribution to high latitude in the Northeastern Pacific.

Unfortunately, the exterior and interior molds of the new Keasey species are difficult to illuminate and photograph, appearing in a common optical illusion that reverses positive and negative features (Fig. 21). Latex casts of these specimens, coated with ammonium chloride (Fig. 21), provide a true indication of negative and positive but fail to capture the natural appearance of specimens as they appear in the field and in museum collections. The diagnosis and description of *P. mistensis* is based microscopic study and drawings combined with data extracted from three different image sets described below.

In spite of the difficulties of specimen illustration, this is the best-preserved fossil propeamussiid species from the Northeastern Pacific, prompting the following note on the image sets.

Image sets—Three kinds of images were assembled for the holotype and each of eight paratypes from the Mist locality. Figure 21A–E illustrates the holotype and four of the paratypes, each represented by a color photograph of the actual specimen paired with a black and white photograph of a latex cast coated with ammonium chloride. Figure 22A–C illustrates three paratypes represented by photographs of uncoated latex casts. In some instances, photographs of actual specimens under different lighting reveal details useful for interpretation. In addition, Fig. 23A–D provides rendered drawings as a summary guide for interpreting future collections of fragments and imperfect specimens.

Etymology—named for the classic crinoid locality,

cold seep, and river bluff outcrops at Mist, Oregon.

Material examined—Although the primary types (collected by Harold Vokes) are all from the carbonate hardground of the main crinoid lagerstätte at Mist, specimens of the propeamussiid occur in float from a higher siliciclastic horizon with abundant spines and tests of two echinoid species. To avoid confusion, a new UCMP locality number is not assigned (see below).

Holotype—USNM 561849, (incomplete) length 8 mm, height 9 mm.

Figured paratypes—USNM 561850, length 5 mm, height 5 mm; USNM 561852, length 6 mm, height 6 mm; USNM 561853, length of hingeline 3.3 mm; USNM 561854, length 7 mm, height 6 mm; USNM 561856, length 8.1 mm, height 8.3 mm. Measurements are approximate, greatest dimensions are all within 5–8 mm.

Unfigured paratypes—USNM 561851, USNM 561855, USNM 561857.

Additional Unfigured paratype—UCMP 110764. This specimen is from a float block with echinoid spines from above the main crinoid layer and is the only specimen preserving shell material.

Type locality—USGS 15318=UCMP A5018. Numbers refer to the generalized Mist locality, including a prominent bench adjacent to the river bluff that was removed by commercial quarrying of the crinoids. For an excellent description of the stratigraphy at Mist see Burns et al. (2005).

LIMOIDA WALLER, 1978

LIMOIDEA RAFINESQUE, 1815

LIMIDAE RAFINESQUE, 1815

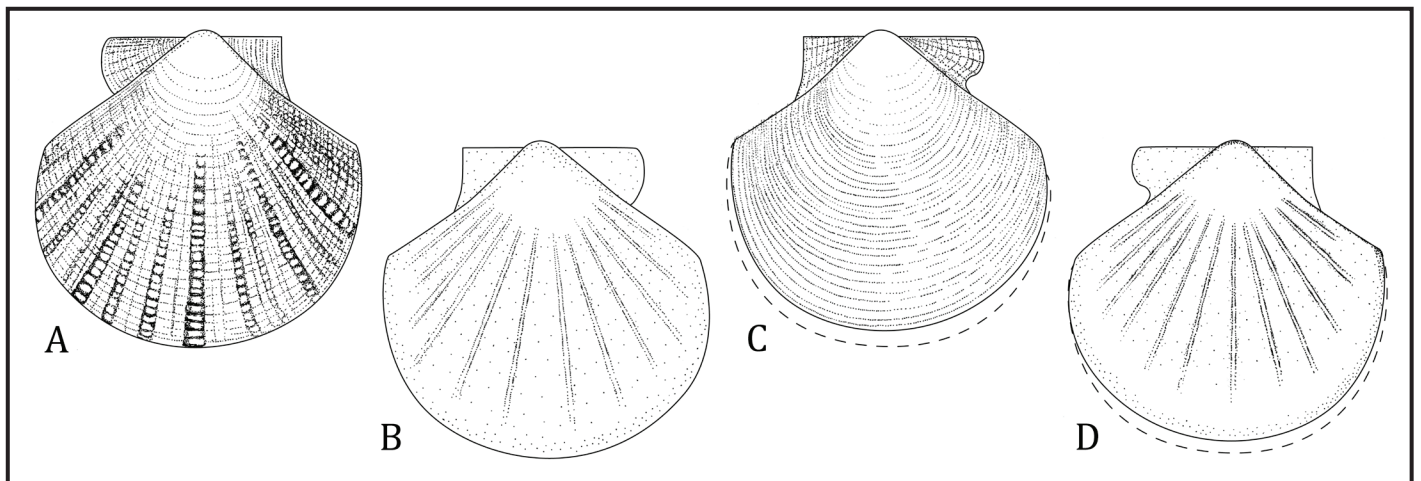


Figure 23. *Propeamussium* (*Parvamussium*) *mistensis* n. sp., reconstruction of major features of shell morphology based on all material examined. A. Left valve exterior. B. Left valve interior. C. Right valve exterior. D. Right valve interior. Dashed lines in C, D indicate extent of the larger left valve and uncalcified flexible apron of right valve.

