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

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Author:
Hickman, Carole S., Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley

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Abstract:

The heteroconch bivalve fauna of the deep-water (>200 m) Keasey Formation in northwestern Oregon records the Eocene–Oligocene climatic transition and replacement of tropical widely-distributed taxa by the cryophilic taxa that dominate modern high-latitude faunas of the North Pacific. Low-diversity assemblages occur in tuffaceous mudstone and siltstone facies of a deep nearshore basin at the onset of subduction on the Cascadia Margin. Six species of anomalodesmatan heteroconchs have been treated separately, and the remaining Keasey heteroconchs treated here include one basal archiheterodont and 13 imparidentian euheterodonts. The families represented are Carditidae, Thyasiridae, Lucinidae, Lasaeidae, Cardiidae, Tellinidae, Basterotiidae, Mactridae and Veneridae. New taxa include the genus *Anechinocardium* and seven new species: *Cyclocardia moniligena*, *Conchocele bathyaulax*, *Conchocele taylori*, *Kellia saxiriva*, *Kellia vokesi*, *Moerella quasimacoma* and *Saxicavella burnsi*. Three species lacking adequate material for formal description are treated in open nomenclature. New features useful for taxonomic discrimination include heretofore unrecognized differences in micro-spines and lamellae on the posterior slope in cardiid bivalve genera and presence of a faint subumbonal ridge in three genera of basterotiid bivalves. Four of the new species are in families in which thiotrophic and methanotrophic chemosymbioses have evolved. Specimens are typically articulated. Shell material is well preserved in the massive units but often chalky or highly altered at cold-seep sites. Fossils are never abundant except for local concentrations in carbonate mounds and associated carbonate lenses, blebs and nodules at cold-seep localities. Multiple lines of evidence of both diffuse and robust flow of fluids rich in reduced compounds are reviewed for three sites where the fauna includes an inner core of chemosymbiotic taxa and peripheral zone of taxa that are opportunistic and tolerant of hypoxia.

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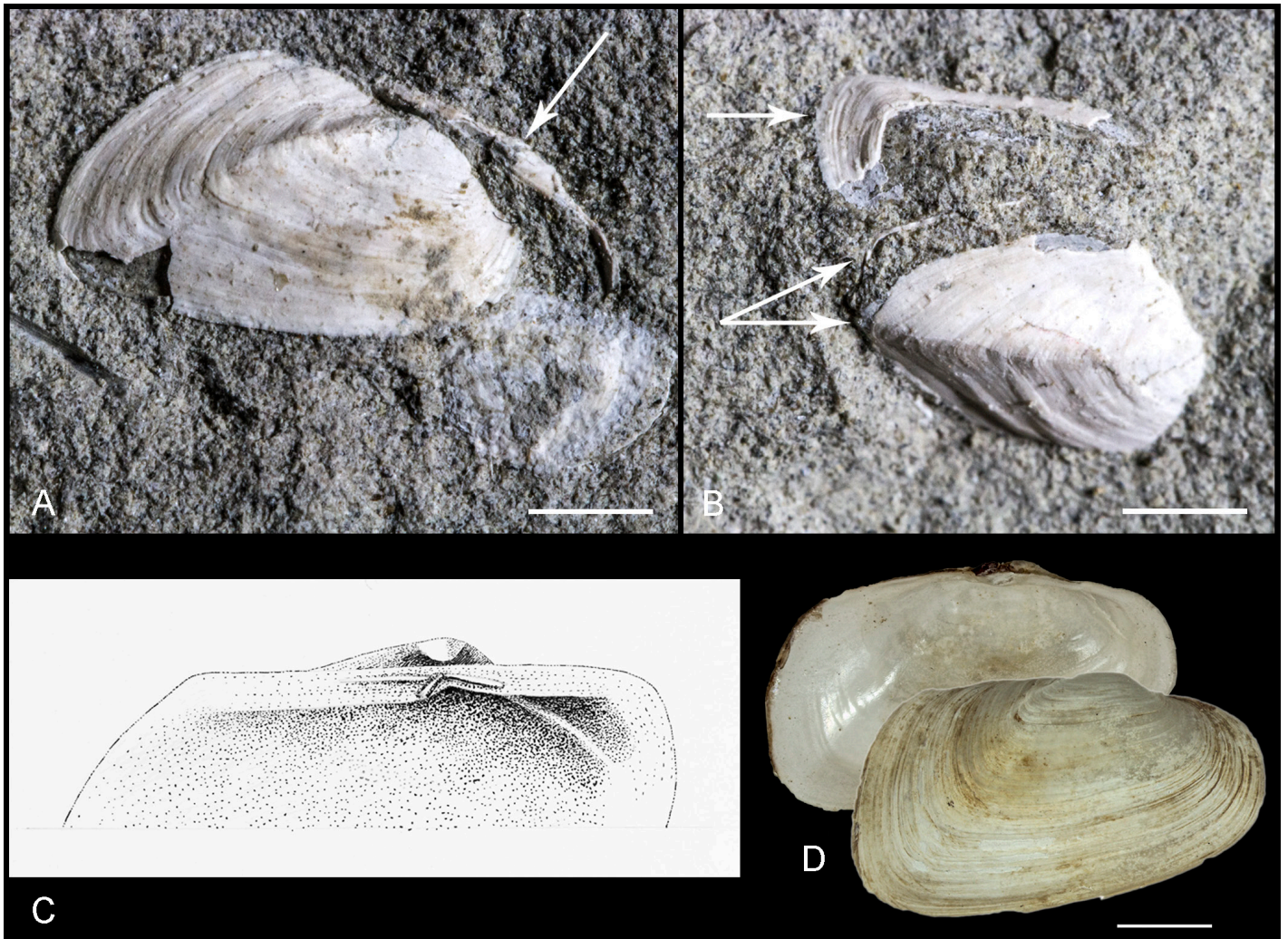
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Cover illustration: *Saxicavella burnsi*, Hickman, n. sp. is one of twelve heteroconch bivalve species from deep-water extreme environments in the Paleogene Keasey Formation in Oregon during a time of global climate change.

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

CAROLE S. HICKMAN

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

The heteroconch bivalve fauna of the deep-water (>200 m) Keasey Formation in northwestern Oregon records the Eocene–Oligocene climatic transition and replacement of tropical widely-distributed taxa by the cryophilic taxa that dominate modern high-latitude faunas of the North Pacific. Low-diversity assemblages occur in tuffaceous mudstone and siltstone facies of a deep nearshore basin at the onset of subduction on the Cascadia Margin. Six species of anomalodesmatan heteroconchs have been treated separately, and the remaining Keasey heteroconchs treated here include one basal archiheterodont and 13 imparidentian euheterodonts. The families represented are Carditidae, Thyasiridae, Lucinidae, Lasaeidae, Cardiidae, Tellinidae, Basterotiidae, Mactridae and Veneridae. New taxa include the genus *Anechinocardium* and seven new species: *Cyclocardia moniligena*, *Conchocele bathyaulax*, *Conchocele taylori*, *Kellia saxiriva*, *Kellia vokesi*, *Moerella quasimacoma* and *Saxicavella burnsi*. Three species lacking adequate material for formal description are treated in open nomenclature. New features useful for taxonomic discrimination include heretofore unrecognized differences in micro-spines and lamellae on the posterior slope in cardiid bivalve genera and presence of a faint subumbonal ridge in three genera of basterotiid bivalves. Four of the new species are in families in which thiotrophic and methanotrophic chemosymbioses have evolved. Specimens are typically articulated. Shell material is well preserved in the massive units but often chalky or highly altered at cold-seep sites. Fossils are never abundant except for local concentrations in carbonate mounds and associated carbonate lenses, blebs and nodules at cold-seep localities. Multiple lines of evidence of both diffuse and robust flow of fluids rich in reduced compounds are reviewed for three sites where the fauna includes an inner core of chemosymbiotic taxa and peripheral zone of taxa that are opportunistic and tolerant of hypoxia.

Keywords: Eocene-Oligocene transition, Cascadia Margin, methanogenesis, cold-seep, chemosymbiosis, hypoxia

INTRODUCTION

Heteroconch bivalves are among the most frequent (occurring at many localities) and abundant (occurring in large numbers at any given locality) mollusks in warm, shallow-water faunas of the Cenozoic. The success of the group is widely attributed to post-Paleozoic evolutionary radiations of siphonate suspension feeders in the Mesozoic. Siphonate survivors of the end Cretaceous mass extinction re-radiated in the Cenozoic. Heteroconchs are less diverse offshore in both fossil and modern deep- and cold-water faunas, although they have been remarkably successful in developing novel morphological and physiological adaptations to physically and chemically extreme environments. They are best known for multiple inventions of nutritional strategies based on chemosynthetic fixation of carbon by archaea and bacteria. They are less well known for novel adaptations to hypoxic conditions and toxic reduced chemicals at effluent sites.

The heteroconch bivalves in the upper Eocene–lower Oligocene Keasey Formation in Oregon provide a window into Paleogene origins of deep-water extremophile communities in the North Pacific and massive faunal turnover at 35.5 Ma in response to global cooling during the Eocene-Oligocene transition.

The anomalodesmatan heteroconchs of the Keasey Formation have been documented separately (Hickman 2014) and include six species in four families. Inclusion of the highly specialized anomalodesmatans within the heteroconchs (Bieler et al. 2014) is strongly supported by morphological and molecular data, although the new classification differs markedly from traditional subdivision of the bivalves, by both paleontologists and neontologists, into four major subclasses.

The remaining Keasey heteroconchs are treated here and include one basal archiheterodont and the remaining non-anomalodesmatan euheterodonts now known as imparidentians. Because the revised classification (Bieler et al. 2014) departs substantially from previous hypotheses of relationships, the systematic paleontology section includes

considerable discussion of the new framework and basis for the constituent clades recognized here.

A major objective of this four-part monographic treatment is to bring paleontololgical and neontological assessments into better alignment. It necessarily requires integration of geological data (e.g., stratigraphy, tectonics, sedimentology, geochemistry, and geochronology) that are largely unfamiliar to neontololgists with biological data (e.g., anatomy, physiology, reproduction, development, and behavior) that are not normally considered relevant to paleontology.

Fourteen species are treated here. Only four are previously described. Of the remaining 10 species, seven are named and diagnosed as new, and three are treated in open nomenclature pending discovery of better material. A new genus is described for the most common bivalve in the formation, a cardiid that was originally described and illustrated more than 100 years ago. At the genus-group level, assignments are based in part on examination of living representatives of the fossil taxa. Comparative illustrations of nine living species are included to show shared diagnostic characters. Comparisons are primarily with similar Paleogene species from the Northeastern Pacific. Neogene and younger species are too easily differentiated to merit detailed comparison. However, some striking similarities to Australasian taxa and species from the Northwestern Pacific are noted either as demonstrably superficial or as potentially relevant to biogeographic reconstruction.

Hickman (2014, pp. 2–4 and references therein) provided a background treatment of the Keasey Formation's location, stratigraphy, depositional and tectonic settings, paleo-bathymetry, paleoecology, age and correlation, and record of the Paleogene greenhouse-icehouse transition. A detailed review and re-assessment of the chronostratigraphy, magnetostratigraphy and molluscan biostratigraphy of the Keasey Formation awaits completion of the bivalve monograph. Correlation must consider a large body of literature providing revised provincial chronostratigtaphic and biostratigraphic frameworks for western Oregon and Washington (Armentrout 1981, Armentrout et al. 1983, Prothero 2003).

Important published data on regional faunal change across the Eocene-Oligocene boundary include (1) an analysis of faunal turnover in marine gastropods on the West Coast of the United States (Squires 2003), (2) analysis of the transition in marine gastropods in the high-latitude North Pacific (Olenik and Marincovich 2003), and (3) documentation of faunal turnover in shallow marine molluscan faunas in the Pacific Northwest (Nesbitt 2003). The latter study highlights significant response in shallow-water bivalve taxa to the tectonically-driven shift from continent-derived feldspathic and arkosic sediments to siliciclastic sediments derived from the onset of Cascade Arc volcanism. Poor chronostratigraphic resolution confounding past analyses is considerably improved by the magnetostratigraphic studies and calibrations of Don Prothero and his students, and provides a new framework for understanding the Eocene-Oligocene transition on the Cascadia Margin (Prothero 2003).

History of the Keasey bivalve project and materials and methods are detailed in the anomalodesmatan treatment (Hickman 2014, pp. 4, 5). Two aspects of Keasey geobiology are especially relevant to the heteroconchs and are treated here in more detail: (1) occurrence of cold-seep carbonate bodies with distinctive bivalve assemblages and (2) combined geological and paleontological inference of faunal response to physically and geochemically extreme environments.

KEASEY COLD-SEEP CARBONATES AND
HETEROCONCH BIVALVES

Unusual bivalve communities appear suddenly in upper Eocene (~35.5 Ma) tuffaceous mudstone and siltstone of the Keasey Formation (Hickman 1984). Designation of novel community types (Hickman 1984) predated previously-overlooked field evidence of their close geological association with carbonate precipitation (Campbell and Bottjer 1993) and with development of multiple lines of evidence for methane seepage in both the fossils and the rocks (Campbell 2006). Inference of microbial chemosynthesis was based initially on the presence of bivalve taxa whose living representatives have established endosymbiotic relationships with sulfide- and methane-oxidizing bacteria (see Taylor and Glover 2010 for a review).

Multiple direct criteria have been established as part of a "seep-search strategy" (Campbell and Bottjer 1993), resulting in documentation of a remarkable temporal and geographic concentration of Paleogene cold seeps associated with the onset of subduction and establishment of the Cascadia Arc in Washington and Oregon. Inference is based on a combination of direct field evidence of carbonate mounds and fluid conduits, biomarker analysis, numerous diagnostic petrographic features and fabrics, and geochemical and isotopic evidence of biogenic and auithigenic carbonate precipitation (Peckmann et al. 2002, Campbell 2006, Nesbitt et al. 2013). In the Keasey Formation stable carbon and oxygen-isotope data ($\delta^{13}C$ and $\delta^{18}O$) from authigenic limestones and biogenic carbonates provide evidence of both robust fluid flow and diffuse seepage of methane (Nesbitt 2003, Martin and Nesbitt 2005, Martin 2010, Nesbitt et al. 2013). Stable isotope analysis of the tests of individual benthic Foraminifera is an especially powerful tool, providing evidence of extreme ^{18}O depletion at one of the Keasey seeps (Martin et al. 2007, Martin 2010).

Three different methane-influenced sites in Oregon of the Keasey Formation illustrate different positions in the spectrum of seep carbonates: (1) Timber-Vernonia, (2) Rock Creek, and (3) Mist.

Timber-Vernonia Seep

This locality in the lower member is exposed in a prominent bluff on the east side of the Nehalem River, bordering the road between Timber and Vernonia. The outcrop has changed over the years. In 1993, it exposed a large limestone block and chimney structures (Fig. 1A) with difficult access. In 2005 the outcrop exposed additional limestone blocks in the deeply-weathered brown tuffaceous siltstone (Fig. 1B) over a lateral distance of approximately 70 meters. The bivalves are zoned at this site, with abundant thyasirids in the limestone core and a rarer solemyid and two lucinids in the adjacent siltstone. The most abundant bivalve in the outcrop is a small carditid species that occurs at a greater distance from the core. It is described below with additional discussion of the relationship of carditids to hypoxic environments.

Modern chemoherm build-ups at Hydrate Ridge on the Cascadia Margin off Oregon (Greinert et al. 2001, Teichert et al. 2005) provide a model for re-interpretation of the carbonate complex at the Timber-Vernonia site in the Keasey Formation (Martin 2010). Although the three-dimensional geometry of the complex cannot be resolved from what is exposed in outcrop, the carbonates represent more organized fluid migration and expulsion than at most other seep sites.

Figure 1A–D. Cold-seep carbonates in the Keasey Formation. **A**. Timber-Vernonia carbonate mound or chemoherm in 1992. **B.** Timber-Vernonia carbonate chemoherm in 2005. **C.** One of five discrete carbonate blocks (arrow), Rock Creek seep. **D.** Carbonate blebs and nodules in siltstone, Rock Creek seep.

Rock Creek Seep

The Keasey carbonate complex at the Rock Creek site consists of a combination of discrete carbonate blocks (Fig. 1C), thin carbonate lenses, and carbonate blebs and nodules (Fig. 1D). The outcrop is in the basal portion of the middle member and is less extensive than the Timber-Vernonia seep. However, we were able to excavate a 25-meter long exposure in overgrown creek bank to expose fresh blue-gray siltstone in sharp contact with five discrete limestone blocks as well as several discrete layers of carbonate blebs, nodules and lenses in the siltstone. Numerous thyasirid bivalves were confined to the limestones, with rare articulated solemyids preserved in living position in the siltstone. Individual unaltered benthic foraminiferal tests from the siltstone yielded δ13C values indicative of carbon-depleted sediment pore water (Nesbitt et al. 2006). We saw no evidence of conduits, suggesting slower and more diffuse flow than at the Timber-Vernonia site. Diffuse seepage appears to be an increasingly ubiquitous feature of post-Eocene fossil seeps on the Cascadia Margin (Nesbitt et al. 2013).

Mist

The crinoid lagerstätte at the base of a 50 m-high bluff on the west side of the Nehalem River is famous for its outstanding preservation and diverse echinoderm fauna. The stem-bearing crinoids described by Moore and Vokes (1953) are especially abundant. They have attracted attention because they were buried *in situ* as completely articulated individuals and form a paleoecological assemblage that is unusual for the Cenozoic. The associated carbonates also have attracted attention. Stable isotope analysis provides clear signatures (-δ18O and +δ13C) of formation in a zone of archaeal methanogenesis (Burns et al. 2005), although formation is not necessarily contemporaneous with the crinoid fauna.

Echinoids, asteroids and ophiuroids are also significant faunal elements at Mist and have been reviewed by Burns and Mooi (2003) in the context of understanding global change and the Eocene-Oligocene transition. Bivalves at Mist have received less attention, but they include a solemyid, a thyasirid, and new heteroconch species (described herein) in families with living forms that are either chemosymbiotic or tolerant of low-oxygen environments. Distinguishing taxa capable of living in seep environments from chemosymbiotic taxa is paleontologically difficult and requires some additional discussion.

Fluid dependence, tolerance, and opportunism at Keasey seeps

Ecological and evolutionary responses to extreme environments and geochemistry are difficult to establish without access to anatomy and physiology. Fossil cold-seep bivalves were not necessarily chemosymbiotic with thiotrophic or methanotrophic bacteria. In the deep-water cold-seep faunas of Japan, deposit-feeding protobranch bivalves of the genus *Acila* H. and A. Adams, 1858 have been a common "background" element since the Cretaceous (Cenomanian) (Majima et al. 2005, Kiel et al. 2008). Deposit-feeding protobranch bivalves in three families are reported in descriptions of Cenozoic seep assemblages on the Cascadia Margin (e.g., Peckmann et al. 2002, Goedert et al. 2003, Kiel 2006, 2010) as well as epifaunal pectinid and propeamussiid pteriomorph bivalves (Kiel 2006). The relationship of these background taxa to seep sediments and geochemistry merits greater attention.

There are three main reasons why non-chemosymbiotic bivalves may be abundant in fossil cold-seep biotopes. The first is an ability to take direct advantage of organic enrichment of sediments by chemosynthetic bacteria. Most of the organic productivity at seeps is by the free-living microbiota, and the abundance of deposit-feeding protobranch bivalves at seep localities is consistent with the hypothesis of trophic opportunism. When present, protobranchs occur peripheral to carbonate bodies and are part of the fauna at both the Timber-Vernonia seep and at Mist.

The second is the ability to tolerate hypoxia and extreme geochemical fluids (especially sulfide) that are normally toxic. Oxygen-binding pigments can occur either within tissues or extracellularly in fluid transport systems. In yoldiid protobranchs, hemoglobin is reported in the bright red gills of *Yoldia hyperborea* (Gould, 1841) (Alyakrinskaya 2003). Hemoglobins are reported from nerve tissue in two tellinids (Alyakrinskaya 2003), and there is experimental evidence that aerobic activity can be sustained by hemoglobin-stored oxygen under anoxic conditions (Kraus and Colacino 1986). Protobranch bivalves and the new tellinid described below are among the most frequent and abundant species in the Keasey fauna.

The most abundant bivalve at the Timber-Vernonia cold seep is a new carditid species described below. It is found peripheral to the main carbonate mounds in glauconitic siltstone, and there is no taxonomic basis for suspecting chemosynthetic capability. However, carditids are members of an ancient bivalve clade that has uniquely-evolved extracellular transport hemoglobin (Terwilliger and Terwilliger 1978). Tolerance of hypoxia is consistent with its occurrence at this seep site.

The study of oxygen-binding proteins and functional specializations for meeting the oxygen needs of bivalves merits greater attention as global warming increases coastal hypoxia and climate-driven oxygen minimum zone (OMZ) expansion.