Placed within their own order and superfamily (Waller 1978), the limid bivalves, commonly known as file shells, have a long geologic history. They appeared in the Carboniferous but failed to diversify to the extent of most pteriomorph groups. The living species are predominantly small-shelled, tropical, epifaunal forms that nestle, attach, or construct byssal nests. Many species are conspicuous in their brightly pigmented hypertrophied mantle tissue and long pallial tentacles, and their ability to swim when disturbed. Internal relationships within the family remain unresolved, despite the remarkable detail with which many living species have been studied. Mikkelsen and Bieler (2003, 2008) and Harasewych and Temkin (2015) provide new data and review previous studies, raising the challenge of a comprehensive worldwide phylogenetic study based on morphological and molecular data. From a deep-time perspective this program must include the fossil record!

Of special interest here are the fossil giant limids (height frequently >200 mm) assigned in this study to five genera. The two species treated below are assigned to *Acesta* H. and A. Adams (1853) and *Plicacesta* Vokes (1963). There are three additional available names for the large-shelled obliquely ovate species—the extinct Cretaceous *Costellacesta* Kauffman (1964), the extinct Eocene *Antarcticesta* Stilwell and Gaździcki (1998), and Oligocene–Holocene *Callolima* Bartsch (1978).

Although members of the family are easily recognized, the genus-group placement of the deep-water species has become increasingly difficult as ROV dives provide in situ video data on ecology and behavior and recover live specimens with new combinations of shell and anatomical features. Extremely thin translucent shells of *Acesta vitrina* Poppe, Tagaro and Stahlschmidt (2015) are uncomfortable in *Acesta*, resulting in description of the new monotypic genus *Acestarica* Dekkers (2022). However, significance of the translucent shell is questionable—anatomical and molecular data from the small deep reef *Mantellina translucens* Haraewych and Tëmkin (2015) place *Mantellina* outside a main limid clade in which *Acesta* and *Lima* are sister taxa. Because the type species of *Mantellina* Sacco (1904) is a Miocene fossil, phylogenetic resolution of the bathyal limids is especially challenging.

Stratigraphic Range—Lower Carboniferous–Holocene.

ACESTA H. AND A. ADAMS, 1853

Type species—By monotypy, *Ostrea excavata* Fabricius (1779). Holocene, Northeastern Atlantic continental

margin, Azores, Canaries; Pleistocene, widespread in Mediterranean.

The oldest reported occurrence is from Upper Jurassic rocks in India (Kanjilal 1990). The Mesozoic record is largely confined to the margins of the southern continents, with a continuous record across the Cretaceous–Paleogene boundary in Antarctica (Stilwell and Zinsmeister 1992) and Cretaceous records from Australia (Darragh and Kendrick 1991, Stilwell and McKenzie 1999) and New Zealand (Beu 1973, Beu and Maxwell 1990). By the end of the Paleogene, the genus had achieved a cosmopolitan distribution, expanding its latitudinal and bathymetric range as global cooling became increasingly pronounced. The type species (Fig. 24A, B) represents an additional trend toward exploiting hard substrates at the shelf-slope break on continental margins in addition to occupying soft substrates at greater depths.

The shell of *Acesta* s.s. is typically thin and fragile despite its large size. Knowledge of the basic biology and life habits of the living species has been limited by their occurrence on vertical rock walls and overhangs in submarine canyons and on seamounts as prominent members of communities of attached suspension feeders. These

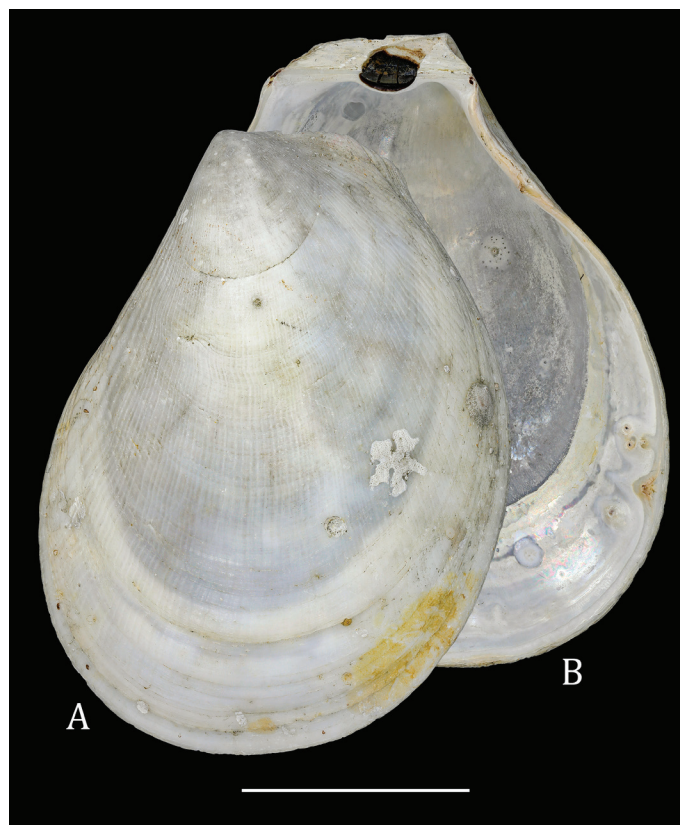


Figure 24. Living type species of *Acesta*, *A. excavata* (Fabricius, 1799), SBMNH 616346. Norway. **A.** Left valve exterior. **B.** Left valve interior. Scale bar=5 cm.

communities have been difficult to sample and have gone undetected until the advent of ROV video observation. Observations of walls of submarine canyons, seamounts, and escarpments on the Eastern Pacific margin of North America have revealed dense populations (e.g., Clague et al. 2012) that show a remarkable degree of genetic connectivity in spite of their disjunct occurrences. The type species is slow-growing, long-lived (5–80 years), and one of the dominant species in deep, cold-water coral reef communities (Schleinkofer et al. 2021). The remarkable ability of these large bivalves to detach and swim (Kohl and Vokes 1994) may account for the preservation of their thin fragile shells in the massive siltstone facies of the Keasey Formation at localities where the hardground habitat is not exposed.