Some minute bivalves (<5 mm) are able to exploit life in anoxic sediments by living in association with invertebrate taxa that ventilate their burrows. This is potentially the case with the first Keasey reports of one basterotiid and two galeommatid bivalves. Bacterial symbionts have been discovered in the gills of living representatives of both families (Oliver 2012, 2013, Oliver et al. 2012) and are discussed in the descriptions of the new Keasey species.

Ability to deal with hypoxia may also serve as a refuge from predation. Naticid gastropods are rare at seeps, and the absence of boreholes in seep bivalves is in marked contrast to evidence of boring predation in non-seep biotopes.

A third potential explanation of an ecological association between bivalves and seep carbonates is the benefit of a hardground for epifaunal taxa. This explanation is consistent with the presence of byssally attached mud pectens. An undescribed mud pecten is one of the most frequent species in the Keasey Formation (>30 localities) and occurs in four distinct assemblages at Mist, although contemporaneity of the Mist carbonates and epifauna has not been established (Burns et al. 2005).

SYSTEMATIC PALEONTOLOGY

Institutional abbreviations

Type numbers and locality numbers in the systematic account are identified as to institution by the following abbreviations: **SBNMH** – Santa Barbara Museum of Natural History, Santa Barbara, California, U.S.A.; **UCMP** – University of California Museum of Paleontology, Berkeley, California, U.S.A.; **USNM** – United States National Museum of Natural History, Washington, D.C.; and **USGS** – United States Geological Survey, Reston, Virginia, U.S.A.

Geographic terminology

There is no consistent terminology for clearly-bounded physical geographic, geologic, and biogeographic regions. Regional designations in the text are applied flexibly as follows:

North Pacific—The Pacific Ocean north of the equator. Fossil and living taxa treated herein are from the high latitude North Pacific margins of Asia and North America. This term is useful for discussing the history of faunal interchange, migrations, ocean currents and gateway events.

Eastern Pacific, Northeastern Pacific—The North American portion of the North Pacific and that portion of the Eastern Pacific ranging from the eastern Bering Sea south to Point Conception. The corresponding Asian portion of the North Pacific, extending from Japan to the western Bering Sea, is referred to as the **Northwestern Pacific**.

Pacific Coast of North America—This term is used primarily to refer to geologic formations and marine fossil faunas exposed on the western continental margin of North America. Geologists and paleontologists have commonly use "Western North America" while neontologists have preferred "Eastern Pacific." There is no consistency in the literature with respect to capitalization of any of these terms.

Pacific Northwest—The modern continental margin of western Washington and Oregon and geologically including the tectonically active **Cascadia Margin** from British Columbia to far northern California.

HETEROCONCHIA J.E. Gray, 1854
ARCHIHETERODONTA Giribet, 2008

Heteroconchia encompasses Keasey species in the most derived and diverse of the extant bivalve groups formerly referred to as "heterodonts." It also includes the previously treated Keasey anomalodesmatans (Hickman 2014), an ancient, large, and predominantly deep-water clade nested within the traditional heterodonts. Living heteroconchs are predominantly infaunal suspension feeders, and although anomalodesmatans are siphonate they have evolved many peculiar specializations that include byssal attachment, tube dwelling, scavenging and active predation. It is therefore of considerable interest that an outstanding multi-locus phylogenetic analyses has established the monophyly and relationships of a set of non-siphonate families comprising the ancient Archiheterodonta (González and Giribet 2015). A single archiheterodont is represented in the Keasey fauna. It occurs at a few localities but is remarkable in its abundance at one of the Keasey cold-seeps in association with two chemosymbiotic bivalves – a solemyid and a thyasirid.

Divergence time estimated from molecular data for the archiheterodont clade (González and Giribet 2015) is consistent with fossil record indications of an Early Paleozoic origin (Allen 1985).

Stratigraphic range—Lower (?) Ordovician to Holocene.

CARDITOIDEA Férussac, 1822
CARDITIDAE Férussac, 1822
CARDITAMERINAE Chavan, 1969c

As noted by González and Giribet (2015), Carditidae cannot be defined phylogenetically without the sampling of many more genera and species. Recognition here of Carditimerinae follows the Treatise classification of Chavan (1969c), who included 24 genus-group names, 11 of which have no living representatives. The new Keasey species belongs to a cosmopolitan genus that occurs predominantly in cold water at high latitudes and which has not yet been sampled in molecular phylogentic study.

Stratigraphic range—Upper Triassic (Carnian) to Holocene.

CYCLOCARDIA Conrad, 1867

Type species—By subsequent designation (Stoliczka, 1871), *Cardita borealis* Conrad, 1832. Holocene, northwestern Atlantic.

Cyclocardia merits special attention as an element of the Keasey bivalve fauna. This is the first appearance of the genus in the Eastern Pacific, coinciding with a dramatic global cooling event and extinction of the widespread tropical Eocene fauna. The tropical Eocene fauna extended from California through the Pacific Northwest and into Alaska included archiheterodont genus *Venericardia* Lamarck, 1801. According to James Perrin Smith (1919) *Venericardia* was the last great migrant from the Atlantic to the Pacific, and the genus was colorfully characterized by Timothy Abbott Conrad as "the finger post of the Eocene" (Gardner and Bowles 1929). If *Venericardia* is the finger post of the Eocene, then *Cyclocardia* is the finger post of the Eo-Oligocene transition and subsequent establishment of the modern cold-water faunas of the North Pacific.

Morphology and preservation—Living species of *Cyclocardia* are more ovate in shape than the trigonal and elongate shapes that are typical in Carditoidea. Coan et al. (2000) recognize nine species in the Northeastern Pacific, but taxonomic characterizations are confounded by high levels of morphological variation. The shells are often thick, strongly inflated, and covered with a hirsute brown or tan periostracum. Strong radial ribs are crossed by commarginal lirae that are stronger on the ribs than in the interspaces. Dredged samples may contain large numbers of individuals in which the periostracum is eroded away and outer crossed-lamellar layer is partially dissolved (Fig. 2B), although the shells remain articulated post-mortem in both fossil (Fig. 2A) and modern (Fig. 2B) populations and the robust hinge plates are commonly well preserved in fossils. Naticid drill holes have not been observed in either fossil or living populations.

Variability—In a review of the northwest American Carditidae, Coan (1997) recognized two major species complexes, one centered in the Bering Sea and the other ranging from the Gulf of Alaska to central Baja California, noting a "bewildering degree of morphological variability" (p. 375). Interpopulation variability in carditids has been attributed to the brooding of young in the mantle cavity and lack of a planktonic larval stage (e.g., Yonge 1969), leading to reduced gene flow between populations (Coan 1997).

Paleobiogeography—Many species of *Cyclocardia* have been described from the Neogene and Quaternary of the
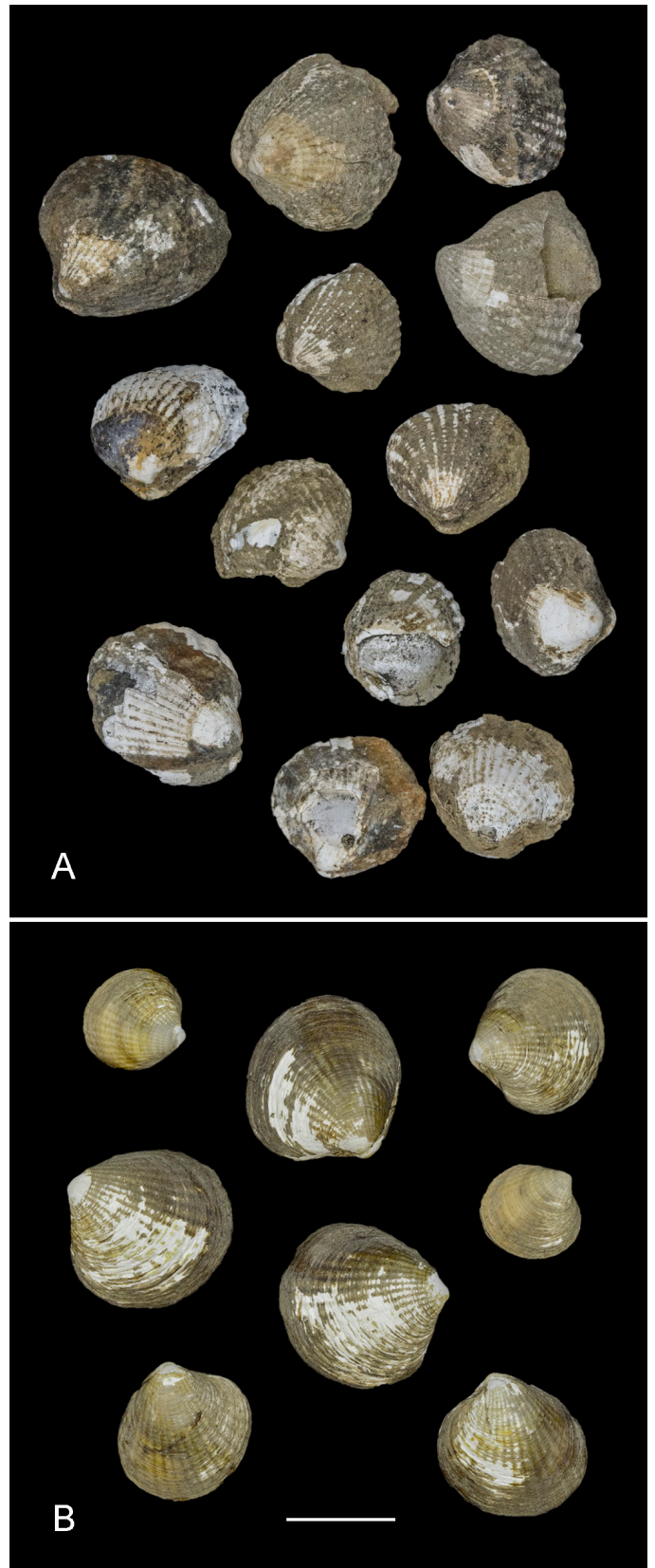

Figure 2A–B. Shell corrosion in *Cyclocardia*. **A**. Double-valved Eocene *Cyclocardia moniligena* n. sp. from Timber-Vernonia cold seep, UCMP IP2286. **B**. Double-valved *Cyclocardia barbarensis* (Stearns, 1890) from the oxygen minimum zone at 500 m in the Santa Barbara Basin, California, SBNHM 44076. Scale bar = 1 cm.

North Pacific. MacNeil (1957) was skeptical of the validity of names attached to similar taxa with high levels of variation and intergradation. However, he saw evidence of connections between Oregon/Washington, the Gulf of Alaska, the Alaska Peninsula, and the Chukchi, Beaufort and Bering Seas. He suggested a North Pacific origin for what he viewed as a *Cyclocardia* species complex, noting that there was "nothing living or fossil in the Atlantic like it" (MacNeil 1957, p. 117). In a detailed study of well-preserved bivalves from remote localities in the far western Alaska Peninsula, Marincovich (1983) documented three species of *Cyclocardia* in the upper Miocene Tachilni Formation and drew connections to both Western North American Miocene faunas and Miocene faunas of Kamchatka, Sakhalin and Hokkaido.

The Cenozoic fossil record of archiheterodonts in Japan is similar to that of the Northeastern Pacific in reflecting a response to climate change from the late Eocene to early Oligocene. *Cyclocardia* is well-represented in the late Paleogene faunas of northeastern Japan, although the nomenclature has a tangled history (Matsubara 2011). Demise of tropical Eocene fauna occurred between 43 and 33 Ma, with onset and progressive establishment of the Tasmanian Seaway and formation of the East-Antarctic Ice Sheet leading to terminal Eocene cooling of deep water. A gateway model of Cenozoic history of the Pacific (Ogasawara 2002) provides an integrative geologic, oceanographic and climatic framework for interpreting changes in the Japanese molluscan fauna.

In New Zealand, Cenozoic archiheterodonts referred to *Cyclocardia* show a strong resemblance to the Conrad's type species, although Beu and Maxwell (1990) conclude that the similarity is "almost certainly fortuitous" (p. 148).

Archiheterodonts, including carditids, are well-represented in the modern temperate faunas of the Magellan and Peru-Chile provinces of South America (Güller and Zelaya 2013), but there are insufficient fossil data to address questions of historical biogeography. In the fjords of southern Chile, two carditid species occur in association with a solemyid and a lucinid (Osorio and Reid 2004), strikingly similar to the association reported below.

Relationship to hypoxic environments—Although there are no reported anatomical modifications directly related to nutrition or chemosymbiosis, living *Cyclocardia* is known to occur abundantly in hypoxic environments. For example, in the oxygen miminum zone (OMZ) at 500 m in the Santa Barbara Basin, *C. barbarensis* co-occurs with two lucinoidean bivalve species (Duplessis et al. 2004). The new Keasey *Cyclocardia* occurs in a similar paleoenvironment at the Timber-Vernonia cold seep. No specimens were observed in the main cold-seep carbonate mounds, but they are locally abundant in "nests" in the allochthonous adjacent siltstone along with less abundant thyasirid, lucinomid and solemyid

bivalves. Discovery of uniquely-evolved extracellular hemoglobin in carditid bivalves (Terwilliger and Terwilliger 1978) and presence of distinctive oxygen transport proteins in other basal bivalve families have potential adaptive significance for persistence in extreme environments as well as potential use in phylogenetic analysis (Terwilliger 1998).

Oxygen transport proteins have been partially co-opted to bind sulfide at sites distinct from the oxygen-binding sites (Terwilliger 1998), and interest in the detoxification, transport, and regulation of the delivery of reduced chemicals (Fe, CH_4, H_2S) in vent and seep organisms has perhaps eclipsed interest in oxygen extraction, transport and storage mechanisms as well as in enzymes facilitating anaerobic metabolism under anoxic conditions. Intracellular tissue hemoglobins in bivalves also contribute to respiratory functional diversity, especially in the ctenidia (Alyakrinskaya 2003). The entire array of functional specializations for meeting the oxygen needs of bivalves merits greater attention as global warming increases coastal hypoxia and ecosystems respond to OMZ expansion.

Stratigraphic range—Upper Cretaceous (Cenomanian) to Holocene. Cosmopolitan.

<div align="center">

Cyclocardia moniligena n. sp.
Figs. 2A, 3A–D

</div>

Diagnosis—Shell small (<20 mm maximum length) thick, typically with eroded chalky surface; valves inflated, nearly equilateral and ovate in shape; anterior dorsal margin slightly concave, posterior dorsal margin slightly convex, and ventral margin evenly rounded; beaks strongly prosogyrous and very slightly anterior to midline; lunule large, broad, recessed and bounded by well-developed incised line; escutcheon elongate, narrow, poorly defined; shell surface chalky where eroded, ornamented by 19 prominent radial ribs that are rounded and strongly beaded medially where crossed by undulating commarginal sculpture; rib interspaces slightly wider than radial ribs, with weak but continuous expression of commarginal elements; commissure crenulate in correspondence with alternating termination of radial ribs; hinge plate heavy and well-developed with two prominent cardinal teeth in each valve, a broadly triangular anterior cardinal and a thin, elongate posterior cardinal paralleling axis of hinge plate.

Description—Shells are insufficiently preserved to describe muscle scars or pallial line. On many shells dissolution of the tops of individual beads on the crossribs increases apparent size and accentuates the coarsely-beaded appearance of valves. In later growth, finer secondary ribs are sometimes intercalated in rib interspaces, especially on the anterior portion of the shell. The width of both ribs and interspaces increases toward the growing shell margin (Fig. 3A).
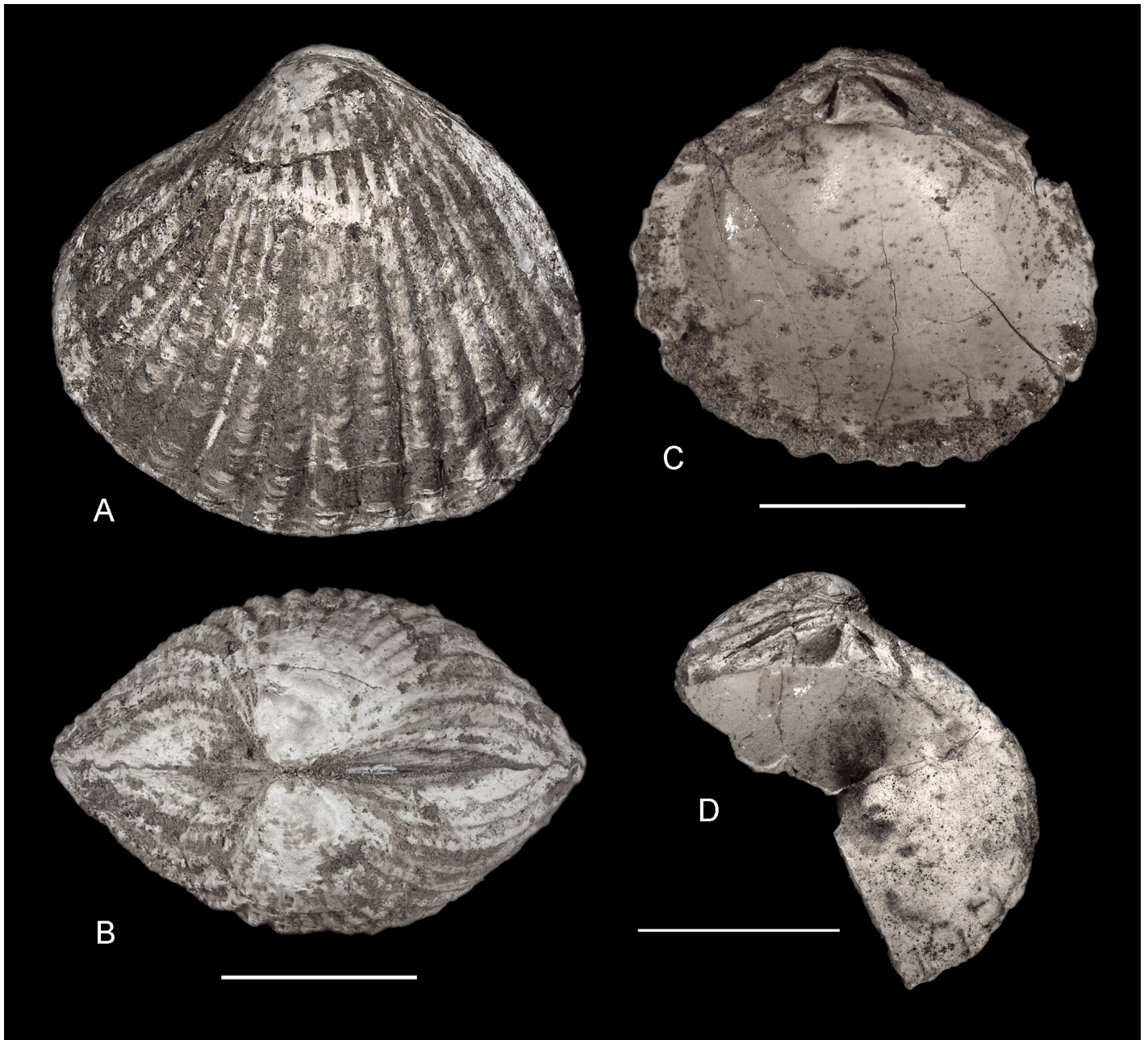
Figure 3A–D. *Cyclocardia moniligena* n. sp. **A.** Holotype, UCMP 110681, Loc. UCMP IP2286, articulated, left valve, length = 13.7 mm. **B.** Dorsal view of holotype, **C.** Paratype, UCMP 110683, Loc. UCMP IP2286, interior view with hinge plate, right valve. **D.** Paratype, UCMP 116684, Loc. UCMP IP2286, interior view with hinge plate, left valve. Scale bars = 5 mm.

Discussion—This is the earliest record of the genus *Cyclocardia* in the fossil record of the Northeastern Pacific. Hertlein and Grant (1972) and Moore (1992) stated the range as Oligocene–Holocene. Seven species are reported from the California fossil record, all but one from Neogene and younger rocks and including three living species.

In the Pacific Northwest, carditids also are known only from Oligocene and younger faunas. Four species were originally described under *Venericardia* prior to recognition of striking differences in the hinge area. The more shallowly-depressed lunule, which does not penetrate beneath the umbones, is not excavated into the hinge plate resulting in a vertical or slightly anterior trend to the anterior cardinals. The excavation of the lunule into the hinge plate in *Venericardiinae* Chavan, 1969c is correlated with a posterior crowding and posterior inclination of the cardinal teeth.

The Keasey species is distinguished easily from all younger species. It is most similar to *Cyclocardia hannibali* (Clark,

1925), which occurs in the overlying Oligocene Pittsburg Bluff Formation and coeval upper portion of the Lincoln Creek Formation as well as in the Miocene Astoria Formation. *Cyclocardia hannibali* has a narrower and more elongate hinge plate and more numerous radial ribs that are more finely beaded. *Cyclocardia hannae* (Tegland, 1933), which occurs higher in the Oligocene Blakeley Formation has fewer radial ribs and is higher in proportion to length. *Cyclocardia castor* (Dall, 1909), also from the Blakeley Formation has a much larger and relatively higher shell with beaks nearer to the anterior margin. *Cyclocardia subteta* (Conrad, 1849) from the Miocene Astoria formation has more numerous radial ribs with relatively narrower interspaces. Although the ribs are crossed by numerous concentric lines, they remain low and do not form beads.