Because these in situ observations and collections of living *Acesta* have special significance for interpreting the fossil record (Upper Jurassic–Holocene) they merit additional discussion. The Mesozoic record is exclusively southern hemisphere, expanding in the late Eocene into the northern hemisphere during dramatic faunal turnover and transition from tropical Eocene fauna to the modern fauna (Hickman 2003). The *Acesta* Community was first recognized and named from peculiar low-diversity, species-dominant fossil assemblages in Late Paleogene deep-water siltstones in Washington and Oregon, typified by the upper member of the Keasey Formation (Hickman 1984). At the time the community was described it was not possible to provide an accurate habitat description, although association with brachiopods and basal root tufts of hexactinellid sponges and the parallelodontid genus *Porterius* (described above) indicated attachment to the substrate.

New habitat discoveries of *Acesta* have been identified as an important element in documenting historical underestimation of deep-sea biodiversity. For example, ROV exploration of a deep submarine canyon system on the Celtic margin has revealed a new biotope dominated by *Acesta excavata* and a species of large deep-sea oyster on vertical surfaces and overhangs (Johnson et al. 2013). ROV mapping of vertical submarine canyon walls document its association with cold-water azooxanthellate corals (Huvenne et al. 2011). It is a dominant and conspicuous member of bathyal cold-water coral bank facies on the northern European continental margin (Lopez Correa et al. 2005) and occurs with cold-water corals on carbonate mounds, pock marks, and craters associated with hydrocarbon seepage (Jensen et al. 2010). The association with cold seeps and reducing environments extends to observations at cold seeps on the Louisiana

slope in the Gulf of Mexico where another *Acesta* species lives attached to the tube openings of vestimentiferan worms and feeds on the lipid-rich eggs (Järnegren et al. 2005). Although there is no clear evidence of chemosymbiosis, a novel intracellular bacterium has been isolated from the gills of *A. excavata* (Jensen et al. 2010). It seems likely that new interest in the deep-water file shells will continue to yield interesting new data.

Phylogeographic studies have likewise contributed useful data for understanding the fossil record. On the Eastern Pacific margin ROV images and samples of live animals from submarine canyons in the Gulf of California have extended the range of two northern species of *Acesta* and documented dense aggregations at greater depths than previously recorded for either species as well as an additional example of strong genetic connectivity with the high latitude populations (Walz et al. 2014). Range extensions have been subject to question and more detailed analyses. Initial collection by submersible of the European *A. excavata* from rock walls of a fjord on the south coast of Newfoundland was hailed as a dramatic range extension (Gagnon and Haedrich 2003). However, a subsequent combination of molecular data and morphometric analysis of the shells of seven *Acesta* species have identified the northwestern Atlantic form as a new cryptic species (Gagnon et al. 2015).

Thus far the Cenozoic fossil species from the Pacific Northwest and California are narrowly endemic, but the new habitat data and phylogeographic analyses of living taxa provide a new context for considering the fossil record.

Stratigraphic Range—Upper Jurassic–Holocene.

ACESTA OREGONENSIS (CLARK, 1925)

FIGS. 25A–D; 26A, B; 27A, B

- Lima (Plagiostoma) oregonensis* Clark (1925). p. 84; pl. 24, figs. 3, 4.
- Lima (Plagiostoma) oregonensis* Clark, Schenck (1936). p. 62.
- Lima (Plagiostoma) oregonensis* Clark, Woodring (1938). p. 48.
- Lima oregonensis* Clark, Weaver (1943). p. 99; pl. 22, figs. 2, 6.
- Lima oregonensis* Clark, Durham (1944). p. 139.
- Lima oregonensis* Clark, Vokes in Warren et al. (1945) (checklist).
- Lima oregonensis* Clark, Vokes in Warren and Norbistrath (1946). p. 227.
- Lima (Plagiostoma) oregonensis* Clark, Hertlein (1952).