Etymology—*monile* (jewel) + *gena* (cheek).

Material examined—The description is based on 42 articulated (double-valved) specimens, 12 pieces of matrix preserving multiple shells, five single valves preserving hinge teeth, and miscellaneous incomplete single valves and shell fragments, all from the Timber-Vernonia cold seep, peripheral to the limestone mounds. Fifteen additional specimens were collected by W. C. Warren from the middle member but not reported by Warren et al. (1945). Four of these are designated herein as paratypes.

Holotype—UCMP 106681, length 13.7 mm, height 12.6 mm, Loc. UCMP IP2286 (=USGS 25028).

Figured Paratypes—UCMP 110683, right valve hinge, locality UCMP IP2286; UCMP 110684, left valve hinge, locality UCMP IP2286.

Unfigured paratypes—UCMP 110682, a small "nest" of shells in matrix, Loc. UCMP IP 2286; USNM 561789 (originally intended by Vokes as holotype), length 7.8 mm, height 7.1 mm, Loc. USGS 15525; USNM 561791, length 10.3 mm, height 10.0 mm, Loc. USGS 15525; USNM 561792, length 8.7 mm, height 8.3 mm, Loc. USGS 15525; USNM 561790, incomplete left valve showing hinge, Loc. USGS 15525.

Keasey Formation localities—UCMP IP2286 (=USGS 25028), USGS 15265 (lower member); USGS 15525 (middle member?).

<div align="center">

EUHETERODONTA Giribet and Distel, 2003
IMPARIDENTIA Bieler et al., 2014
LUCINIDA J.E. Gray, 1854
THYASIRIDAE Dall, 1900a

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Suspicion that Thyasiridae may be polyphyletic (e.g., Williams et. al. 2004, Dufour 2005) arose from insufficient access to material for molecular analyses and comparative anatomical study. With increased taxon sampling, there is strong analytic support for monophyly of the family (Taylor et al. 2007). However, internal relationships remain unresolved. Taxa that are restricted to cold deep-water habitats remain poorly sampled and are potential reservoirs of undetected variation. Although shell morphology is highly conservative, there is considerable anatomical variation between species that have been examined for chemosymbiotic bacteria: some taxa lack bacteria, and when present they may be arranged and housed in different ways (Dufour 2005).

Large thyasirids of the genus *Conchocele* Gabb, 1866 appear in deep-water communities during the late Eocene greenhouse-icehouse transition on the Pacific Coast of North America (Hickman 1984, 2003). They are core taxa at cold-seeps, typically in association with species of *Solemya* Lamarck, 1818 and *Lucinoma* Dall, 1901 (Hickman 1984). They occur directly in seep limestones as well as on the periphery in sediments indicative of oxygen minimum conditions and the presence of sulfide or methane seepage.

Extant *Conchocele* have ctenidia that place it among the chemosymbiotic thyasirids with the most highly modified ctenidia (Dufour 2005, Taylor and Glover 2010). Oliver (2014) describes and illustrates this most derived condition in which tubular structures with densely packed bacteriocytes greatly expand the surface area of the bacteriocyte zone.

Discoveries of new and unusual deep-water thyasirids suggest previously unrecognized evolutionary radiations. They include new genera from the west coast of North America (Coan and Valentich-Scott 2012), the west coast of Africa (Oliver 2014), and the Arctic Ocean (Valentich-Scott et al. 2014). A review of Magellanic and Antarctic thyasirids (Zelaya 2009) includes one new species and new generic assignments for four other species . Two new taxa have been described from >7,000 m in the Japan Trench (Okutani et al. 1999). The environmental setting for Arctic Ocean species is notably similar to that of the Keasey thyasirids: shells were recovered from a sediment core with authigenic carbonates and methane hydrates (Valentich-Scott et al. 2014). The active Cascadia Margin also contains sites of unusual of crustal fluid discharge that are neither cold seeps nor hydrothermal vents. Lithoautotrophic microbes at one such a site on the east flank of the Juan de Fuca Ridge share a unique geochemical habitat with infaunal protobranch bivalves and a new thyasirid with gill bacteriocytes (Oliver and Holmes 2007).

Revision of Cenozoic fossil thyasirids of the North Pacific is long overdue, and it is time to question the traditional bulk-allocation of fossil populations to a single geographically-widespread and long-ranging species.

Stratigraphic range—Cretaceous to Holocene.

CONCHOCELE Gabb, 1866

Type species—By original designation, *Conchocele disjuncta* Gabb, 1866. "Pliocene," Dead Man's Island, San Pedro, California.

Conchocele has been treated by many authors as a subgenus of *Thyasira* Lamarck, 1818. The type species of *Thyasira* (by monotypy) is *Tellina flexuosa* Montagu, 1803, a circumboreal and pan-Arctic species that has been difficult to define and which may represent a species complex (Coan et al. 2000). As pointed out by Stewart (1930, p. 194), it is a small-shelled species (approximately 10 mm in height), suggesting that Gabb's name *Conchocele* may be "useful for the large North Pacific Species". Gabb's holotype of *C. disjuncta* was lost, and Stewart designated a lectotype (labeled in Gabb's handwriting) that is 90.5 mm in height. Gabb's species is usually synonymized with the previously-described *Venus bisecta* Conrad, 1849 (based on a fossil from the Miocene Astoria formation in Oregon), and most authors have not been able to justify differentiating the two taxa on conchological features. *Conchocele disjuncta* (Gabb, 1866, p. 28; 1869, pl. 7, figs. 48a, b), *Conchocele bisecta* (Conrad, 1849, p. 724, pl. 17, figs. 10, 10a) and some Japanese species, notably *T.* "*bisecta* var." *nipponica* Yabe and Nomura (1925, p. 84, pl. 23, fig. 3; pl. 24, figs. 2–4) are all large. A specimen of *T. nipponica* was reported by Yabe and Nomura (1925, p. 86) to have a "longest diameter" of 170 mm. Grant and Gale (1931, p. 282) stated that specimens of *T. disjuncta* "sometimes attain a length of 130 mm (about 5 inches)".

Oliver and Frey (2014, p. 465-466) revise the generic diagnosis of *Conchocele*, maintaining the synonymization of *C. disjuncta* with *C. bisecta.* However, they do not comment on the allocation of all of the Paleogene and Neogene fossils from the north Pacific to this single species. In the Northwestern Pacific (notably Kamschatka and Japan) additional species-group names have been proposed under both C. *disjuncta* and C. *bisecta* for Cenozoic fossils (e.g., Krishtofovich 1936).

Revision of living and fossil populations of *Conchocele* will be a large undertaking for three reasons. First, there is considerable shape variation in character pair plots for thyasirids, and there is considerable overlap in plots between populations (Kauffman 1967). Second Orientation of thyasirids for illustration and measurement is difficult to standardize. Specimen measurements given in the literature cannot be used for morphometric comparison. Third, the geographic and stratigraphic range of the *Conchocele* complex is immense. In addition to populations from the Northeastern Pacific, it will be crucial to review of studies by Russian scientists of *Conchocele* from cold seeps in the Sea of Okhotsk (Kamenev et. al. 2001 and references therein). It also will be crucial to review the entire Upper Cretaceous to Holocene fossil record in Japan. Majima et al. (2005) summarize literature reports 75 chemosynthetic fossil assemblages. They report fossil thyasirids (identified as *C. disjuncta*, *C. bisecta*, or *C. nipponica*) from 30 fossil localities. The majority of occurrences are autochthonous, in deep-water forearc sequences. Articulated shells are reported to be in living position and associated with cold-seep carbonates. The Japanese occurrences are classified as a Type III chemosynthetic assemblage that is considered seep-dependent (Majima et al. 2005).

Two new species are described and figured here from the Keasey Formation to call attention to distinctive features and to break with a tradition that requires genetic stasis on an unprecedented temporal and geographic scale.

Stratigraphic range—Eocene to Holocene.

Conchocele bathyaulax n. sp.
Fig. 4A–D

Thyasira bisecta Conrad, Schenck, 1936, p. 62.
Thyasira n. sp. Vokes in Warren, Norbisrath and Grivetti 1945, checklist
Thyasira n. sp. Moore and Vokes 1953, p. 115, 118.
Conchocele bisecta (Conrad) Campbell and Bottjer 1993
Conchocele bisecta (Conrad) Squires and Gring 1996, p. 69.

Diagnosis—Shell large (>55 mm in length), thin, equivalve, inflated, subquadrate, and chalky; length and height nearly equal, with prominent terminal umbones; ventral margin evenly rounded, anterior margin almost straight, with median convexity marking lunar ridge and concavity marking shallow subumbonal groove; Posterior slope convex and paralleling very deep radial sulcus; shell surface with low undulations and numerous fine, closely-spaced commarginal growth lines; edentulous and lacking true hinge plate; long, narrow and deeply grooved ligament plate.

Description—Although the shells of fossil thyasirids are often chalky, some specimens in the Keasey Formation preserve the outer shell layer (Fig. 4A–D). Specimens are typically articulated, which has made it difficult to observe internal features. The adductor muscle scars and pallial line are not clearly preserved on any of the material examined.

Discussion—This species is relatively higher and more quadrate in outline than *Conchocele bisecta* and has a more evenly and more broadly rounded ventral margin and more nearly straight anterior margin. It also differs in the presence of low undulations on the shell surface. In these respects, it also differs from younger Oligocene specimens from the Blakeley Formation figured by Tegland (1933, pl. 7, figs. 18–22). Thyasirids are absent from the lower Oligocene Pittsburg Bluff and Eugene formations in Oregon. In a review of the fossil record of large Paleogene thyasirids of the Northeastern Pacific, Squires and Gring (1996, p. 68–69)
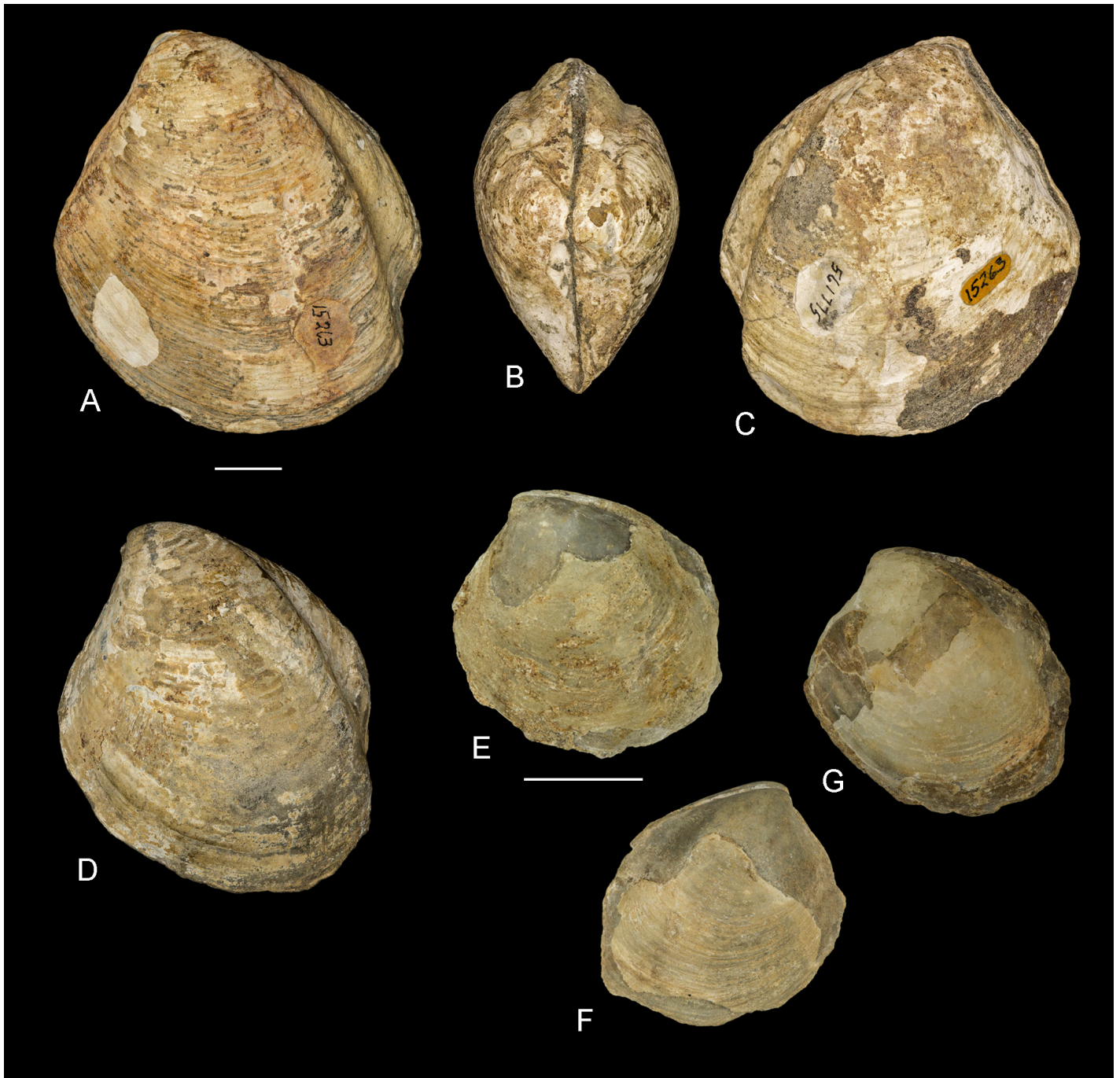
Figure 4A–F. Thyasiridae, *Conchocele*. **A–D.** *Conchocele bathyaulax* n. sp. **A–C.** Holotype, USNM 561775, Loc. USGS 15263, articulated, left, dorsal and right valve views. **D.** Paratype, USNM 561776, Loc. USGS 15263, articulated, left valve view. **E–G.** *Conchocele taylori* n. sp. **E.** Holotype, UCMP 110688, Loc. UCMP IP16004, articulated, left valve view. **F.** Paratype, UCMP 110689, Loc. UCMP IP16004, articulated right valve view. **G.** Paratype, UCMP 110690, Loc. UMP IP16004, articulated, left valve view. Scale bar for A–D = 1 cm, E–G = 1 cm.

referred material from the Keasey Formation to *Conchocele bisecta* and broadly defined the species to include 11 junior synonyms.

Etymology—from the Latin *bathy* (deep) + *aulax* (furrow), referring to the unusually deep posterior sulcus.

Material examined—In addition to the designated type material, the description is based on examination of >50 Keasey specimens in various states of preservation.

Holotype—USNM 561775 (articulated), maximum height (umbone to posterior ventral margin) 65.2 mm;

length (distance from posterior dorsal margin to anterior dorsal margin 55.4 mm; diameter (both valves) 33.7 mm, Loc. USGS 15263.

Figured Paratype—USNM 561776 (articulated), maximum height 61.8 mm; length 49.2 mm; diameter, 30.9 mm, Loc. USGS 15263.

Unfigured Paratypes—USNM 561777 (an atypically small specimen), Loc. USGS15263; USNM 561778 (left valve partially excavated in attempt to expose hinge region), Loc. USGS 15263; UCMP 110685, 110686, 110687 (three large double-valved specimens showing typical preservation), Loc. UCMP IP2286.

Keasey Formation localities—Type locality: USGS 15263 (=UCMP IP2286) (lower member). Other localities: USGS 15265 (lower member), USGS 15267, 15318 (middle member).

Stratigraphic range—upper Eocene to lower Oligocene.

Conchocele taylori n. sp.
Fig. 4E–G

Diagnosis—Shell small (< 25 mm in length) , thin, equivalve, ovate and strongly inflated; radial sulcus weak; umbones prominent; anterior dorsal margin markedly concave, posterior dorsal margin convex; shell surface with numerous fine prominent growth increments except posterior to radial sulcus; ligament sunken in a deep groove; lunule broad but shallow and poorly-developed; dentition unknown.

Description—Specimens are invariably articulated and seldom distorted. Taphonomic alteration is primarily in the form of varying degrees of exfoliation of the thin shell and mineral infilling of the shell interior so that muscle scars and pallial line are not preserved.

Discussion—This species is abundant in the cold-seep limestone bodies at a single locality in the lower part of the middle member of the Keasey Formation on Rock Creek. It occurs in dense monospecific populations in the limestone, and individual specimens are difficult to extract from the hard indurated limestone. Distinguishing this species by size from the large *Conchocele bathyaulax* is based on having observed no specimens in the field or among those collected exceeding 40 mm in maximum width. The species is further distinguished by its more ovate shape, stronger inflation of the valves, shallowly convex anterior dorsal slope, and shallower posterior radial sulcus. The holotype (Fig. 4E) and two illustrated paratypes (Fig. 4F–G) are >25 mm wide and reflect the range of variation in the type lot.

The Rock Creek cold seep is unusual in the low diversity of the fauna. The thyasirid was the only species observed in the nodular carbonate mounds, and a large solemyid bivalve occurs in the immediately adjacent blue-gray muddy siltstone

(Nesbitt et al. 2006). Individual foraminifera of two species collected from the siltstone yielded markedly depleted ^{13}C values suggesting biogenic and thermogenic methane seepage contemporaneous with the limestone containing the thyasirids (Martin and Nesbitt 2005, Nesbitt et al. 2006).

Etymology—Named in honor of David G. Taylor who discovered the Rock Creek cold seep and participated in excavation, collection, measurement and mapping of the exposed section.

Material examined—40 specimens in the type lot; hundreds observed in the field.

Holotype—UCMP 110688 (articulated), maximum height (umbone to posterior ventral margin) 25.0 mm; length (distance from posterior dorsal margin to anterior dorsal margin) 22.4 mm; diameter (both valves) 14.2 mm, Loc. UCMP IP16004.

Figured Paratypes—UCMP 110689 (articulated), maximum height 24.9 mm; length 22.8 mm. diameter 14.9 mm; UCMP 110690 (articulated), maximum height 23.2 mm; length 21.0 mm; diameter 12.1 mm, both from Loc. UCMP IP16004.

Keasey Formation locality—known only from the type locality near the base of the middle member.

Stratigraphic occurrence—upper Eocene.

LUCINIDAE J. Fleming, 1828

Lucinid bivalves have an exceptionally long history, with a low-diversity record in the Paleozoic dating from the Late Silurian of Gottland (Liljedahl 1991) and an increasingly diverse and abundant post-Paleozoic record in paleoenvironments that include shallow anoxic seagrass sediments, oligotrophic coral reef sediments, and cold-seep limestone and hydrocarbon seep deposits in massive deep-water mudstones, especially forearc sequences on convergent plate margins. Obligate chemosymbiosis with intracellular sulfide-oxidizing bacteria appears to be universal in living lucinids. The three-dimensional relationships between these bivalves and seep-plumbing, fluid migration features, mineralogy and petrology, isotopic signatures, and diagenetic sequences can be examined over long (million-year) timescales that add a new dimension of interest to the Keasey Formation and its extremophile-dominated bivalve fauna.