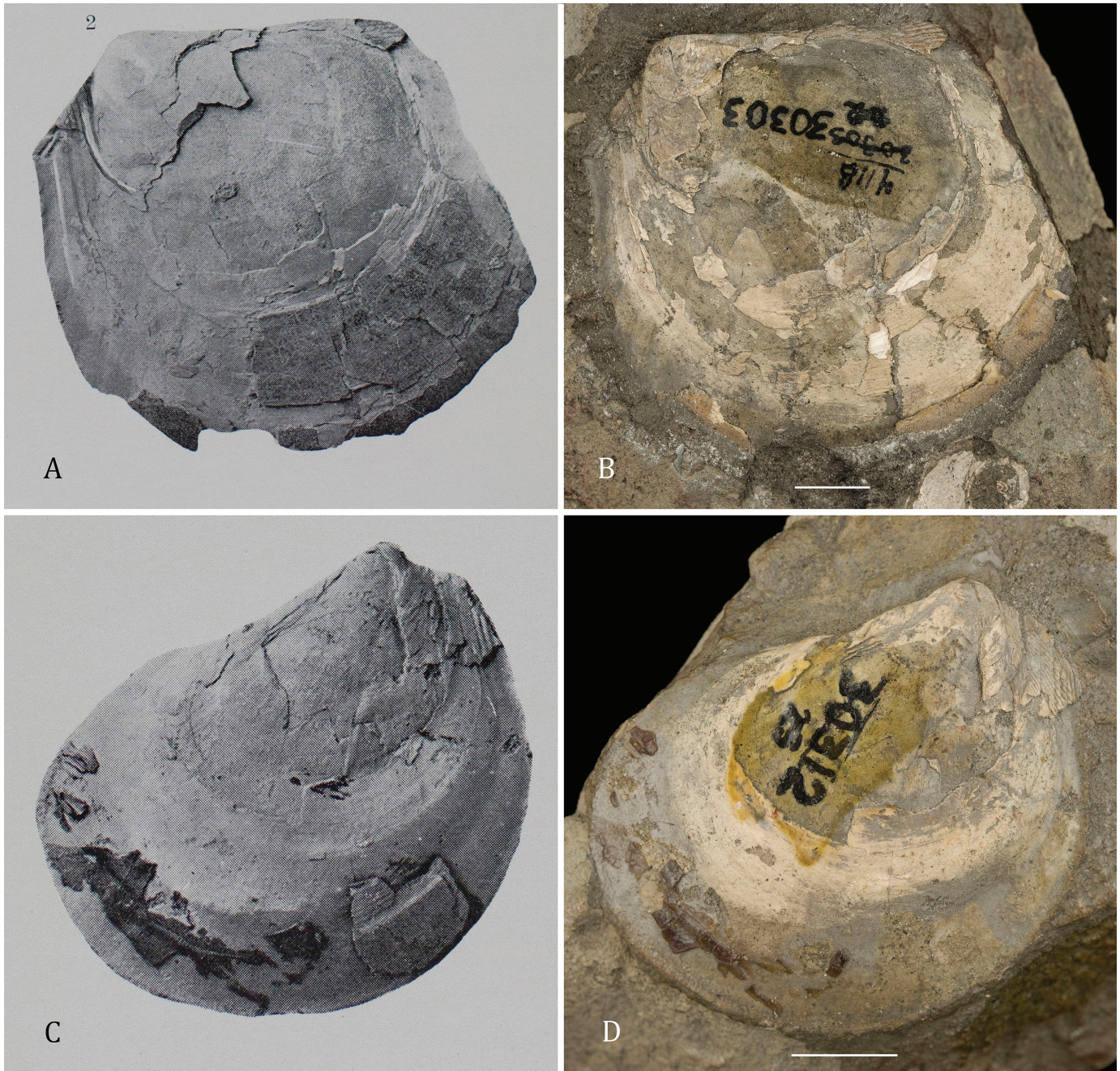


Figure 25. Holotype and paratype of *Acesta oregonensis* (Clark, 1925). **A.** Clark's trimmed and retouched original figure of Keasey holotype, right valve, UCMP 30303. **B.** Unmodified color image of holotype in matrix. **C.** Clark's original figure of the paratype, left valve, UCMP 30312. **D.** Unmodified color image of paratype in matrix. Scale bars=1 cm.

p. 379.

Lima (Acesta) oregonensis (Clark), R.C. Moore and Vokes (1953). pp. 115, 118.

Lima (Acesta) oregonensis (Clark), Vokes (1963), pp. 85–86.

Discussion—In the original description, Clark assigned this species to *Plagiostoma* J. Sowerby (1814), a genus based on an Early Jurassic species with a thicker

shell, a broad cardinal area, and a triangular resilifer located beneath the beaks. The diagnostic features of *Plagiostoma* are in marked contrast to the thin shell, narrow cardinal area and posteriorly oblique ligament pit of the Paleogene species, which here is assigned to *Acesta*. Clark's original illustrations are misleading photographs in which the holotype (Fig. 25A) and paratype (Fig. 25C) were trimmed to eliminate the matrix in which they are

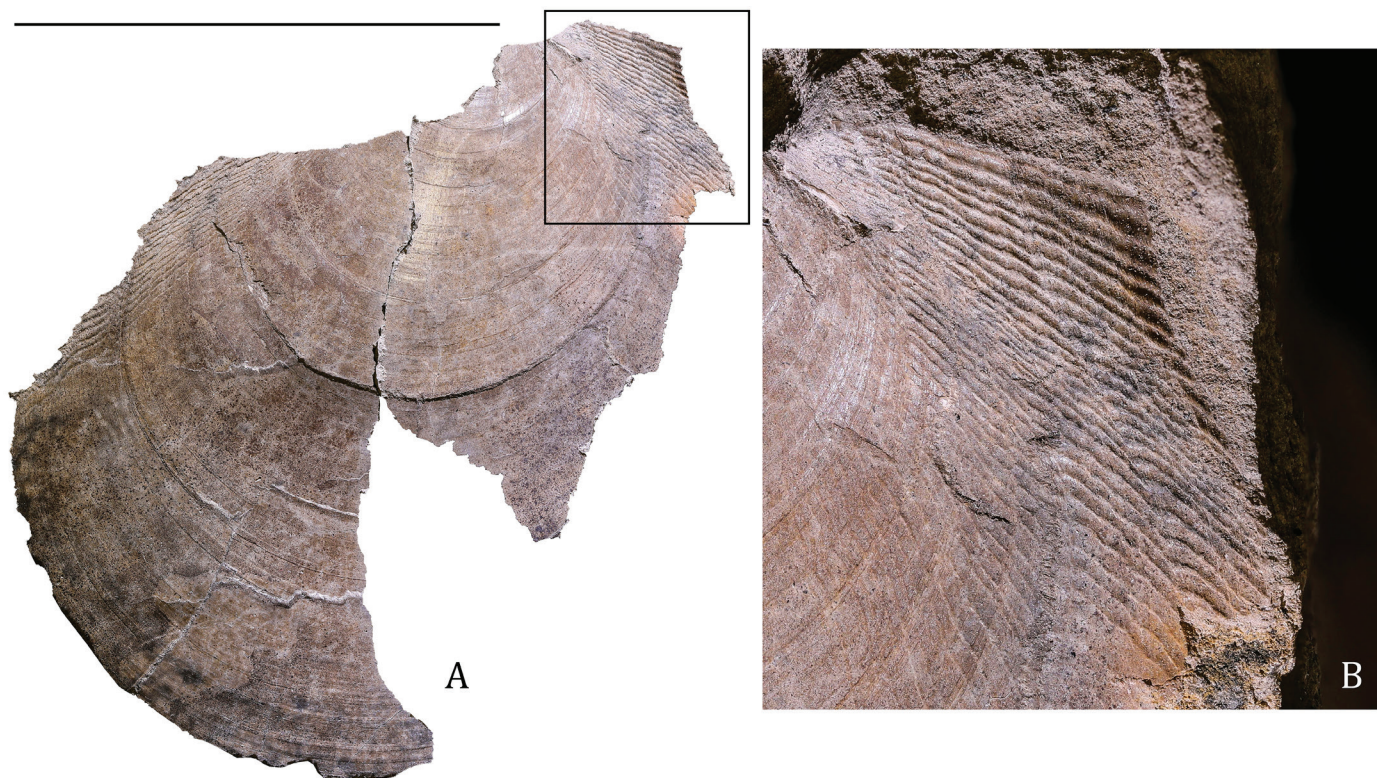


Figure 26. *Acesta oregonensis* (Clark, 1925), Keasey hypotype UCMP 110740. **A.** Original shell, left valve exterior, fitted together from two siltstone blocks, matrix digitally removed. Scale bar=5 cm. **B.** Detail of posterior ear.

imbedded, and fail to show the distribution of adhering, poorly-preserved shell fragments. New photographs of the types (Figs. 25B, D) are provided here. Clark also reversed the orientation of the ears in his description, describing the larger posterior ear as anterior and the smaller anterior ear as posterior.

Subsequent specimens collected by Hans Norbistrath, R.M. Grivetti and Harold Vokes as well as specimens collected in preparation of this monograph are all from the upper member of the Keasey Formation, where original shell material is typically well preserved and the dominant (occurring at most localities) element in assemblages along with basal root tufts of hexactinellid sponges, less frequent specimens of *Porterius gabbi*, and poorly-preserved terebratulid brachiopods. Failure to collect thin, delicate shell fragments undoubtedly accounts for under-representation of the species in both museum and private collections.

Careful examination of all available material is most informative in a composite characterization of the exterior ornamentation. Shells are smooth or with faint radial lines on the central part of the shell but pronounced on the anterior and posterior dorsal margins where numerous, finely incised radial lines are irregular in width

and spacing (Fig. 26A). A peculiar disjunct pattern of interrupted ribbing develops at intersections with commarginally bunched growth lines (Fig. 26B). The glossy, pale brown exterior calcitic layer is underlain by a white chalky inner aragonitic layer (Fig. 27A, B).

The Keasey species is most similar in shell shape and ornamentation to *Acesta hamlini* (Dall, 1900) from the Pliocene of the Los Angeles Basin where it was carefully documented and figured by Woodring (1938). Durham (1944) described *Lima twinensis* and *Lima robertsae* from younger Oligocene horizons in the Twin River and Blakeley formations in northeastern Washington, but preservation is inadequate to permit detailed comparisons with the Keasey species other than to note that they are large-shelled species more appropriately assigned to *Plicacesta* Vokes (1963). Durham's species are more similar to *Plicacesta wilsoni* E.J. Moore (1984a) from the uppermost exposed portion of Lincoln Creek Formation along with the Keasey-equivalent giant limid treated and figured separately below.

Material examined—11 partial to nearly-complete valves and numerous shell fragments suitable for investigation of shell microstructure.