The majority of living lucinids are small, ranging from 5–30 mm in length (Taylor and Glover 2009). Although there is a misconception that large size is characteristic of lucinids at seeps and vents, Taylor and Glover (2009) list 14 fossil species that exceed the size of any living species (105–220 mm in length). More than half of these are from confirmed or suspect seep paleoenvironments. However, the size award for gigantism goes to *Superlucina* Taylor and Glover, 2009
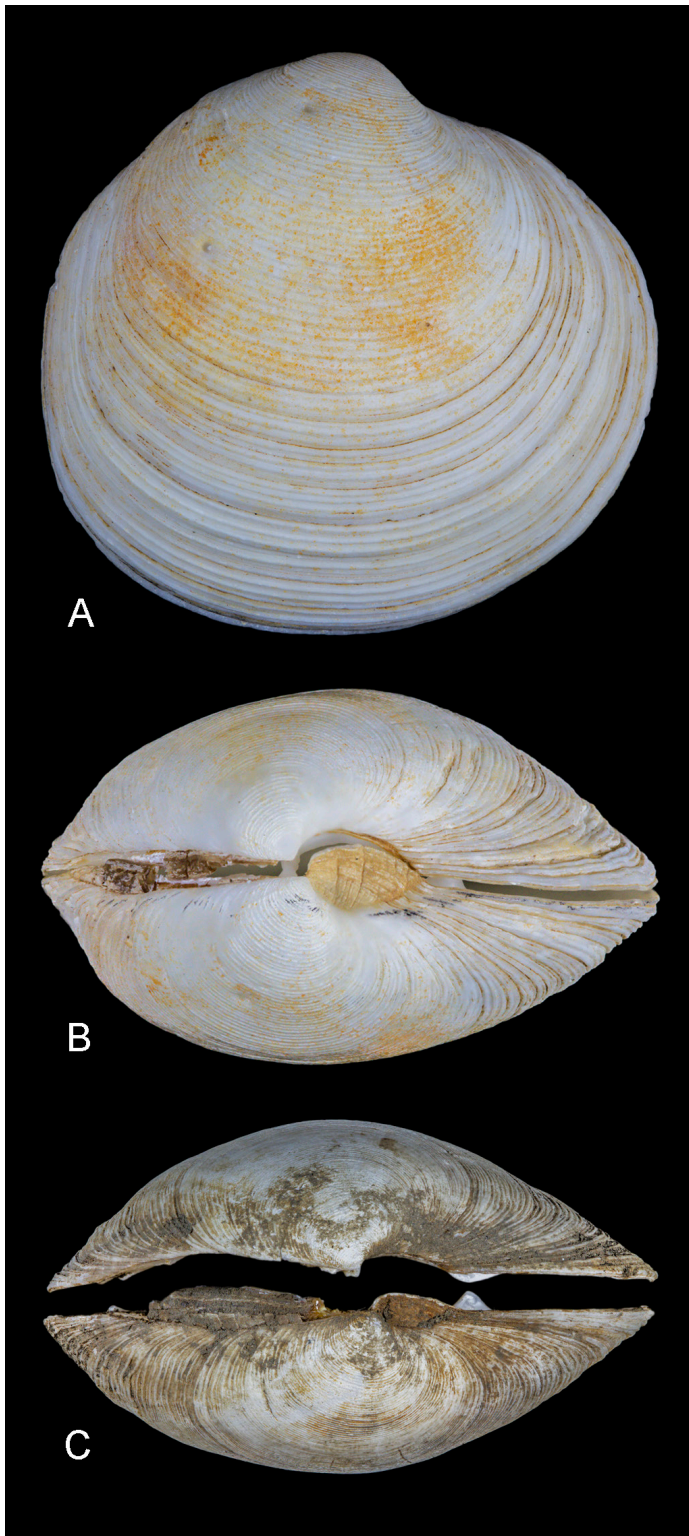
Figure **5A–C.** Lucinidae, *Epilucina californica* (Conrad, 1837), hypotypes of living species. **A.** Right valve, SBNHM 537630, length = 37.3 mm. **B.** Dorsal view of A illustrating ligament and asymmetric lunule. **C.** Hypotype, SBNHM 454406, length 40.3 mm, dorsal view with valves slightly separated.

attaining heights >300 mm in Eocene shallow seagrass settings in the Caribbean region.

The Eocene marks the first appearance of large chemosymbiotic bivalves at cold seeps on the Cascadia Margin of North America. The first stratigraphic occurrence is in middle Eocene cold- seep limestones of the Humptulips Formation in the Southern Olympic peninsula (Saul et al. 1996). Articulated specimens of the distinctively elongate and thick-shelled type species of *Cryptolucina* (Saul et al. 1996) measure up to 180 mm in length and are preserved in a bathyal environment with cold-seep limestone and pyritic mudstone indicative of dysaerobic conditions.

Although they are rare in the Keasey Formation, remains of two the two lucinids documented here also are coincident with onset of subduction on the Cascadia Margin along with the occurrence at two Keasey cold seeps with the abundant thyasirid species also described above.

Stratigraphic range—Upper Silurian to Holocene.

CODAKIINAE Korobkov, 1954
EPILUCINA Dall, 1901

Type species—By original designation, *Lucina californica* Conrad, 1837. Miocene –Holocene, California and Japan.

In addition to the relatively large, thick shell with coarse commarginal sculpture, the genus is distinguished by a prominent, deep-set, asymmetric lunule in the right valve, projecting into a corresponding indentation in the left valve anterior to the beak. Radial ribs are lacking, and there is a moderate to strong posterior truncation of the valves. The type species is illustrated here to show these diagnostic features (Fig. 5A–C).

Neogene (upper Miocene and Pliocene) occurrences of the type species in California are reviewed by Moore (1988). She treated *Epilucina* as a subgenus of *Codakia* Scopoli, 1777, which also has an asymmetric lunule. Although recognition of *Epilucina* in the Pacific coast Paleogene was hindered for many years by poor preservation an outstanding study by Squires and Gring (1996) connects occurrences in California with upper Eocene cold-seep carbonate bodies and an associated fauna of chemosymbiotic bivalves. The present study confirms the same geologic and faunal association in the Keasey Formation.

A large-shelled *Epilucina* also appears in the upper Eocene of Colombia, a form described as *Lucina (Epilucina) gabrielensis* Clark, 1946. The Paleogene biogeographic history of *Epilucina* is restricted to the Eastern Pacific. However, *E. californica* appears in Japan in the Miocene and persists through the Pliocene as an inferred westward expansion across the North Pacific during the Mid-Neogene Climatic Optimum (Kurihara 2007).
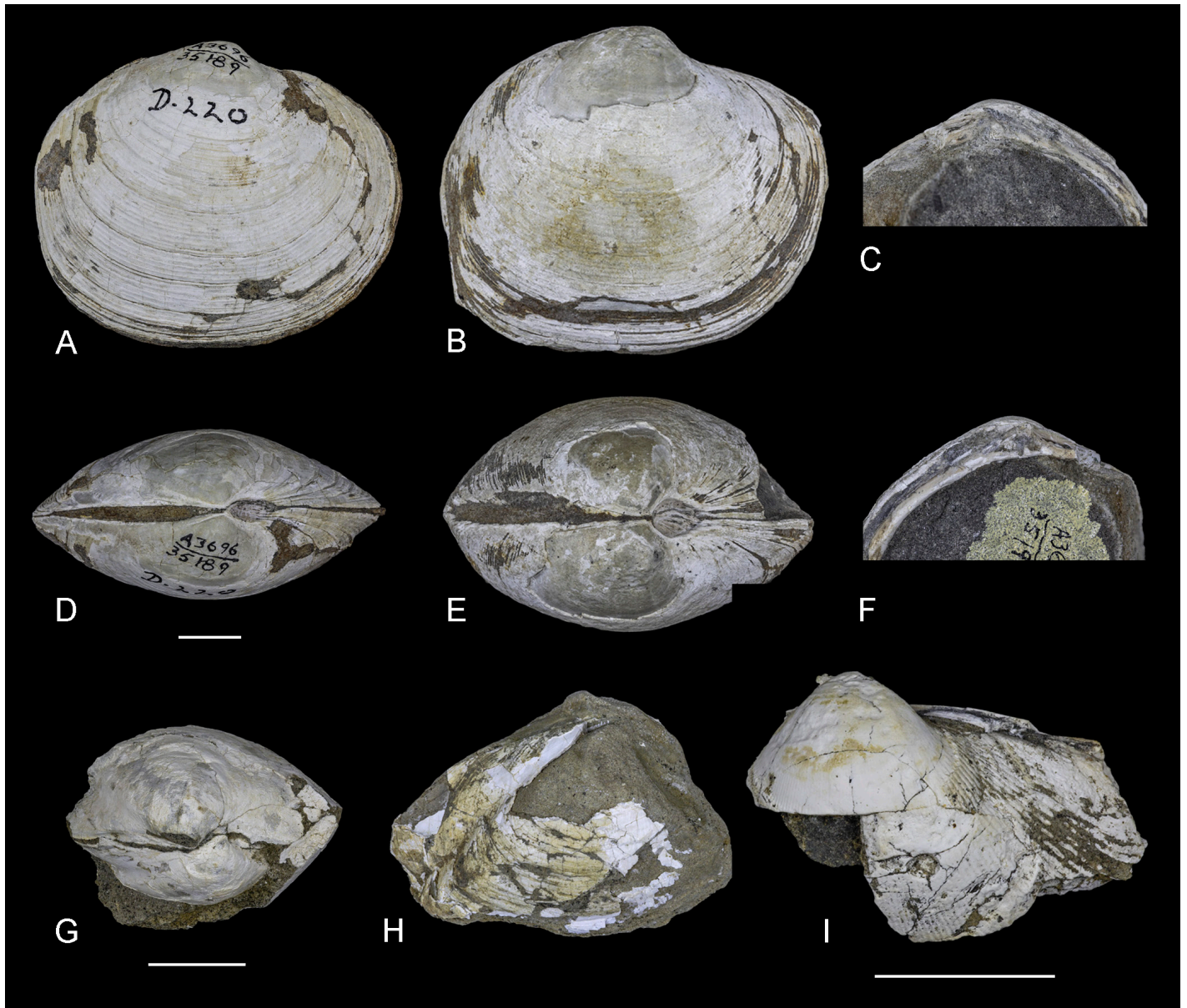
Figure 6A–I. Lucinidae, *Epiluicina* and *Fimbria*. **A–H.** *Epilucina washingtoniana* (Clark, 1925). **A,D.** Right valve and dorsal views of double-valved hypotype, Lyre Conglomerate, UCMP 110693, Loc. A-1070. **B, E.** Right valve and dorsal views of double-valved hypotype, Marrowstone Shale, UCMP 35189, Loc. A-3696. **C.** Prepared right hinge plate, hypotype, Marrowstone Shale, UCMP 35190, Loc. A-3696. **F.** Prepared left hinge plate, hypotype, Marrowstone Shale, UCMP 35191, Loc. A-3696. **G.** Dorsal view, incomplete and distorted double-valved hypotype, Keasey Formation, UCMP 110691, Loc. UCMP IP2286. **H.** Incomplete double-valved hypotype, Keasey Formation, UCMP 110692, Loc. UCMP IP2286. **I.** *Fimbria* sp. Fragment with characteristic fimbriid radial ribs, UCMP 110694, UCMP IP2286. Scale bar for A–F = 1 cm, G, H = 1 cm, I = 1 cm.

Stratigraphic range—Upper Jurassic to Holocene.

Epilucina washingtoniana (Clark, 1925)
Fig. 6A–H

Corbis washingtoniana Clark, 1925, p. 90; pl. 20, figs. 1–4.
Corbis washingtoniana Clark, Weaver 1942, p. 152–153, pl. 37, figs. 1,3.

Corbis washingtoniana Clark, Durham 1944, p. 144.
Corbis washingtoniana Clark, Weaver and Kleinpell 1963, p. 201, pl. 33, figs. 10, 11.
Corbis washingtoniana Clark, Vokes in Warren and Norbisrath 1946, p. 227.
Fimbria washingtoniana (Clark), Moore and Vokes 1953, p. 118, 119.

Lucina (Myrtea) aff. *L. diegoensis* Dickerson, Weaver and Kleinpell 1963, p. 200–201, fig. 6.

Codakia (*Epilucina*) *washingtoniana* (Clark), Squires 1990, p. 553–554.

Epilucina washingtoniana (Clark), Squires and Gring 1996, p. 66–68, fig. 4.1–4.4.

Discussion—Twelve poorly-preserved specimens from the lower member of the Keasey Formation represent a species originally described by Clark (1925) from seacliff exposures of the Marrowstone Shale on the northeastern Olympic Peninsula of Washington. When well preserved, this distinctive species is easily recognized by its large size (length up to 7 cm), thick and strongly inflated shell, posterior truncation, asymmetric lunule, and coarse commarginal sculpture. However, it is often poorly-preserved and difficult to recognize as fragments and when the shell is diagenetically altered or dissolved. Inadequate illustration of the original type material has hindered recognition, and material from the type area is illustrated here (Fig. 6A–F) along with a discussion of its distinctive association with chemosymbiotic taxa and cold-seep geologic occurrences.

Epilucina washingtoniana was described from a thick Paleogene sequence that subsequently became the basis for several molluscan biostratigraphic zones (e.g., Durham 1944, Armentrout 1975, 1981). Magnetostratigraphic analyses of the Marrowstone Shale and Keasey Formation (Prothero and Hankins 2000, Prothero et al. 2009) suggest that the *E. washingtoniana* occurrences could both be late Eocene. However foraminiferal faunas indicate a younger, early Oligocene age for the Marrowstone (Armentrout and Berta 1977).

Clark's original figures of the holotype are overexposed and heavily retouched, and the dorsal (hingeline) view does not provide an accurate representation of the lunule. Weaver's illustrations of the same specimen are also overexposed and lack detail. Figures of three hypotype specimens from the Wagonwheel Formation in central California (Squires 1990) provide the best published illustrations to date. Durham (1944) did not figure material from the Marrowstone Shale, but he listed numbers for four hypotypes that are, incorrectly labeled in the type collection as "Oligocene, Lincoln Fm." Three of these specimens are illustrated here (Fig. 6A, C, D, F) along with one specimen from an earlier collection in the Lyre Formation (Fig. 6B, E), an older, thick conglomerate, sandstone and siltstone sequence in the northern Olympic Peninsula (Brown et al. 1956).

Material examined—Twelve articulated but poorly-preserved specimens and numerous fragments from three localities in the lower member of the Keasey Formation and ten specimens from the Marrowstone Shale and two from the Lyre Formation in Washington.

Figured Keasey hypotypes—UCMP 110691, maximum dimension of incomplete specimen 29.2 mm, Loc. UCMP IP2286; UCMP 110692, maximum dimension of incomplete specimen 37.2, Loc. UCMP IP2286.

Figured Marrowstone Shale hypotypes—UCMP 35189, length 60.2 mm, height 50.2 mm, maximum diameter 28.9 mm, Loc. UCMP A-3696; UCMP 35190, prepared right hinge, Loc. UCMP A-3696; UCMP 3591, prepared left hinge, Loc. UCMP A-3696.

Figured Lyre Conglomerate hypotype—UCMP 110693, length 67.3, height 50.2 mm, maximum diameter 28.9 mm, Loc. UCMP A-1070.

Keasey Formation Localities—USGS 15263, 15265, UCMP IP2286 (all lower member).

Stratigraphic range— middle (?) to upper Eocene.

FIMBRIINAE Nicol, 1950
FIMBRIA Megerle von Mühlfeld, 1811

Type Species—By original designation, *Fimbria manga* Megerle von Mühlfield, 1811 (= *Venus fimbriata* Linnaeus, 1758). Holocene, tropical Indo-Pacific, Austraila, Indonesia, Hawaii.

Fimbria is the sole remaining genus in a group of shallow-water tropical bivalves in a small lucinoidean group that proliferated during the Mesozoic, when it was represented by extinct Triassic and Jurassic genera and species with localized geographic distributions (Monari, 2003). It is represented by only two living species.

The group was accorded full familial status when proposed (Nicol 1950). Most paleontologists and neontologists have followed Nicol (e.g., Boss 1969, Chavan 1969b, Morton 1979, Reid and Slack-Smith 1998, Monari 2003). The contradictory assertion by Allen and Turner (1970) that that *Fimbria* is a lucinid is reviewed in detail by Morton (1979). The controversy is largely resolved by molecular data that place it within Lucinidae (Williams et al. 2004), which is consistent with shell microstructural data (Taylor et al. 1973) and details of the intracellular housing of symbiotic bacteria within the enlarged ctenidia (Williams et al. 2004)

Fimbria has been regarded as a Tethyan element in Paleogene molluscan faunas of the Gulf Coastal Plain (Givens 1989) and as a Tethyan migrant into Eocene faunas of southwestern North America (Squires 1990). Although the presence of *Fimbria* in deep-water Paleogene faunas of the Pacific Northwest would be anomalous, the thick shell, massive hinge and radial ornamentation on fragmental specimens from a cold seep locality in the Keasey Formation merits illustration (Fig. 6I) and brief discussion.

Stratigraphic range—Lower Jurassic (Hettlangian) to Holocene.

Fimbria ? sp.
Fig. 6I

Discussion—An incomplete and poorly preserved fragmental right valve of lucinoidean bivalve from one of the Keasey cold seeps differs from *Conchocele bathyaulax* and *Epilucina washingtoniana* in the presence of distinctive radial sculpture. This sculpture also occurs on small fragments collected in talus. Similar fragments of radial sculpture may have been the basis for the assignment of "*Corbis washingtoniana*" to *Fimbria* by Moore and Vokes (1953). It is possible that the radial sculpture is an artifact of preservation, although the specimen figured here is distinct from all of the specimens of *Epilucina washingtoniana* examined in the course of this study.

Figured specimen—UCMP 110694, maximum dimension of fragment of left valve 22.6 mm, Loc. UCMP IP2286 (Timber-Vernonia cold seep).

Stratigraphic occurrence—Lower member (upper Eocene).

GALEOMMATOIDEA J.E. Gray, 1840

Minute to small bivalves (length <10 mm) whose modern representatives are predominantly commensal or symbiotic with larger marine invertebrates have been studied for >200 years, with increasing emphasis on ecology, functional morphology, host specialization and reproductive strategy and peculiarities (e.g., Oldfield 1961, 1964, Boss 1965, Ó Foighil 1985, 1987, Morton 1988, Mikkelsen and Bieler 1989, 1992, Morton and Scott 1989, Ponder 1998, Goto et al. 2011, Oliver 2012).

The ecological association of many of these small bivalves with deep-sea burrowing echinoids (Gage 1966b) is especially interesting for three reasons. Firstly, spatangoid echinoid remains are abundant at several Keasey localities (Burns and Mooi 2003). Secondly, the reducing environment in which this echinoid-bivalve relationship occurs (Gage 1966a) is consistent with the suggestion that many elements of the Keasey bivalve fauna are adapted not only to tolerate, but also to engineer their geochemical environment. Thirdly, elegant documentation of symbiotic bacteria in bacteriocyte cells in modified gill filaments of a deep-sea echinoid-associated galeommatoid bivalve (Oliver et al. 2012) adds another bivalve lineage to the growing list of chemosymbiotic taxa.

Less attention to taxonomy and relationships has resulted in a bewildering proliferation of genus-group names, while poorly-documented levels of intraspecific variation confound species identification. Many authors have suspected an internal tangle of polyphyly (e.g., Coan et al. 2000). Bieler and Mikkelsen (1992) defined useful new anatomical characters for galeommatids but their preliminary cladistic analysis yielded 164 equally parsimonious trees, primarily because of lack of data and ambiguity for species outside of their own investigations. However subsequent analyses combining molecular and morphological characters support higher-level monophyly of the group (Bieler et al. 2014).

The fossil record compounds taxonomic difficulties because diagnostic features of the hinge plates and shell interiors are seldom preserved. However, extraordinary preservation in Paleogene faunas of Europe resulted in many of the genus-group names subsequently and currently used for living species (Chavan 1969a).

The treatment herein provisionally recognizes two family-group taxa: Galeommatidae J.E. Gray, 1840 and Lasaeidae J.E. Gray, 1842. Some authors have recognized more (e.g., Boss 1982; Morton and Scott 1989), although distinctions are so poorly defined that more cautious recognition of single family group name also has been advocated pending "proper comparative studies based on key taxa" (Ponder 1998 p. 316). Five unnamed clades were recovered in a recent molecular phylogenetic analysis of 33 putative galeommatoidean species from Japan (Goto et al. 2012), but none these clades corresponds to an available family group, indicating that considerable additional work is required to resolve internal structure.

Only four galeommatoid species have been described from the Paleogene of the Eastern Pacific, three from California and one from the Oligocene the Pacific Northwest. All occur in shallower facies and are based on very few specimens.

Stratigraphic range—? Upper Cretaceous to Holocene.

LASAEIDAE J.E. Gray, 1842
(=LEPTONIDAE J.E. Gray, 1847; KELLIIDAE Forbes and Hanley, 1849; ERYCINIDAE Deshayes, 1850; MONTACUTIDAE W. Clark, 1855)

The use of Lasaeidae is adopted following a long tradition of treatment of Paleogene fossil galeommatoideans of the Pacific coast of North America under the genus *Kellia* Turton, 1822. *Kellia* is effectively used here as a form genus because hinge plates and interior shell features are not known for the Eocene fossils.

Stratigraphic Range—Cretaceous to Holocene.

KELLIA Turton, 1822

Type species—by subsequent designation (Récluz, 1844), *Mya suborbicularis* Montagu, 1803. Holocene, circumboreal.

The type species of *Kellia* is a thin-shelled free-living form with thoroughly documented functional anatomy (Oldfield 1961). The genus is cosmopolitan, and the type species is recognized in the fauna of the Eastern Pacific from Alaska to Peru (Coan et al. 2000; Coan and Valentich-Scott 2012).
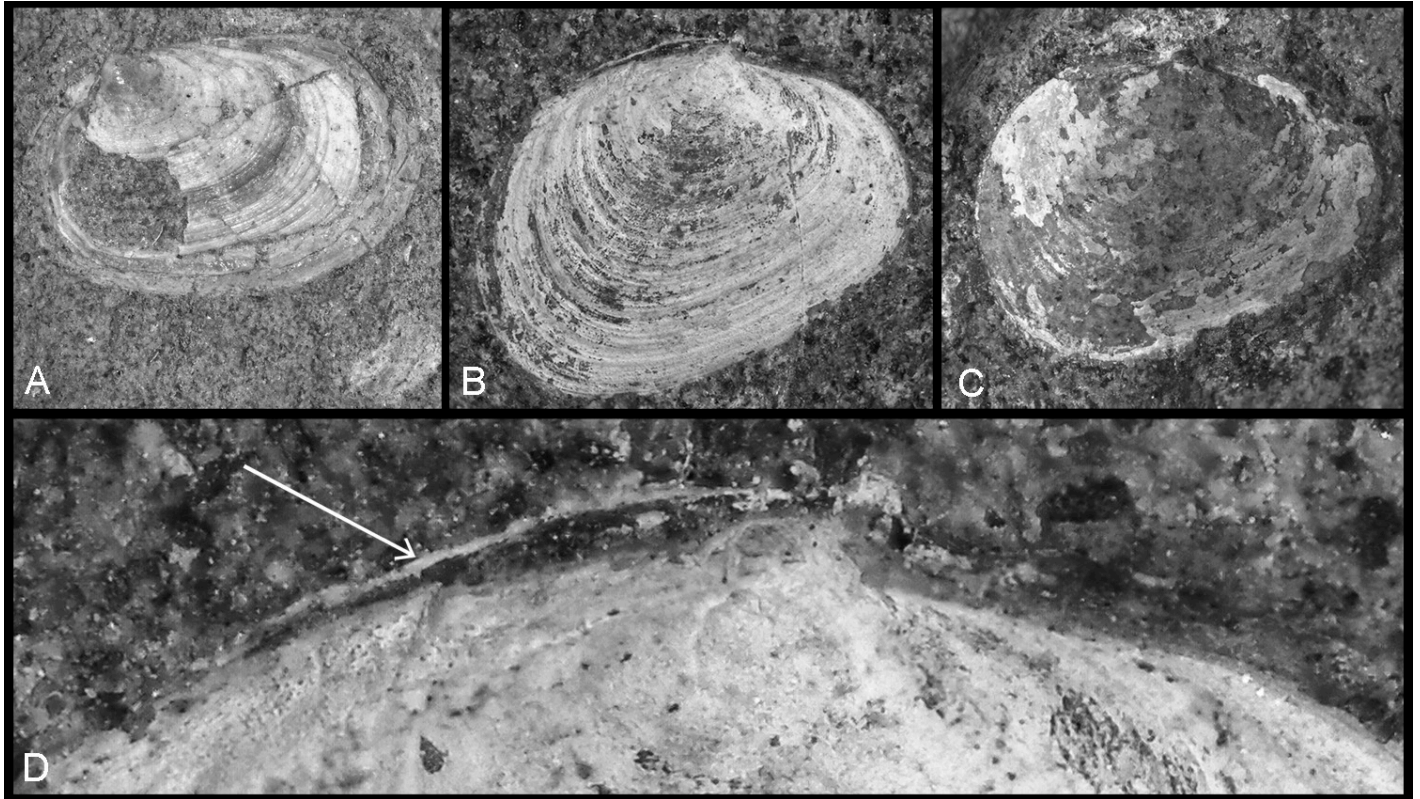
Figure 7A–D. Lasaeidae, *Kellia*. **A.** *Kellia saxiriva* n. sp., holotype, USNM 561800, Loc. USGS 15309, right valve in matrix, length 4.4 mm. B–D. *Kellia vokesi* n. sp. **B**. Holotype, USNM 561798, Loc. USGS 18285, left valve in matrix, length 4.9 mm. **C**. Paratype, USNM 561799, Loc. USGS 18285, left valve in matrix, length 4.3 mm. **D**. Detail of B with arrow at offset dorsal margin of right valve.

The genus is a cosmopolitan and relatively unspecialized group of free-living lasaeids. Six living species have been distinguished in cold-water intertidal and shallow subtidal habitats at high latitudes of the Northwestern Pacific and Bering Sea, where population densities of 1,190 individuals/m² have been recorded (Kamenev 2004).

Stratigraphic Range—Eocene to Holocene.

Kellia saxiriva n. sp.
Fig. 7A

Diagnosis—Shell small, thin, ovate-elongate, inequilateral, with prominent umbone at one third of length from posterior end; posterior dorsal margin convex, merging gradually with evenly-rounded posterior margin; anterior dorsal margin shallowly-convex, merging uninterrupted with more broadly rounded anterior margin; ventral margin shallowly convex; exterior surface nearly smooth but with many fine growth increments that increase in prominence ventrally.

Discussion— *Kellia saxiriva* Hickman n. sp. is described from a single right valve in matrix. The hinge and interior are unknown. The shell is slightly crushed and cracked, with some shell missing. However, the outline of the margin where shell is missing is clearly preserved in the matrix. Shell proportions clearly distinguish it from a second species of *Kellia* described below in which the umbo is more centrally situated, the shell is relatively shorter and the anterior end is more broadly expanded. The specimen was collected by Harold Vokes, from the lower member of the Keasey Formation on Rock Creek during geologic mapping of northwestern Oregon (Warren et al. 1945).

Etymology—A compounded reference to the type locality, *Sax-* (Rock) + *riva* (creek). It is the name Harold Vokes assigned to the USNM specimen that he intended to describe as *Erycina saxiviva*.

Holotype—USNM 561800, Length 4.4 mm, height 2.8 mm, Loc. USGS 15309.

Keasey Formation Occurrence—Lower member in association with mud pectens and a diverse assemblage of protobranch bivalves.

Kellia vokesi n. sp.
Fig. 7B–D

Diagnosis—Shell minute, ovate, nearly equilateral, with umbones situated slightly closer to posterior end; anterior

and posterior dorsal slopes of approximately equal length, shallowly convex, and merging gradually with sharply-rounded anterior and posterior shell margins; ventral margin nearly straight, merging gradually with anterior and posterior margins; shell surface with numerous fine growth lines; hinge not exposed.

Discussion—*Kellia vokesi* Hickman n. sp. is known from two right valves in matrix from the upper part of the middle member. Shell proportions are distinct from those of *K. saxiriva* from the lower member. The shell is proportionally higher, the anterior end more broadly rounded and the beaks more centrally placed. Length/height ratios of the holotype and paratype are nearly identical. A thin ridge of shell material paralleling and offset from the anterior dorsal margin of the holotype (arrow, Fig. 7D) may represent a slightly offset corresponding margin of the right valve. Although the original shell material is highly altered, the growth increments are distinctly preserved.

Etymology—Named in honor of the late Harold Vokes, who collected the specimens and had given them the prospective type name of *Erycina solicadentia*.

Holotype—USNM 561798, left valve, length 4.9 mm, height 3.5 mm.

Paratype—USNM 561799, left valve, length 4.3 mm, height 3.2 mm.

Keasey Formation type locality—Middle Member, Loc. USGS 18285.

<div align="center">

Cardioidea + Tellinoidea Bieler et al., 2014

Cardioidea Lamarck, 1809

Cardiidae Lamarck, 1809

Protocardiinae Keen, 1951

</div>

Cardiid bivalves comprise an easily-recognized cosmopolitan group of shallowly-burrowing infaunal bivalves, commonly known as cockles. They occur abundantly in warm, shallow water. Cardiids originated in the Triassic, underwent a Mesozoic radiation, survived the end Cretaceous mass extinction, and underwent a second, predominantly Tethyan, diversification beginning in the Paleogene. Shells are often exceptionally well preserved in Tertiary fossil faunas, especially in the condensed shellbeds of the Atlantic and Gulf coastal plains. Vokes (1977) documented 15 species in the Pilocene Chipola Formation in Florida, illustrating diagnostic fine details of sculpture and noting that cardiids were present in collections from every locality in the type area of the formation. Moore (2002) reviewed the fossil record of 31 cardiid species from the Tertiary of California and Baja California Sur. By contrast, only 15 species are documented from the Tertiary formations of Oregon and Washington. Cardiids reported from Paleogene strata of northern Alaska

(e.g., Marincovich 1996) have been considered relict Mesozoic taxa that survived into the Cenozoic in a geographically isolated Arctic Ocean (Schneider and Marincovich 2000).

The family has been studied most intensively by paleontologists who have included both living and fossil taxa in their treatments (e.g., Stewart 1930, Keen 1937, 1951, 1969a, 1980, Marwick 1944, Kafanov and Popov 1977, Schneider 1992, 1994, 1995, 2002, Schneider and Carter 2001). Many family-group and genus-group names have been proposed. However, internal relationships are very poorly resolved and controversial. Keen (1980) recognized six cardiid subfamilies and accepted 77 out of 109 available genus group names, illustrating the major shell features for each genus based on its type species. Schneider (1995) provided the first cladistic hypothesis for Cardiidae based on 36 taxa and 54 morphological characters. Results of his subsequent cladistic analysis of the type subfamily Cardiinae (Schneider 2002) demonstrated the adequacy of the fossil record and its unique ability to combine taxonomic, stratigraphic and paleobiogeographic data in revisionary phylogenetics.

The other traditional subfamilies have been more difficult to revise. There are no combined morphological and molecular studies addressing internal relationships, although a well-supported sister-group relationship has been established between Cardioidea and Tellinoidea (Bieler et al. 2014). A single large-scale molecular study (Hererra 2013) reported rampant paraphyly in six subfamilies, but the study does not address the considerable extinct diversity crucial to resolving relationships and evolutionary history.

Subfamily allocation of the Keasey cardiids is tentative, and the rational requires some additional discussion of (1) paleontological treatment of fossil taxa and (2) studies extant taxa that have dismantled both Protocardiinae Keen, 1951 and Laevicardiinae Keen, 1951, and (3) the restricted definition of *Nemocardium*.

Paleontological treatment—Paleogene cardiid species of the Pacific Northwest have been treated for many years under *Nemocardium* Meek, 1876 (e.g., Stewart 1930, Schenck 1936, Durham 1944) and classified under Protocardiinae (e.g., Moore 1963, 1976, Hickman 1969). *Nemocardium* has been construed broadly as the oldest living cardiid genus, originating in the Early Cretaceous, surviving the end Cretaceous mass extinction, and persisting in the modern fauna. Its' major evolutionary radiation was during the Eocene with a post-Paleogene decline. The early appearance of the genus may have contributed to its classification with protocardiids in a cosmopolitan subfamily along with other genera that became extinct at the end of the Cretaceous. Scott (1986) noted the confusion surrounding taxonomy and nomenclature of Lower Cretaceous cardiids but recognized "at least
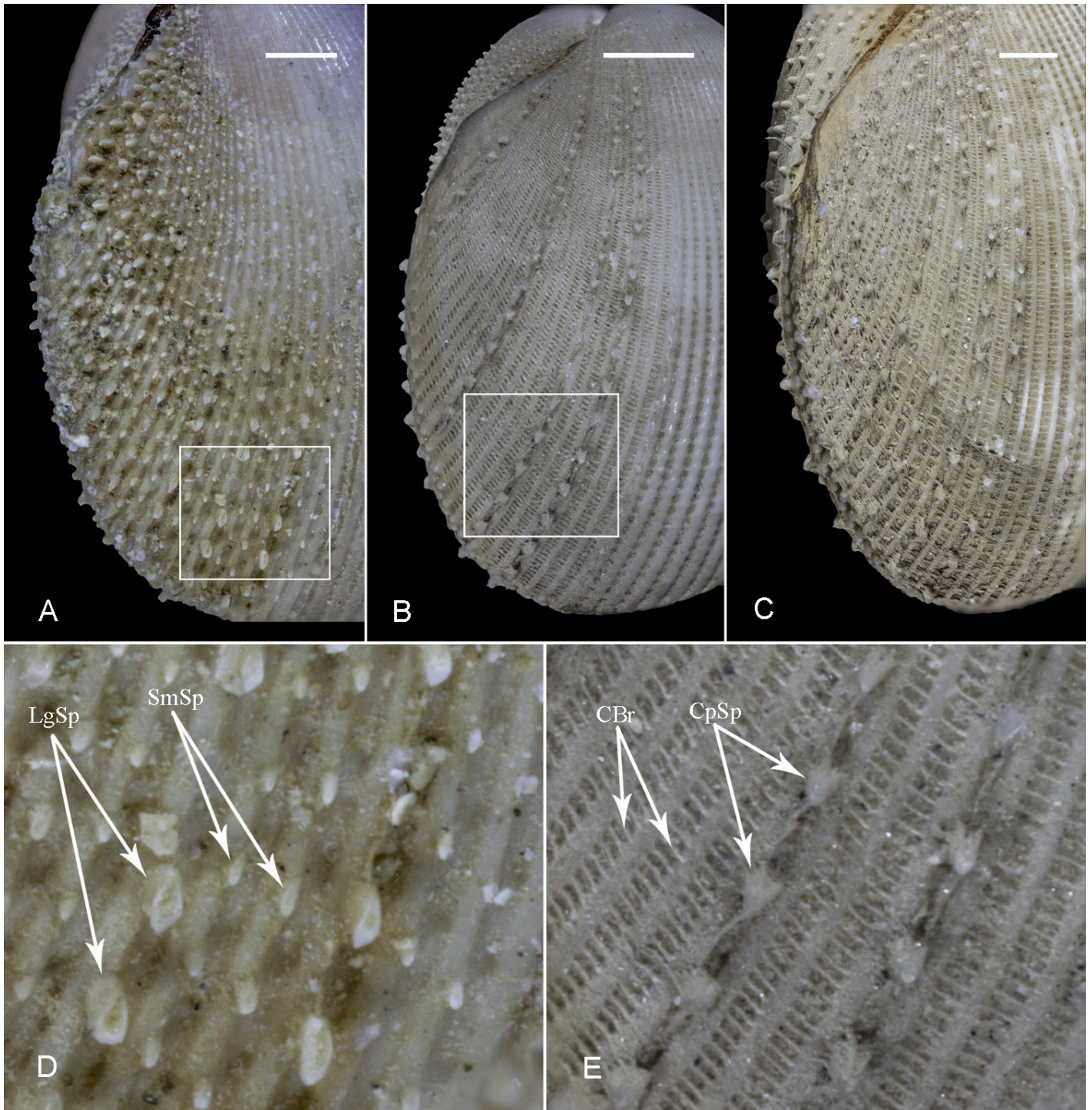
Figure 8A–E. Cardiidae, diagnostic features of posterior slope microsculpture of *Pratulum* and *Microcardium*. **A,D.** *Pratulum pulchellum* (J.E. Gray, 1843), SBNHM 235666, large spines (LgSP) and small spines (SmSP) (at arrows) are confined to radial ribs. **B,E.** *Microcardium panamense* (Dall, 1908), SBNHM 352702, radial ribs smooth, ornament confined to rib interspaces as cross bridges (CBr) and occasional complex spines (CpSp). **C.** *Microcardium panamense*, specimen from same lot as B illustrating variation in location and number of spines. Scale bars = 1 mm.

six Cretaceous species" of *Nemocardium*. Stewart (1930, p. 273) considered the genus to be "chiefly of the early Tertiary," noting abundant representation in the Eocene of California and disappearance by the end of the Oligocene in the Pacific Northwest. *Nemocardium s.s.* is not recognized in the living fauna of the Northeastern Pacific (Coan et al. 2000).

Figure 9. Diagnostic features of posterior slope microsculpture of *Anechinocardium* n. gen. smooth radial ribs, crossbridges confined to interspaces, frequently offset from one interspace to the next (circle). Scale bar = 1 mm.

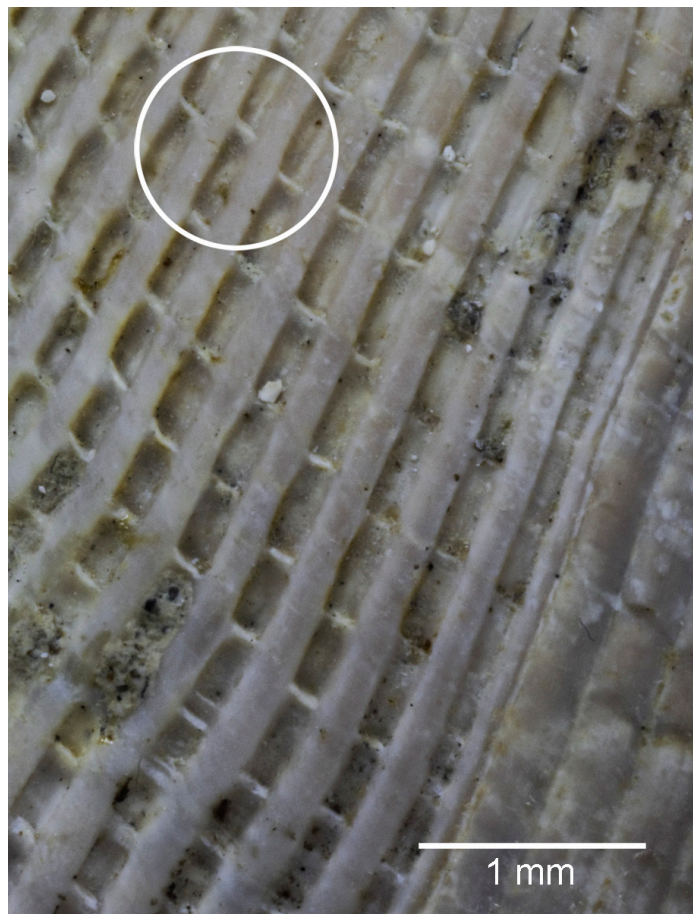In a parallel recognition of greater similarity to extinct Mesozoic species, at least eight Paleogene species from the Atlantic and Gulf Coastal Plain have been assigned to the genus *Protocardia* von Beyrich, 1845. These species were reassigned to *Nemocardium* based on Keen's (1950) assessment that *Protocardia* did not survive the end Cretaceous mass extinction and is not present in the Cenozoic of North America (Hughes 1961).

In the Southern Hemisphere paleontologists and neonatologists have recognized a protocardiine fauna. In a review of the Australasian Protocardiinae, Poutiers (1992) identified a suite of living taxa as inhabitants of relatively deep (upper bathyal), warm-water refugium on the eastern margin of Gondwana. The hypothesized relicts add to growing evidence for a diverse New Caledonian upper bathyal "lost world" (Bouchet 1987) at the eastern edge of Gondwana.

Recognition of a Southern Hemisphere a deep-water remnant Mesozoic protocardiine fauna mirrors the relict high-latitude Mesozoic survivors in the Northern Hemisphere described by Schneider and Marincovich (2000). The Keasey protocardiines described here are identified as part of a bipolar survival of Mesozoic taxa as distinct from the Tethyan progenitors of the low-latitude Cenozoic cardiid evolutionary radiation.

Dismantling of Protocardiinae and Laevicardiinae—In his reinvestigation of the status and constituency of cardiid subfamilies, Schneider (1995) determined that the traditional subfamily Protocardiinae Keen, 1951 was polyphyletic if the genus *Nemocardium* Meek, 1876 was included. He removed *Nemocardium* recognizing support from cladistic analysis for a sister-group relationship with Laevicardiinae. Ter Poorten (2013) considered Laevicardiinae Keen, 1951 to be polyphyletic but declined to erect a new subfamily for *Nemocardium*. Leaving *Nemocardium* provisionally in Laevicardiinae, he provided a very clear and restrictive redefinition of the genus, advocating full generic status for taxa previously treated as subgenera.

Partial dismantling of higher taxa may be a constructive step at this time. In terms of both fossil and living species it invites critical re-examination of shell features that have been vaguely described in the past. More explicit definition of characters and character states holds promise of unmasking convergence. Examples of new diagnostic characters for genera are given below as rationale for proposing a new genus based of the most abundant and frequent species in the Keasey fauna.

Restricting the definition of *Nemocardium*—The type species of *Nemocardium* Meek, 1876 is *Cardium semiaspersum* Deshayes, 1858 from the lower Eocene (Ypresian) of France (by subsequent designation, Sacco, 1899). The superficial feature characterizing the genus is the division of the relatively large ovate-quadrate shell into two distinct regions: a smooth anterior portion with subsurface radial ribs and a clearly-demarcated posterior region with prominent spinose ribs. On close examination of the posterior region, there are striking differences in how the posterior sculptural elements are secreted.

In his diagnosis of *Nemocardium*, ter Poorten (2013, pp. 48-49) specifies that spines are present only *on* the posterior ribs and that the intercostal spaces lack spines and transverse lamellae. This condition is illustrated here by the posterior ornamentation on the New Zealand species *Pratulum pulchellum* (J.E. Gray, 1843) in which some posterior radial ribs have slightly hooked spines while others have finer nodules (Fig. 8A, D). However, the anterior two thirds of the shell have distinct radial ribs, eliminating it from *Nemocardium*, and *Pratulum* is treated as a distinct genus (ter Poorten 2013), with a fossil record extending back to the early Paleocene (Beu and Maxwell 1990).

A different condition is illustrated here on the posterior region of the tropical American species *Microcardium panamene* (Dall 1908), which is even more distinct in lacking costal spines while developing complex spines (CpSp) between some of the ribs as well as a system of fine intercostal cross-bridging (CBr) striae (Fig. 8B, C, E). Both species in the Keasey formation lack spines of any kind (Fig. 9) and do not fit any previously-described genus group. The new name proposed here is consistent with geographic and bathymetric restriction to deep water in the Northeastern Pacific and temporal restriction to the Paleogene.