Figured hypotypes—UCMP 110740 (left valve), length

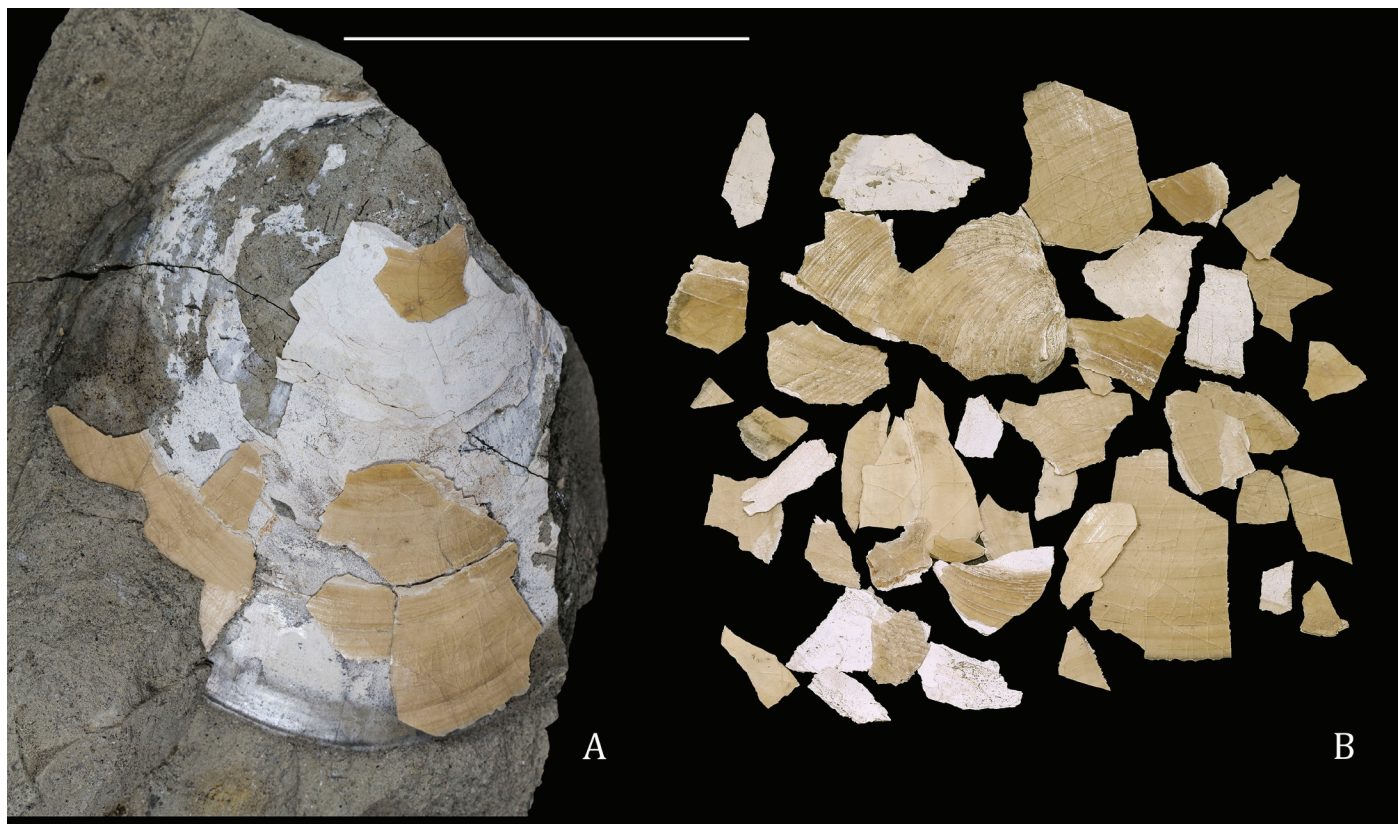


Figure 27. *Acesta oregonensis* (Clark, 1925). Hypotype, UCMP 110741. **A.** Right valve in matrix with adhering interior (aragonitic) and exterior (calcitic) shell layers. Scale bar=5 cm. **B.** Fragments of exfoliated aragonitic layers from **A.**

7.3 cm, height 7.8 cm., Loc. UCMP IP2540. UCMP 110741 (right valve), length 7.8 cm, height 7.7 mm, Loc. UCMP 110740.

Unfigured hypotype—UCMP 110742 (incomplete righty valve in matrix), Loc. UCMP IP2540.

Localities—USGS 15269, 15315, 15518, 15601, UCMP 4118 (Clark's type locality), UCMP IP2540, 2549, 2550. The type locality is an abandoned railroad tunnel with outcrops that are no longer accessible, but the beds fall within the stratigraphic interval represented by the upper member.

Stratigraphic range—Restricted to the upper member of the Keasey Formation.

PLICACESTA VOKES, 1963

Type species—By original designation, *Lima smithii* G. B. Sowerby III (1888). Holocene, Japan.

Discussion—*Plicacesta* is usually treated as a subgenus of *Acesta*, along with the extinct Upper Cretaceous *Costellacesta* Kauffman (1964) and extinct Eocene *Antarcticesta* Stilwell and Gaździcki (1998). It is treated here as a distinct genus that includes similarly large-shelled limids with prominent sculpture of well-developed

radial ribs and interspaces over the entire shell and most strongly developed on the central portion. The hingeplate is thick, with a strongly oblique (opisthocline) resilifer with curved margins. As noted by E.J. Moore (1987, p. C15) the Eastern Pacific fossil species assigned to *Plicacesta* have considerably thicker shells than the living species, and it is possible this is a paraphyletic group. These thick-shelled forms first appear in the Paleogene of central and southern California. A specimen from the Keasey-equivalent Gries Ranch Formation provides new documentation of both exterior sculpture and the interior hinge plate and strongly oblique resilifer.

Stratigraphic range—Paleocene–Holocene.

PLICACESTA BELA (DICKERSON, 1917)

FIGS. 28A–C

Lima bela Dickerson (1917). pp. 172–173; pl. 29, fig. 11.

Lima (Radula) oakvillensis Clark (1925). p. 84; pl. 14, figs. 1, 3.

Lima bela Dickerson, Effinger (1938). pp. 368–369.

Lima bela Dickerson, Weaver (1943). pp. 97–98; pl. 21,

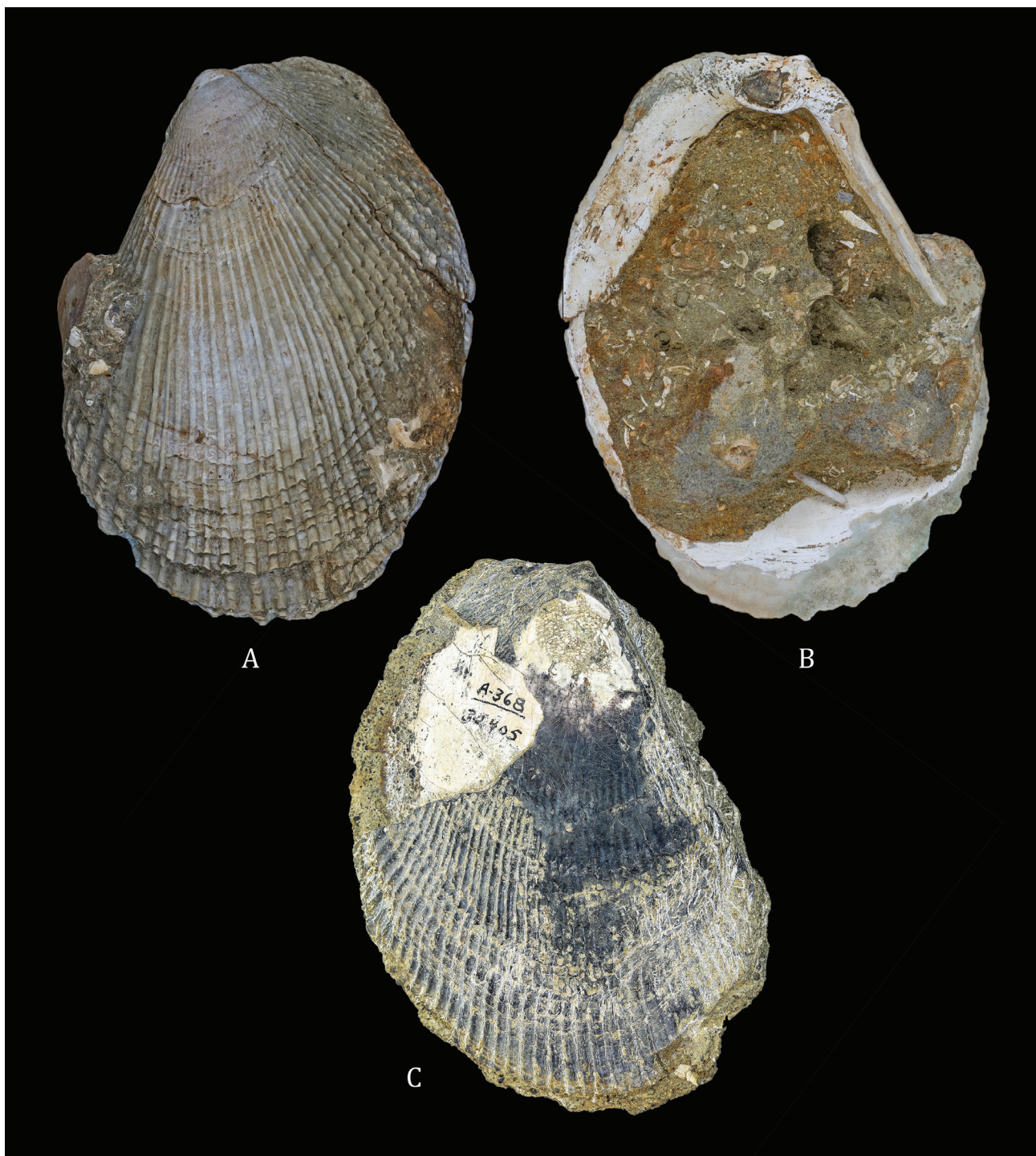


Figure 28. *Plicacosta bela* (Dickerson, 1917). **A, B.** Gries Ranch Formation hypotype UCMP 110743, length 8.4 cm. **A.** Left valve exterior calcitic layer, **B.** Left valve interior with calcitic layer (white) and interior portion of aragonitic layer (gray). **C.** Lincoln Creek Formation hypotype UCMP 32405. Right valve exterior, length 8.4 cm.

fig. 3.

Lima oakvillensis Clark, Weaver (1943). p. 98; pl. 21, fig. 1; pl. 22, fig. 7.

Acesta (Plicacosta) oakvillensis Clark, E.J. Moore (1984a). pp. 27–28; figs 118, 132, 134.

Not *Acesta* cf. *A. oakvillensis* Clark, Addicott (1976a). p. 441; fig. 6ac.

Discussion—The resilifer is clearly posterior to the beak. The posterior ear is well-developed on the rounded posterior dorsal margin. The anterior dorsal margin is

straight, anterior to the beaks, and lacking evidence of a discrete ear. The radial ribs are strongly developed, with flat-bottomed interspaces that are wider than the radial ribs on the central portion of the shell. The ribs become scabrous at intersections with concentric growth increments. Shells are more similar in shape, ornamentation, and cardinal area to those of the Japanese type species of *Plicacesta* than to other species that have been assigned to the genus. The robust sculpture is more typical of the Cretaceous (Maestrichtian) species of *Costellacesta* illustrated by Kauffman (1964), although interspaces lack the fine secondary radial threads characteristic of the geologically older genus. The monotypic and endemic Antarctic genus *Antarcticesta* is distinguished by its thin shell and sculpture of very broad, scaly, and widely-spaced radial ribs. Recognition of four distinct genus group taxa has considerable morphological support as a working hypothesis.