Stratigraphic range—Upper Triassic (Norian) to Holocene.

ANECHINOCARDIUM n. gen.

Type species: *Cardium weaveri* Anderson and Martin, 1914. Middle member, Keasey Formation, northwestern Oregon. Upper Eocene.

Diagnosis—Strong posterior radial ribs smooth, lacking spines or granules typical of genus; very fine ladder-like cross striae present in intercostal spaces in early stages of development, disappearing during subsequent growth; lamellae not always aligned from one interspace to the next.

Discussion—The diagnostic interlamellar cross-striae and their lack of alignment are illustrated in Figure 9.

The New Zealand genus *Varicardium* Marwick, 1944 is superficially similar to *Anechinocardium* Hickman n. gen. However, the Miocene type species (by original designation) *Varicardium patulum* (Hutton, 1873), has a more massive shell with strong concentric ribs on the anterior and ventral portion of the shell as well as a heavier hinge plate and tubercles on the anterior margins of the posterior ribs. It has been synonymized with *Nemocardium* (ter Poorten 2013).

In addition to the type species, *Anechinocardium* includes two younger Eocene to early Oligocene species: *Nemocardium formosum* Hickman, 1969 from the Eugene Formation in Oregon and *Cardium lorenzanum* Arnold, 1908, which replaces the type species in the upper member of the Keasey Formation and overlying Pittsburg Bluff Formation.

Anechinocardium may include an undescribed species from the lower Oligocene Quimper Sandstone in Washington, but preservation of a large shell originally assigned to *Nemocardium weaveri* (Durham, 1944 in part) is inadequate

to permit detailed comparison. Although the Quimper is partially equivalent to the Keasey in age (Armentrout et al. 1983), the specimen in question is from a shallower sand facies and associated with species typical of the Pittsburgh Bluff Formation. Durham's (1944) unfigured hypotype (UCMP 35200), a single right valve in matrix, is proportionally higher than typical Keasey specimens. Radial ribs are worn but sufficiently well-preserved on the posterior slope to confirm absence lack of spines or granules and the presence of fine cross-striae in intercostal spaces during early ontogeny. Armentrout (1973) returned to Durham's Quimper locality but did not find the species.

Etymology—*a*(*n*)(Latin prefix, not) + *echinos* (Latin, spiny), referring to the absence of spines on the smooth ribs of the posterior slope.

Stratigraphic range—upper Eocene to Oligocene.

Anechinocardium weaveri (Anderson and Martin, 1914)
Fig. 10A–J

Cardium weaveri Anderson and Martin, 1914. pp. 57–58; pl. 1, figs. 3a, b.
Cardium weaveri Anderson and Martin, Schenck 1928. p. 36.
Nemocardium weaveri (Anderson and Martin), Stewart 1930. p. 274.
Nemocardium weaveri (Anderson and Martin), Schenck 1936. pp. 3, 44, 62, 63.
Nemocardium weaveri (Anderson and Martin), Weaver 1942. p. 161; pl. 36, figs. 1, 2.
Nemocardium weaveri (Anderson and Martin), Durham 1944. p. 116, 146 (in part).
Nemocardium weaveri (Anderson and Martin), Vokes, *in* Warren et al. 1945. checklist.
Nemocardium weaveri (Anderson and Martin), Vokes, *in* Warren and Norbisrath 1946. p. 227.
Nemocardium weaveri (Anderson and Martin), Moore and Vokes 1953. p. 215, 218.
Nemocardium (Nemocardium) weaveri (Anderson and Martin), Keen 1954. p. 10.
Not *Cardium weaveri* Anderson and Martin, Clark 1925. p. 105.
Not *Nemocardium weaveri* (Anderson and Martin), Durham 1944. p. 119, 146 (locs. A-1811, A-1824, Quimper Sandstone).

Figure 10 A–J. *Anechinocardium weaveri* (Anderson and Martin, 1914). **A–C.** Right valve, left valve and dorsal views of articulated hypotype, UCMP 110695, Loc. UCMP IP7984, length = 51.3 mm. **D–F.** Right valve, posterior view of both valves, and detail of offset of posterior radial ribs at commissure of smaller articulated hypotype, Loc. UCMP 110696, UCMP IP7984, length 34.2 mm. **G, H.** Interior view and detail of prepared hinge, right valve hypotype, UCMP 110697, Loc. UCMP IP7984. **I, J.** Interior view and detail of prepared hinge, left valve hypotype, UCMP 110698, UCMP IP7984. Scale bars in details **H, J** = 2 mm. ▶
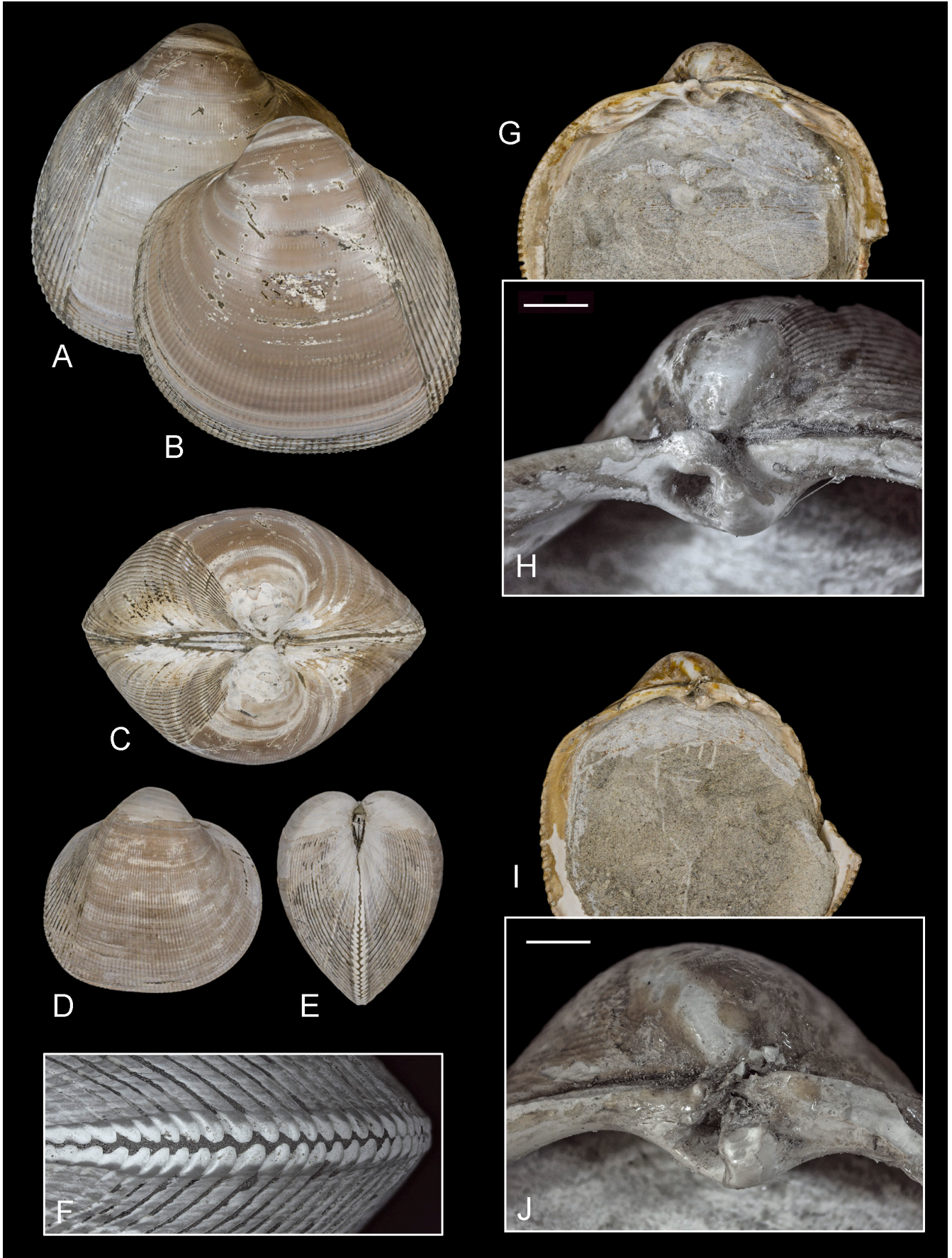
Discussion—This is the most abundant and well-preserved bivalve in the Keasey Formation. Unlike many other Keasey bivalves, the large quadrate shells are typically well preserved with the valves articulated, not crushed or distorted, and the original shell surface in good condition. The best specimens are those collected from unweathered matrix. The shells are relatively thin, brittle, and unreinforced by the ornamentation typical of many cardiids, tending to break and occur as fragments on weathering.

The hinge is more resistant to fragmentation than the rest of the shell, the right and left hinge plates are illustrated here for the first time (Fig. 10G–J). The cardinal teeth are of markedly unequal size in the left valve, and the anterior cardinal is much stronger than the posterior. The cardinal teeth are more nearly equal in size in the right valve and are partially fused. The interlocking of the cardinals is what Keen (1980, p. 9) referred to as "cruciform". The laterals are elongate parallel to the hingeline and are separated at some distance from the cardinals. The elongate escutcheon is well developed posterior to the beaks.

Allometric growth produces a change in proportions from immature individuals in which length is slightly greater than height to large adult shells (height >50 mm) in which height exceeds length. The commissure is stabilized by well-developed interdigitating crenulations (Fig. 10F) that are coarser at the termination of the heavier ribs with wider interspaces on the posterior slope than at the termination of finer subsurface ribs with narrower interspaces on the middle and anterior slopes. The crenulations extend into the interior ventral margins of the shell.

The major feature of *Anechinocardium weaveri* that has not been noted and figured previously is the absence of nodes, granules or concentric ornamentation *on* the smooth heavier ribs of the posterior slope and restriction of periodic ornamentation to very fine intercostal lamellae that are well developed during early ontogeny, becoming less prominent and disappearing during later growth. These fine cross-bridging lamellae (Fig. 9) are the primary feature distinguishing the new subgenus from other subgenera of *Nemocardium*. The lamellae are not always aligned from one interspace to the next. The lack of alignment is especially prominent in *A. lorenzanum* from the upper member of the Keasey (circled on Fig. 9).

Two other large-shelled fossil *Anechinocardium* species from the Pacific Northwest occur stratigraphically higher and in shallower facies in the Eugene Formation [*A. formosum* (Hickman, 1969)] and the Quimper Sandstone and coeval strata (?) at Fiddler's Bluff, Washington (*Anechinocardium* n. sp. ? Hickman, this report). Hickman (1969) provided a detailed comparison with the Eugene species, and the Quimper specimen is discussed and figured herein.

Material Examined—>100 double-valved specimens plus hinge plates of five left valves and four right valves. Specimens also were examined for evidence of predation. Naticid drill holes were observed in the umbonal region of six juvenile specimens: two on right valves and four on left valves. No drill holes are present on adults, and their absence suggests a size refuge for the species. This species is restricted to the middle member of the Keasey Formation.

Type Information—Figured hypotypes, all from Loc. UCMP IP7984 (= USGS 25031): UCMP 110695, length 51.3mm, height 52.6 mm, diameter 36.8 mm; UCMP 110696, length 34.2 mm, height 32.4 mm, diameter 30.5 mm; UCMP 110697, length of right hinge plate 31.8 mm; UCMP 110698, length of left hinge plate (incomplete) 25.6 mm. Unfigured UCMP hypotypes (both from UCMP IP7984): UCMP 110699, length 50.6 mm, height 51.3 mm, diameter 38.5 mm; UCMP 110700, length 45.1 mm, height 45.0 mm, diameter 35.1 mm. USNM Hypotypes: USNM 561767, length (incomplete) 43.0 mm, height 42.5 mm, diameter (right valve) 16.4 mm, Loc. USGS 15282; USNM 561768, length 33.2 mm, height 32.3 mm, diameter (left valve) 12.2 mm, Loc. USGS 15282; USNM 561769, length 19.3 mm, height 18.0 mm, diameter 13.6 mm, Loc. 15282; USNM 561770, length 29.3 mm, height 27.5 mm, diameter 20.2 mm, Loc. 15282; USNM 561771, length 49.7 mm, height 50.5 mm, diameter 34.9 mm, Loc. 15282; USNM 561772, length 46.7 mm, height 48.8 mm, diameter 37.0 mm, Loc. 15517.

Keasey Formation Localities—USGS 15267, 15274, 15275, 15279, 15280, 15281, 15282, 15283, 15284, 15313, 14314, 15316, 15318, 15508, 15509, 15525, 15602, 2712, 2723, 5390; USGS M3854, M3862; USGS 25030, 25036; UCMP IP7984 (=USGS 25031).

Stratigraphic occurrence—Upper Eocene, restricted to the middle member of the Keasey Formation.

Anechinocardium lorenzanum (Arnold, 1908)
Fig. 11A–D

Cardium cooperi Gabb, var. *lorenzanum* Arnold, 1908. p. 366; pl. 33, fig. 6.
Cardium cooperi Gabb, var. *lorenzanum* Arnold, Arnold 1909. p. 4, fig. 17.
Cardium cooperi Gabb, var. *lorenzanum* Arnold, Weaver 1912. p. 18.
Cardium lorenzanum Arnold, Arnold and Hannibal 1913. pp. 581, 588.
Cardium lorenzanum Arnold, Clark 1915. pp. 14, 18.
Cardium lorenzanum Arnold, Weaver 1916. pp. 35, 51.
Cardium lorenzanum Arnold, Van Winkle 1918, p. 75.
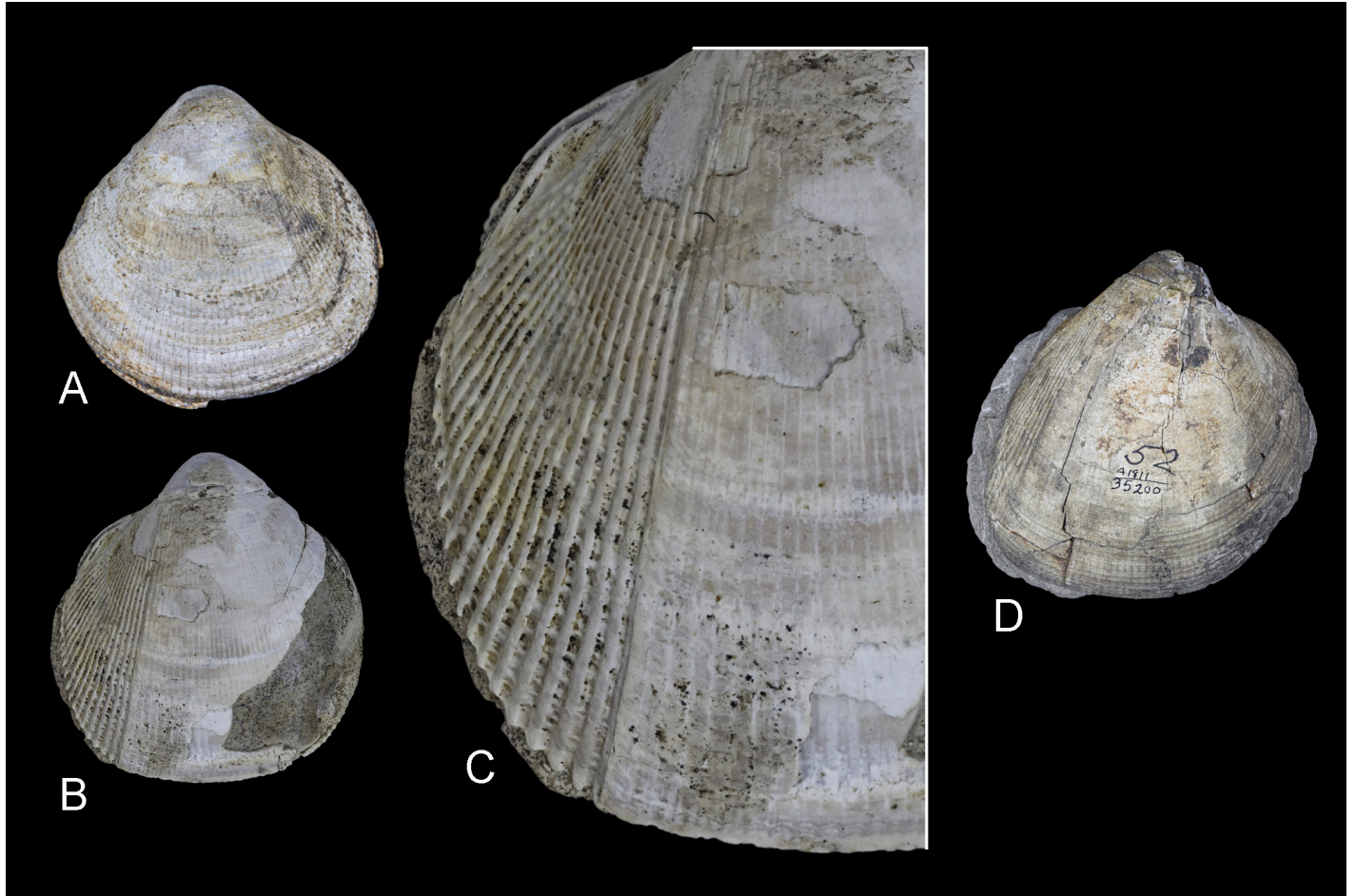*Cardium lorenzanum* Arnold, Clark 1918. pp. 90, 96, 101, 104, 141.

Figure 11A–D. *Anechinocardium lorenzanum* (Arnold, 1908) and *Anechinocardium* sp. **A.** *Anechinocardium lorenzanum*, hypotype from the Blakeley Formation, UCMP 32116, Loc. UCMP 681, length = 16.0 mm. **B.** *Anechinocardium lorenzanum*, hypotype from the Keasey Formation, UCMP 110701, Loc. UCMP IP2288, length = 16.7 mm. **C.** Detail of sculpture from B. **D.** *Anechinocardium* sp. from the Quimper Sandstone, UCMP 35200, Loc. UCMP A-1811, length 54.9 mm.

Cardium lorenzana Arnold, Clark 1925. pp. 82, 88, 89.
Cardium lorenzanum Arnold, Clark 1925. p. 106.
Nemocardium lorenzanum (Arnold), Stewart 1930. p. 274.
Cardium lorenzanum Arnold, Tegland 1933. pp. 92, 93, 116, 117; figs. 16, 17.
Nemocardium lorenzanum (Arnold), Schenck 1936. pp. 69, 71.
Nemocardium lorenzanum (Arnold), Weaver 1942. pp. 160, 634; pl. 35, fig. 22; pl. 36, figs. 3, 5.
Nemocardium lorenzanum (Arnold), Durham 1944. pp. 120, 122, 127, 146.
Nemocardium lorenzanum (Arnold), Vokes in Warren and Norbisrath 1946. p. 227.
Nemocardium lorenzanum (Arnold), Moore and Vokes 1953. pp. 115, 118, 119.
Nemocardium (Keenaea) lorenzanum (Arnold), Keen 1954. p. 11.
Nemocardium (Keenaea) lorenzanum (Arnold), Hickman 1969. p. 38; pl. 2, fig. 7.

Nemocardium (Keenaea) lorenzanum (Arnold), Moore 1976. p. 47, pl. 10; figs. 12–14.
Nemocardium (Nemocardium) lorenzanum (Arnold), Moore 2002 (e-book, no pagination).

Discussion—The features distinguishing this species from *A. weaveri*, the type species of *Anechinocardium*, are smaller shell size (height <30 mm), greater variation in the ratio of width to height, and persistence of fine ladder-like cross striae in intercostal spaces throughout growth (Fig. 11C). It replaces *A. weaveri* in the upper member of the Keasey Formation.

Although Arnold described this species in a report on the San Lorenzo Formation of California, his type specimen is from the Lincoln Creek Formation in Washington. As suggested by the extensive (but not exhaustive) synonymy above, it has a considerably broader geographic and stratigraphic range and also occurs in shallower facies. Specimens of this species are more variable in proportions and rib counts than *A. weaveri*, and may represent a species complex.

The earliest recognition of fine cross-striae in intercostal spaces on the posterior portion of the shell (Hickman, 1969) was based on a study of eight specimens from tuffaceous siltstone beds in the Eola Hills north of Salem, Oregon, interpreted as Eugene Formation. Although Hickman (1969) assigned the species to the subgenus *Keenaea* Habe, 1951, it is now clear that periodic concentric sculptural elements do not cross the ribs as in *Keenaea*, but are restricted to the interspaces.

Material Examined—The species is represented by 11 specimens from upper member of the Keasey Formation. Five of the specimens are double-valved and well preserved and four have a naticid drill hole. Two of the drill holes are in the right valve and two in the left. Eight specimens from the Eugene Formation were examined earlier and one was figured (Hickman 1969, pl. 2, fig. 7). Specimens from the Pittsburg Bluff Formation are most comparable to those from the Keasey. One of Tegland's specimens from the Blakeley Formation is refigured here (Fig. 11A). Other reported occurrences are noted below.