Dickerson described *Lima bela* from a small, left valve. Specimens of large adults collected subsequently from the type locality (Fig. 28A, B) cannot be distinguished from *Plicacesta oakvillensis*, described by Clark (1925) from the coeval beds in the lower part of the Lincoln Creek Formation at the Oakville Quarry (Fig. C). Unfortunately, both Dickerson and Clark confused anterior and posterior in stating that there was well-developed anterior ear and a straight posterior margin. This is clearly not the case with the specimens illustrated here.

Co-occurrence of *Plicacesta bela* and *Porterius gabbi* in Gries Ranch assemblages is consistent with a deep-water depositional environment as discussed above in the treatment of *Porterius*.

Figured Gries Ranch hypotype—UCMP 110743 (left valve), length 8.4 cm, height 10.4 cm., Loc. UCMP IP2289.

Figured Lincoln Creek hypotype—UCMP 32405 (right valve), length 8.9 cm, height 11.3 cm, Loc. UCMP A-368.

Stratigraphic range—Although this species has not been collected in the Keasey Formation, it is narrowly restricted to the Gries Ranch Formation and coeval beds in the Lincoln Creek Formation, where it co-occurs with *Porterius gabbi*. As noted above, the narrow restriction of *P. gabbi* includes the upper member of the Keasey Formation.

SUMMARY AND CONCLUDING REMARKS

Four-part monographic treatment of the Keasey bivalves was originally conceived and designed on traditional taxonomic divisions—protobranchs, pteriomorphs, heterodonts, and anomalodesmatans. New data

sets and analytic methods have altered the traditional classification and generated new phylogenetic hypotheses and alternative classifications.

Preceding treatments of the anomalodesmatans (Hickman 2014) and heteroconchs (Hickman 2015) included revised estimates of relationships between and within major groups. The pteriomorphs continue to emerge as a well-supported clade, although the analysis of internal relationships is ongoing and vigorous. Molecular analyses have been especially useful in identifying clades. However, new morphological and paleontological data continue to produce significant refinements and an exciting integration of knowledge by combining data from fossil and living species.

In the above treatment, relationships within the pteriomorphs enter the discussions of each of the taxa. However, no further discussion is provided here, as with the two previous papers. A comprehensive summary is slated for the fourth and final paper in the series, the protobranchs, along with an overview of Keasey paleoecology, biostratigraphy, and paleobiogeography.

Productive future research on the Keasey pteriomorphs will emerge from strategic search images based less on entire specimens and more on recognition of morphological detail and collection of incomplete specimens and fragments that are typically left behind in the field. Attention to preparation and advancements in image acquisition and illustration continue to be important, especially for microscopic sculptural patterns on many mud pecten and glass scallop shells. These future directions invite and encourage avocational paleontologists and collectors with a long history of interest in the Keasey fauna.

The concept of a peri-seep biotope as a distinct physical and chemical region of habitat and fauna will be accepted and useful only if there is increasing evidence in both modern and ancient settings of a zone of transition. The existence of intermediate conditions and intermediate fauna will replace the traditional binary distinction between seep fauna and background fauna only with broader recognition in both modern and ancient settings. For the geologist it is a concept that can be extended vertically and temporally into the sedimentary record. For the biologist it is a concept that can be extended upward into the water column.

ACKNOWLEDGEMENTS

Many contributions of colleagues and institutions during fifty years of field and laboratory study of the Keasey bivalves are acknowledged in the earlier

anomalodesmatan and heteroconch monographs (Hickman 2014, 2015). For the pteriomorphs, I am especially grateful for specimens donated by Casey Burns, Dave Taylor and Bruce Welton. Geologic, taxonomic, structural, functional, and ecological interpretations have benefited from wide-ranging discussions with Liz Nesbitt, Judy Terry Smith, Paul Valentich-Scott, Tom Waller, and the late Brian Morton. For discussions of paleobiogeography and striking similarities to Eocene pteriomorph taxa in Australia and New Zealand, I thank Alan Beu, Tom Daragh and the late George Kendrick.

For digital photography, image manipulation, and assistance with final preparation of the color figures, I am especially thankful for the outstanding work of Dave Strauss. Line drawings and difficult reconstructions are the work of Marla Coppolino. Micrographs by the author were recorded digitally with the Hitachi Field Emission Scanning Electron Microscope in the Biological Electron Microscope Facility at the University of Hawai'i, Manoa; and the interest, valuable advice, and assistance of Tina Weatherby Carvallo are gratefully acknowledged.

Designation of the peri-seep biotope is an outgrowth of detailed field study of Rock Creek carbonate and associated mudstone facies with Dave Taylor and Liz Nesbitt, Ruth Martin and Kathy Campbell. Work in The Rock Creek section was made possible by the Keasey Family Foundation and members of the Keasey family. I am grateful for years of encouragement by residents of Vernonia, Oregon. Toby Finzel of the Vernonia Pioneer Museum provided helpful historical information on regional history of the now defunct Smithwick and Empire quarries that have been a major source of Keasey mollusk material.

In continuing recognition of his encouragement and generosity, this monograph is dedicated to the late Harold Vokes, who provided the foundational geological expertise, specimens, and initial identification of the Keasey bivalves collected during geological mapping in northwestern Oregon.

I appreciate the valuable reviews and suggestions of Elizabeth Nesbitt, Paul Valentich-Scott, and an anonymous reviewer. I am especially grateful to Diane M. Erwin for her meticulous editing and for overseeing the entire editorial process and final production for *PaleoBios*.

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