Type Information—Figured hypotype: UCMP 110701, length 16.7 mm, height 17.7 mm, Loc. UCMP IP2288 (=USGS 15269 and 25039). Unfigured hypotypes: USNM 561773, length (slightly incomplete right valve) 11.9 mm, height 11.5 mm, Loc. USGS 15518; USNM 561774, length (incomplete right valve) 9.5 mm, height 9.8 mm, Loc. USGS 15518.

Keasey Formation Localities— USGS 15518, 25032; UCMP IP2288 (all upper member).

Occurrence elsewhere—In addition to the additional occurrences noted above, Moore (1976) reported the species from the Alsea Formation in Oregon and the Rices Mudstone Member of the San Lorenzo Formation in California. Vokes (personal communication) reported it from the Scappoose Formation in Oregon and from USGS collections from Bear Creek, near the junction with Beaver creek, one mile south of Hemlock in Tillamook County, Oregon.

Stratigraphic occurrence—Oligocene.

Anechinocardium sp.
Fig. 11D

?*Cardium weaveri* Anderson and Martin, Clark 1925, p. 105.

Nemocardium weaveri (Anderson and Martin) Durham 1944, p. 119 (checklist), 146 (in part, not "Keasey").

Discussion—A previously unfigured specimen from the Quimper Sandstone, designated by Durham (1944) as a hypotype of *Nemocardium weaveri*, is figured here for comparison. It is a right valve in matrix and is larger and relatively higher than any of the specimens from the Keasey

Formation. They are finer and more numerous on the posterior area of the shell, and the umbo projects higher above the hinge line. The specimen occurs in strata that are younger than the middle member of Keasey Formation (late Eocene) and closer in age to the overlying Pittsburg Bluff Formation (early Oligocene). There are no comparable specimens that can be assigned to *Anechinocardium* in extensive collections from Pittsburg Bluff localities.

Figured Specimen—UCMP 35200, length 54.9 mm, height 59.1 mm.

Occurrence—Quimper Sandstone, lower Oligocene, Clallam County, Washington, Loc. UCMP A-1811.

TELLINOIDEA Blainville, 1814

Telliniform bivalves from Lower Mesozoic strata have been classified in extinct family groups of uncertain affinities. Taxa appearing in the Cretaceous are more reliably recognized as precursors of a largely tropical evolutionary radiation in the Cenozoic, but including some distinctive high latitude forms and extending to bathyal depths in the Holocene fauna of the Northeastern Pacific (Coan et al. 2000).

Stratigraphic range—?Upper Triassic to Holocene.

TELLINIDAE Blainville, 1814

In contrast to the shallow-burrowing cardiids, the tellinids, commonly known as tellins, are deep-burrowers with relatively thin, compressed shells, long separate siphons, and large labial palps. They are often the most abundant bivalves in the infauna of organic-rich soft sediments and occur as prominent faunal elements over a broader latitudinal range as well as a broader bathymentric range than cardiids. The shells are typically smooth with fine commarginal growth lines as the only ornament in contrast to the more elaborately ornamented cardiids. Many of the living species are noted for their brilliantly-pigmented shells. The animals are highly active and rapid burrowers. Two aspects of tellinid ecology are noteworthy in the Keasey bivalve fauna, which is dominated by taxa that are able to live in extreme environments and to derive their nutrition through deposit feeding or chemosymbiosis. The first is the presence of hemoglobin, an oxygen carrying pigment, nerve ganglia and muscle (Kraus and Colacino 1986). The second is the secondary shift in the tellinids from obligate suspension feeding in early Mesozoic family-group taxa to deposit feeding and combined feeding modes in the late Mesozoic and Cenozoic (Pohlo 1982), in part through versatility in orientation and behavior of the long inhalant siphon. The opening of the siphon can be pressed directly to the sediment to suck up organic-rich particles or it can stir the sediment and ingest resuspended particles from the water column (Yonge 1949). Statements

in the literature that tellinids have abandoned suspension feeding altogether are unwarranted (see Pohol 1969 for a review), although the ability to thrive in hypoxic settings and environments that provide little nutrition from the water column is a key evolutionary triumph for the group. Ability to colonize a sulfide-rich environment is also reported (Laurent et al. 2013) although there is no evidence of chemical dependence or a chemosymbiotic relationship.

Although Tellinoidea appears to be monophyletic (Bieler et al. 2014), the internal relationships are universally regarded as chaotic, in large part because taxonomy has been based primarily on shell features. Tellinidae, traditionally divided into Tellininae Blainville, 1814 and Macominae Olsson, 1961, is not monophyletic (Bieler et al. 2014). There are more than 100 available genus group names, more than 50 of which have been treated as subgenera of *Tellina* Linnaeus, 1758. Although heroic attempts at supraspecific classification include the Mesozoic and Cenozoic taxa (Afshar 1969, Keen 1969b), the results have not been tested cladistically. Placement of the Keasey tellinoidean species into a genus-group is based on its remarkable similarity of the shell to that of the type species.

Stratigraphic range—Lower Cretaceous to Holocene.

MOERELLA Fischer, 1887

Type species—By monotypy, *Tellina donacina* Linnaeus, 1758, Holocene, North Sea, Atlantic coasts of Europe, Mediterranean, Adriatic and Black Seas.

Assignment of the following species to *Moerella* is based primarily on the similarities in shell shape, proportions and hinge structure, with two lateral teeth in the right valve. In the type species the ventral limb of the very deep pallial sinus is confluent with the pallial line to greater extent. However the degree of confluence can be highly variable among species, and Dall (1900b) considered it to be of little taxonomic value in tellinids.

Stratigraphic range—lower Eocene to Holocene.

Moerella quasimacoma n. sp.
Fig. 12A–J

Macoma hoffmanniana Gabb, Dall in Diller 1896, p. 548. (not *Tellina hoffmanniana* Gabb, 1864, pp. 156, 230; pl. 22, figs. 133, 138a.
Macoma sp. Dall in Washburne 1914, p. 31.
Macoma n. sp. Vokes in Warren et al. 1945, checklist.
Tellina n. sp. Moore and Vokes 1953, pp. 115, 119.

Diagnosis—Shell thin (thickness 0.2 mm), compressed, subovate-elongate, and strongly inequivalve, with more inflated left valve and posterior flexure to right of both valves; umbones low, beaks prosogyrate and small but sharply pointed, right beak slightly higher than left; almost equilateral, with slightly concave anterior and posterior dorsal margins nearly equal length; exterior surface glossy and smooth with numerous faint growth lines and growth checks; pallial sinus faint but deep, broadly U-shaped, almost touching anterior adductor, with ventral limb confluent with pallial line to varying degree; sunken external ligament prominently developed, escutcheonal region broad but not clearly demarcated; lunule absent; hinge plate with thin, elongate posterior and anterior lateral teeth and two cardinal teeth in each valves.

Description—The anterior end of the shell is broadly rounded, and the posterior end is more sharply rounded. In the right valve the anterior cardinal is simple and relatively heavy, and the posterior cardinal is broadly triangular, strongly developed and deeply bifid (Fig. 12I). In the left valve the posterior cardinal is also simple but thinner than the equivalent right anterior cardinal, and the left anterior cardinal is narrower and less deeply bifid than the posterior right cardinal (Fig. 12J). The thin, elongate lateral teeth in the left valve are at the valve margins and fit into sockets on the left valve dorsal to the submarginal laterals (Fig. 12G–H). The average umbonal angle measured on 50 specimens is 126°. The adductor muscle scars are relatively large, shallowly impressed, and situated closer to the dorsal margins. The posterior scar is smaller and sub-rounded in outline than the larger, more elongate anterior scar. There is a broad but very shallow groove and ridge along the posterior dorsal valve margins where growth lines change direction more abruptly than on the more evenly rounded anterior dorsal margin (Fig. 12A, B, D, E).

Discussion—*Moerella quasimacoma* Hickman n. sp. is one of the most frequent and abundant bivalves in the Keasey Formation, and it is remarkable that it has lacked a name for more than 100 years. Specimens in the United States National Museum in the Diller and Washburne collections were labeled, apparently by William Healey Dall (see synonymy), as "*Macoma* sp." and in preliminary study by Vokes (Vokes in Warren et al. 1945), although he subsequently recognized the presence of lateral teeth and listed it as an undescribed species of *Tellina* (Moore and Vokes 1953). The species occurs in all three members but is restricted to the Keasey Formation.

This is apparently the earliest occurrence of *Moerella* in the Eastern Pacific. It is readily distinguished from other tellinid species from the west coast Paleogene. *Tellina vancouverensis* Clark and Arnold, 1923 from the Oligocene Sooke Formation of Vancouver Island and *T. merriami* Weaver, 1912 from the Miocene Montesano Formation of Washington are both more strongly inequilateral, with more posteriorly situated
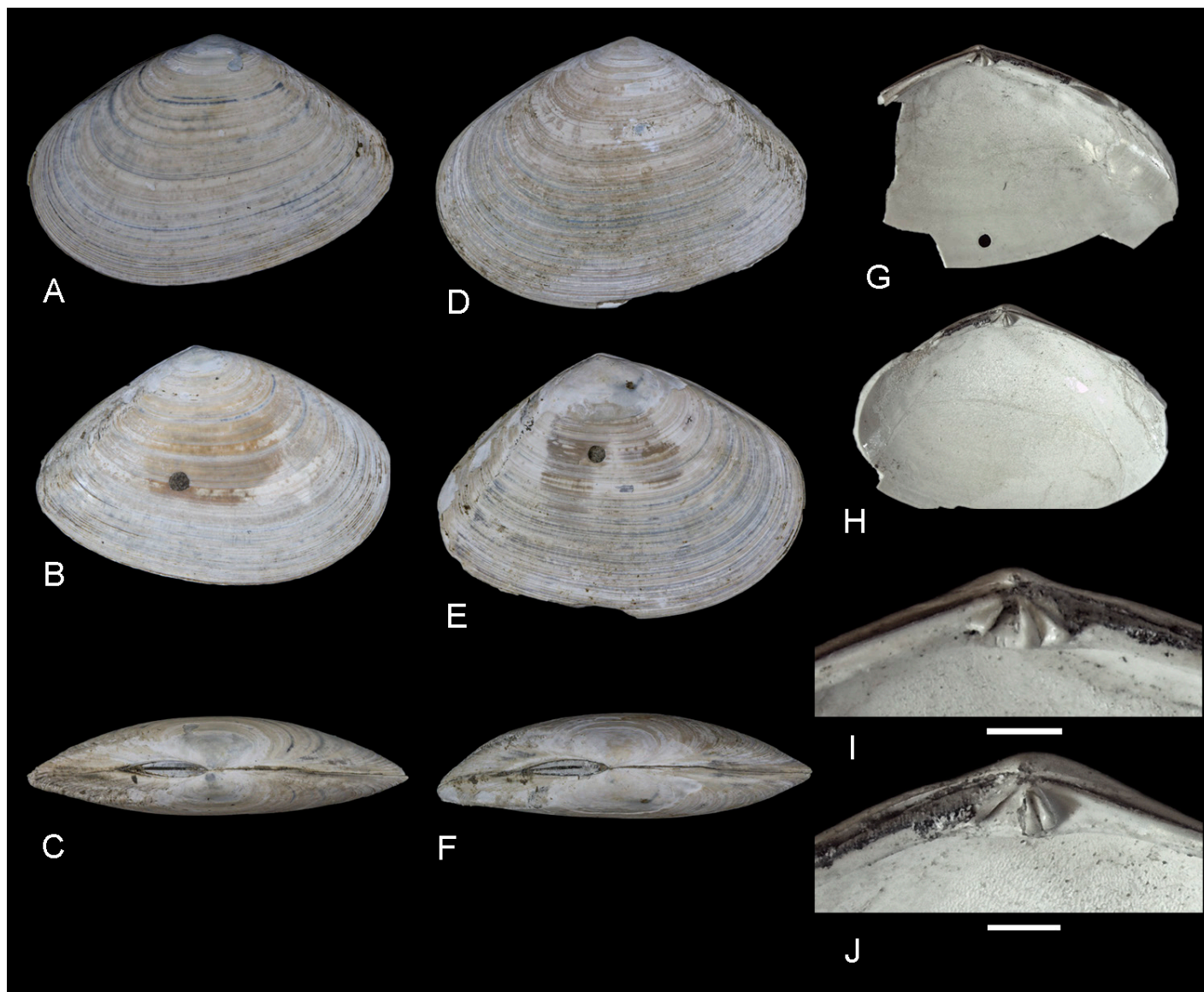
Figure 12A–J. Tellinidae, *Moerella quasimacoma* n. sp. **A–C.** Left valve, right valve, and dorsal view of holotype, UCMP 110702, Loc. UCMP IP7984, length 30.7 mm. **D, E.** Left valve, right valve, and dorsal view of paratype, UCMP 110703, Loc. UCMP IP7984, length 30.7 mm. **G.** Interior of right valve of paratype, UCMP 110704, Loc. UCMP IP7984, length (incomplete) 15.4 mm. **H.** Interior of left valve of paratype, UCMP 110705, Loc. UCMP IP7984, length (incomplete) 21.4 mm. **I.** Detail of cardinal teeth in right valve, J. Detail of cardinal teeth in left valve. Scale bars for I, J = 1 mm.

beaks and longer anterior end. *T. lorenzoensis* Arnold, 1908 was referred to *Macoma* by Clark (1925) and Tegland (1933), but the hinge structure remains unknown, and the outline is subtrigonal. The shell of *"Macoma" lorenzoensis arnoldi* Tegland, 1933 from the Oligocene Blakeley Formation is proportionately higher than the Keasey species. Moore (1976) was unable to find lateral teeth in the hinge of *T. pittsburgensis* Clark, 1925 from the overlying Oligocene Pittsburg Bluff Formation, and *T. aduncanasa* Hickman, 1969 from the Eocene-Oligocene Eugene Formation are more elongate and have a sharply attenuated posterior end.

Taphonomically it is remarkable that the new Keasey species is invariably double valved and never crushed, in spite of the thinness and brittle nature of the shell. Deep burrowing and long siphons, as inferred from the depth of the pallial sinus, may have afforded protection against postmortem exposure and transport, but specimens commonly have naticid drill holes that are not consistent with respect to valve drilled or placement on the valve. Naticids are among the most abundant gastropods in the Keasey Fauna (Hickman 1980), and three naticid species co-occur at localities with drilled *M. quasimacoma*.

Etymology—Named in recognition of the shell outline that led to identification as a species of *Macoma* in early collections. It is the name that Harold Vokes attached to intended USNM type specimens.

Material examined—The description is based on detailed examination of 55 double-valved specimens and hinge plates of two right valves and one left valve.

Holotype—UCMP 110702, length 30.0 mm, height 18.7 mm. Loc. UCMP IP7984 (=USGS 25031). (articulated)

Figured paratypes—UCMP 110703, length 30,7 mm, height 22.4 mm, Loc. UCMP IP7984 (articulated); UCMP110704, length (incomplete) 15.4 mm, height (incomplete) 12.1 mm (right valve with hingeplate), Loc. UCMP IP7984; UCMP 110705 length incomplete 21.4 mm, height 11.8 mm, (left valve with hingeplate), Loc. UCMP IP7984; USNM 561784.

Unfigured paratypes—USNM 561784, 561785, 56186, 561787, 561788.

Keasey Formation localities—USGS 2717, 25263, 15265, 15305, 15307, 15308, 15309, 15584; UCMP IP2286 (=USGS 25028), IP7983 (=USGS 25026) (lower member). USGS 1513, 2712, 2716, 15134, 15267, 15268, 15274, 15275, 15279, 15280, 15281, 15282, 15283, 15284, 15316, 15318, 1508, 15517, 15582, 15602, 25036, 25038, M3682; UCMP IP7984 (middle member). USGS 15315, 15518, 15581, 16601 (upper member).

Stratigraphic range—upper Eocene to lower Oligocene.

macoma Leach, 1819

Type species—by monotypy, *Macoma tenera* Leach, 1819 = *Tellina calcarea* Gmelin, 1791. Holocene, North Atlantic.

Tellinoideans lacking lateral teeth and occurring primarily in cold-water faunas at high latitudes have been treated by many authors under a separate subfamily Macominae Olsson, 1961. Until the relationships of tellinoidean genera are better understood, subfamilial designations do not seem warranted, and the Keasey shell treated here in open nomenclature is tentatively assigned to *Macoma* based primarily on shape.

Stratigraphic Range—Eocene to Holocene.

Macoma? sp.
Fig. 13A–C

Discussion—A single articulated shell of a compressed inequilateral tellinoidean with prominent beaks differs from the abundant *Moerella quasimacoma* in being equivalve and in having a strongly convex anterior dorsal margin and slightly concave posterior dorsal margin. The shell surface is chalky, in contrast to the typically glossy appearance of the shells of the Keasey *Moerella* and the growth increments are less well defined. The shell was collected along with several shells of *M. quasimacoma*, and its distinctive features were discovered only during careful study of the lot.

Figured Specimen—UCMP 110706, length 23.3 mm (almost complete), height 18.1 mm. Loc. UCMP IP2287 (=USGS 15267, USGS 25034) (uppermost middle member).
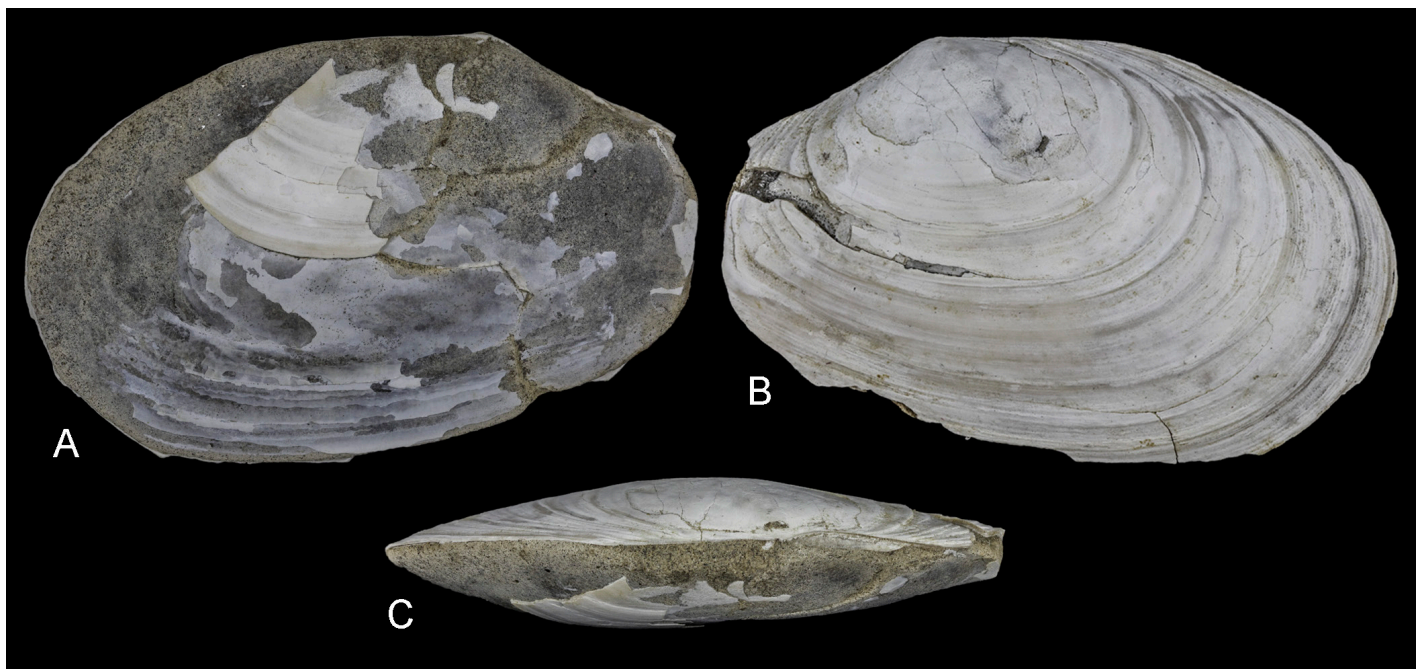

Fig. 13A–C. *Macoma*? sp. **A.** Left valve, **B.** Right valve, **C.** Dorsal view of UCMP 110706, Loc. UCMP IP2287, length = 23.3 mm.

CYAMIOIDEA G.O. Sars, 1878

Cyamioideans, like galeommatoideans, are small marine bivalves whose taxonomy and phylogenetic relationships poorly resolved. Different authors have shifted the alignment of genus groups and species between family groups and shifted family groups between Galeommatoidea and Cyamioidea. Conflicts between morphological and molecular data have increased the uncertainty of placement of Basterotiidae and Saxicavellinae which recently have been allocated on morphological grounds to Cyamioidea (Coan and Valentich-Scott 2012) and on sequence data to Galeommatoidea (Oliver 2013). The tentative classification adopted here for the new Keasey Formation species is consistent with the record of taxa in deep, cold-water settings, longer geologic record, and evidence of adaptations for chemosymbiosis and life in extreme or hypoxic environments.

Stratigraphic range—Jurassic to Holocene.

BASTEROTEIIDAE Cossmann, 1909
SAXICAVELLINAE Scott, 1994
SAXICAVELLA P.-H. Fischer, 1878

Type species—by monotypy, *Saxicavella jeffreysi* (Winckworth, 1930), Northeastern Atlantic.

Saxicavella has been variously treated a subgenus of *Hiatella* Daudin in Bosc, 1801 (e.g., Thiele 1935) a separate genus in a distinct subfamily of Hiatellidae J.E. Gray, 1824 (e.g., Scott 1994, Coan et al. 2000), and most recently transferred out of Hiatellidae to Basterotiidae (Oliver 2013). The earliest study of anatomy led Yonge (1971) to conclude differences were so great as to merit separate generic status. The major difference noted by Yonge was the absence of siphons (or presence of only very short siphons), in contrast to the long siphons of (other) hiatellids. It was much later that the reproductive peculiarities of simultaneous hermaphroditism and brooding (Scott 1994) and additional peculiarities of the shell and anatomy (Oliver 2013) confirmed growing suspicion of a distinct evolutionary lineage far removed from Hiatelloidea. The broad, sometimes cosmopolitan, geographic distributions and many forms of reproductive and developmental specializations are characteristic of minute brooding bivalve species (e.g., Ó Foighil and Eernisse 1988). This opens the possibility that fossil taxa can occur at great distances from their closest relatives and represent genetic lineages that will confound taxonomic allocation based solely on shell features.

Some peculiarities of saxicavellines are atypical of the majority of minute-shelled hermaphroditic bivalves. They include the following: (1) high latitude occurrence in the Atlantic and Pacific, (2) active burrowing ability, (3) free living, but with infrequent evidence of symbiotic association with invertebrate host species, (4) occurrence in offshore sand and mud, and (4) bathymetric ranges extending below shelf depths (>200 m). The type species is reported to occur as deep as 1,207 fathoms (= 2,207 m) (Winckworth 1930). These features are consistent with the otherwise unusual occurrence of the Keasey bivalve described below.

The most interesting peculiarity, however, is a new saxicavelline genus and species recovered from >1,000 m with highly modified ctenidia with bacteriocytes packed with what appear to be symbiotic bacteria (Oliver 2013). The new Keasey species described below co-occurs with a thyasirid and solemyid at a locality with independent geological and geochemical evidence of carbonates that formed in a zone of archeal methanogenesis (Burns et al. 2005).

Schneider and Kaim (2011) describe two exquisitely-preserved small shells from a Middle Jurassic (Bathonian) wood fall in southern Poland as a hiatellid in the genus *Pseudosaxicava* Chavan, 1952. Their new species may, in fact, be a basterotiid. They interpreted the shells as juveniles, but the diagonal carination separating the anterior and posterior area and microtubercles on the shell are both characteristic of living carinate and pustulose species currently classified in Basterotiidae (see Coan and Valentich-Scott 2012). Based on associated wood-fall fauna and fine-grained clay and silt sediment Schneider and Kaim (2011) inferred a deep-water (outer slope) setting and potential hypoxic conditions. The conclusion that Jurassic sunken logs supported non-actualistic, pre-chemosymbiotic communities (Kaim 2011) is based on the absence of xylophagan bivalves and other taxa whose living representative harbor chemosynthetic bacteria. However, more recent discovery, noted above, of bacterial chemosymbiosis in a deep-water basterotiid (Oliver 2013) opens the possibility of a longer history of modification of the gills of basterotiids, possibly as part of the Jurassic recovery from the end Triassic mass extinction.

The living type species and two extinct species of *Saxicavella* have been reported from the Pliocene and Pleistocene faunas of the Coralline and Red Crag of Europe (e.g., Wood 1850), where they have been used as stratigraphic and paleoclimatic indicators (Graham 1989).

Stratigraphic range —Paleocene?, Eocene to Holocene.

Saxicavella burnsi n. sp.
Fig. 14A–C

Diagnosis—Shell length <10 mm, thin and fragile, equivalve, inequilateral, with beaks anterior to midline; shape modioiliform (obliquely rhomboidal), anterior end narrower than posterior, posterior dorsal margin straight, posterior margin sub-truncate, ventral margin very shallowly convex; posterior area clearly demarcated by oblique rounded ridge extending from umbo to posterior-ventral margin. Interior
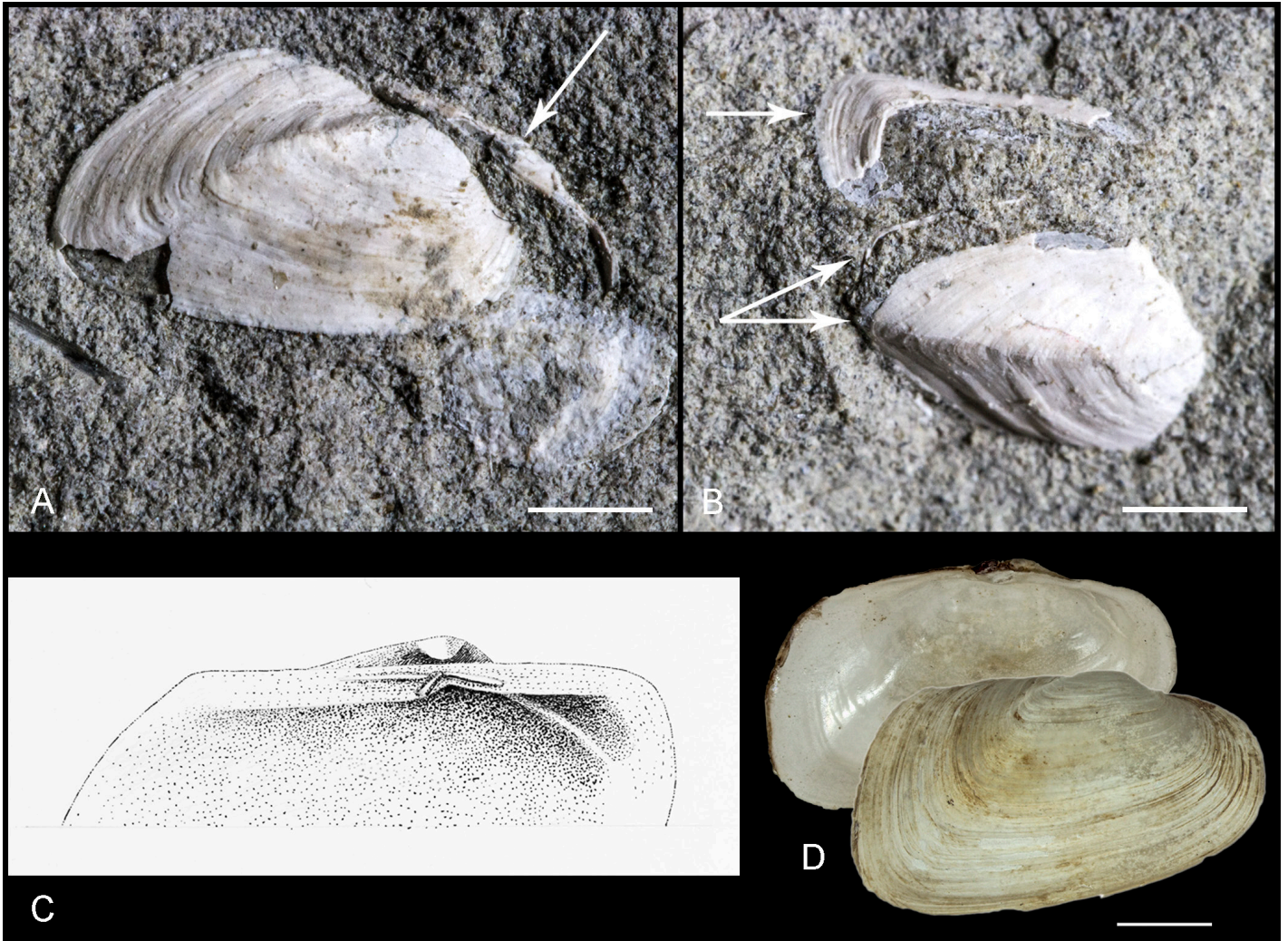
Fig. 14 A–D. Basterotiidae, *Saxicavella.* **A–C.** *Saxicavella burnsi* n. sp. **A**. Holotype, UCMP 110707, Loc. UCMP IP16005, left valve and offset dorsal margin of right valve (at arrow) in matrix . **B**. Two paratypes in matrix, UCMP 110708 (incomplete left valve and offset posterior dorsal margin of right valve, lower arrows) and UCMP 110709 (fragment of left valve in matrix, upper arrow), UCMP IP16005. **C.** Paratype, USNM 561802, Loc. USGS 15318, drawing of hinge plate and subumbonal ridge from latex peel of interior mold. **D.** *Saxicavella pacifica* Dall, 1916, SBNHM 43578, paired valves. Scale bars = 2 mm.

of left valve with weak subumbonal ridge; surface with fine concentric growth lines and growth checks.

Discussion—The prominent radial ridge setting off the posterior end of the shell contributes most to its distinctive shape and distinguishes *Saxicavella burnsi* Hickman n. sp. from both of the similarly minute Keasey species of *Kellia*.

Hinge structure is indistinctly preserved only in the internal mold of the left valve of one of the paratypes. A drawing made from a latex peel (Fig. 14C) shows two rudimentary cardinal teeth and a faint horizontal structure posterior to the cardinals that may be either a third cardinal or a weak nymph plate. The anterior cardinal is slightly oblique to the straight posterior dorsal margin. The posterior (or median ?) cardinal is shorter but more strongly-developed than the anterior cardinal. There is a weak indentation in the hinge plate between the cardinals. The subumbonal ridge accentuates the visibility of a faintly-impressed anterior muscle scar, but the posterior muscle scar is not visible on the latex peel from the internal mold. The interior ventral margins of the valves are smooth, showing no sign of indentations. There is no sign of a ventral sinus or posterior gape.

The most interesting and unique feature of the shell of *S. burnsi* is the subumbonal ridge, a faint oblique line in the shell interior, extending from beneath the umbone along the posterior edge of the anterior adductor (Fig. 14C). The ridge is easily overlooked because it is visible only under some angles of illumination and difficult to photograph. However, it is present in the type species of *Saxicavella*, *S. jeffreysi*

Winckworth 1930. It is not present in Yonge's illustration (1971, fig. 10) of the shell interior, but it is clearly illustrated here (at arrows in Fig. 15A). The relationship of *Saxicavella* to *Basterotia* is further supported by the presence of this ridge in *Basterotia obliqua* Coan, 1999. Again, the ridge is not figured or mentioned in the original description, but it is illustrated here (at arrow in Fig. 15B). Of greater interest regarding the new Keasey basterotiid is discovery of the ridge in the deep-sea basterotiid *Atopomya dolobrata* Oliver, 2013. This new genus and species, from 1,200 m off the coast of Ireland, has highly modified ctenidia with bacteriocytes containing symbiotic bacteria (Oliver 2013). The ridge is not convincingly visible in the original illustrations of valve interiors (Fig. 1B, C), but high-resolution original images provided by Graham Oliver (pers. comm. 2015) confirm that it is present in both valves. Of perhaps greater interest is the association of *Atopomoya* with glass sponge beds (G. Oliver, pers. comm. 2015), because the new Eocene species occurs at Keasey storage locker locality with abundant basal root tufts of hexactinellid sponges.

The overall shape, including the oblique demarcation of the posterior portion of the shell, is similar to that of some shallow-water tropical Eastern Pacific taxa assigned to Sportellidae Dall, 1899, as reviewed by Coan (1999). On the basis of photographs of the Keasey material, Winston Ponder (pers. comm. 2013) suggested a similarity to some New Zealand and Subantarctic sportellids (Ponder 1971). However comparisons with North Pacific and Atlantic basterotiids have proved more compelling. A shell of the subtidal *Saxicavella pacifica* Dall, 1916 is illustrated here (Fig. 14D) to show the similarity in shape as well as the faint but distinctive subumbonal ridge.

Etymology—Named in honor of Casey Burns, who collected and donated the piece of blue-gray siltstone containing the holotype and two paratypes as well as additional material that has helped clarify the stratigraphic distribution of distinctive faunal assemblages in the Keasey Formation.

Material examined—Four specimens. The holotype and two paratypes are imbedded in the same block of matrix and preserve original (but altered) shell material. The holotype (Fig. 14A) is partially disarticulated, but the left valve provides the best indication of shell outline, the oblique radial demarcation, and the shell surface. A double-valved paratype (Fig. 14B) is similarly partially disarticulated with the left valve mostly visible and the offset posterior dorsal margin of the right valve partially visible. A fragment of left valve (Fig. 14B) is preserved alongside the second paratype, and its position and orientation indicate that it is part of a third specimen. The fourth paratype is from an earlier collection by Moore and Vokes in the main crinoid layer at Mist. It is a butterflied specimen, part and counterpart, containing no original shell material. However, the interior mold retained adequate detail for the latex peel from which the hinge plate and subumbonal ridge are reconstructed (Fig. 14C).

Holotype—UCMP 10707.

Paratypes—UCMP 110708, 110709, USNM 561802

Type locality—UCMP IP16005 (≈USGS 15315) (upper member).

Other Keasey locality—USGS 15318 (uppermost middle member, the main crinoid-bearing layer at Mist).

Stratigraphic occurrence—This is the first report of *Saxicavella* from the fossil record of the Eastern Pacific and extends its regional stratigraphic range back to the upper Eocene.
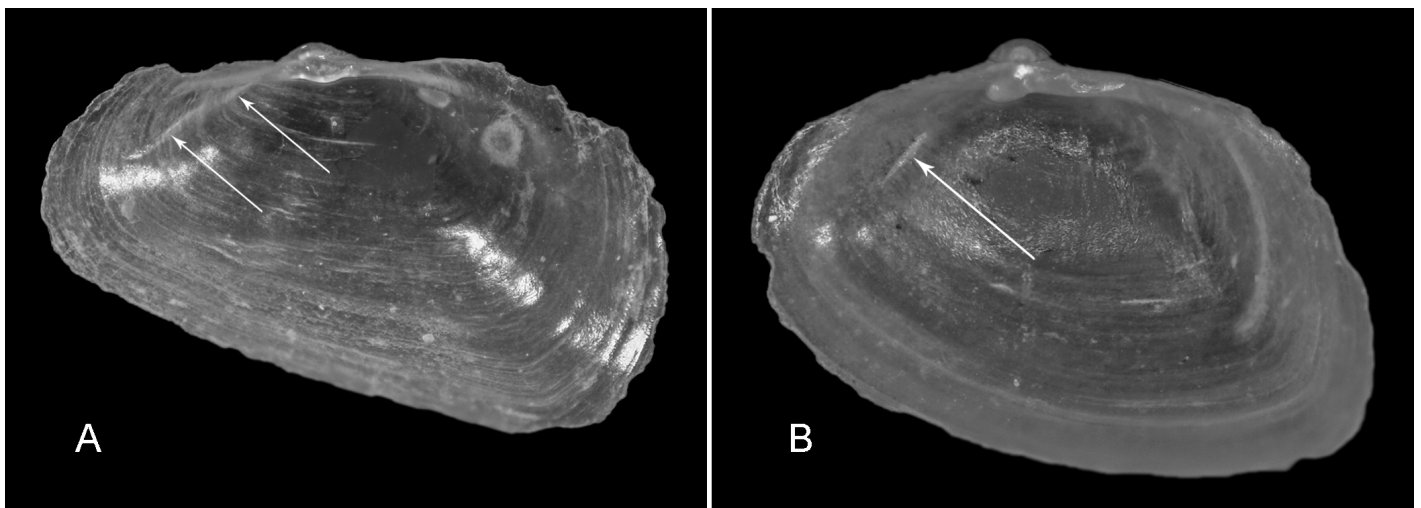

Fig. 15A–B. Cyamioidean subumbonal ridges. **A**. *Saxicavella jeffreysi* Winkworth, 1930, SBNHM 424690, length = 3.5 mm, interior of left valve, ridge at arrows. **B**. *Basterotia oblioqua* Coan, 1999, SBNHM 454104, length = 2.4 mm, interior of left valve, ridge at arrow.

MACTROIDEA Lamarck, 1809

Mactroideans, including the species commonly known as surf clams and gapers, are a prominent element of the living littoral marine fauna, occurring in greatest abundance in coarse, shifting sediment. They are active and often deep burrowers and include species that are commercially valuable. In the Northeastern Pacific relatively large-shelled inflated mactroideans are a dominant element in many shallow-water temperate Neogene fossil assemblages, but they are uncommon prior to the demise of the tropical Eocene fauna. Of the four mactroidean families, only Mactridae Lamarck, 1809, is represented the Northeastern Pacific.

Stratigraphic range—Lower Cretaceous (Aptian) to Holocene.

MACTRIDAE Lamarck, 1809

Pacific Coast mactrids have been variously treated under genus-group names that include *Mactra* Linnaeus, 1767; *Hemimactra* Swainson, 1840; *Mactromeris* Conrad, 1868; *Mulinea* J.E. Gray, 1837; *Pseudocardium* Gabb, 1866; *Simomactra* Dall, 1894; *Spisula* J.E. Gray, 1847 and *Teresus* J.E. Gray, 1853. A checklist of California Tertiary marine mollusks includes 50 entries under *Spisula* (Keen and Bentson 1944), although classification of the fossil species requires considerable revision based on reassessment of the living Northeastern Pacific taxa (Coan et al. 2000).

Fewer fossil species are reported from the Pacific Northwest, although large, heavy-shelled species are an abundant element in shallow facies of the latest Eocene and Oligocene. For example, *Mactromeris eugenensis* (Clark, 1925) is the most frequent and abundant bivalve in the Eugene Formation (Hickman 1969) along with smaller populations of *M. pittsburgensis* (Clark, 1925) and a large, undescribed species of *Pseudocardium*. *Mactromeris pittsburgensis* is abundant at many localities in the Pittsburg Bluff Formation (Moore 1976) and also occurs in the Alsea, Blakeley, and Tunnel Point formations in Oregon, the Lincoln Creek Formation and Quimper Sandstone in Washington, and the Poul Creek and Yakataga formations in Alaska. These Paleogene taxa are part of the cool-water fauna that replaced the tropical Eocene fauna during the Eocene-Oligocene transition (Hickman 2003).

Literature references for the extant northern mactrids are given by Coan et al. (2000) and for the extant Panamic species by Coan and Valentich-Scott (2012). An important and well-illustrated paper on Mesozoic and Cenozoic mactrids of the Northeastern Pacific (Packard 1916) continues to be useful for species identification. Most of the 38 species treated are from the Neogene, with three from the Cretaceous (Chico Formation), five from the Eocene and two from the

Oligocene. Taxonomic treatments of the Neogene mactrids (e.g., Grant and Gale 1931, Hertlein and Grant 1972) are generally useful for species discrimination but do not contribute to a satisfying higher level supraspecific classification or historical perspective on warm- and cold-water taxa. Cenozoic mactrids from California and Baja California were reviewed by Moore (2002) and include both warm- and cold-water taxa. Saul (1991) was perceptive in using hinge features to distinguishing six supraspecific Pacific Coast taxa and in her rejection of the presence of both *Spisula* and *Mactra* in the Northeastern Pacific.

The least well-known mactrids in the temperate fauna are the smaller- and thinner-shelled species of *Simomactra* that may occur abundantly in finer sediment and extend well below the surf zone. It is not clear when or where they originated, and the occurrence of a single shell in the Keasey Formation is therefore of special interest.

Stratigraphic range—Lower Cretaceous (Aptian) to Holocene.

SIMOMACTRA Dall, 1894

Type species—by monotypy, *Mactra dolabriformis* Conrad, 1867. Holocene, Panamic Province, tropical Eastern Pacific.

This Eastern Pacific genus includes three species with shells that are smaller, thinner, and less inflated than those of the surfclams and gapers. They have a fragile but distinctive hinge structure that includes three cardinal teeth in each valve, the posterior two forming a inverted "V" flanked by transversely elongate lateral teeth with very fine pustules on the dorsal surface. The pustulose surface (Fig. 16B) readily distinguishes the lateral teeth from the transversely ridged-and-grooved surfaces of the lateral teeth of *Spisula* (Fig. 16A).

Stratigraphic range—upper Eocene–Holocene. This is the first unequivocal report of *Simomactra* from the Paleogene. It has been reported in species lists from the Eocene of the Gulf Coast (e.g., Dockery and Lozouet 2003) as *Simomactra praetenuis* (Conrad, 1833). This species was described originally under *Mactra* and treated subsequently under *Spisula* (e.g., Harris 1919, Palmer and Brann 1965). It is not clear that anyone except Moore (1962) ever examined Conrad's material, which she noted as "3 probable syntypes" labeled by Conrad. The hinge has not been described or figured, and confident allocation to *Simomactra* is therefore not possible.

Simomactra n. sp.
Fig. 17A, B

Discussion—A single left valve partially imbedded in matrix (Fig. 17B) was prepared to reveal a distinctive mactrid
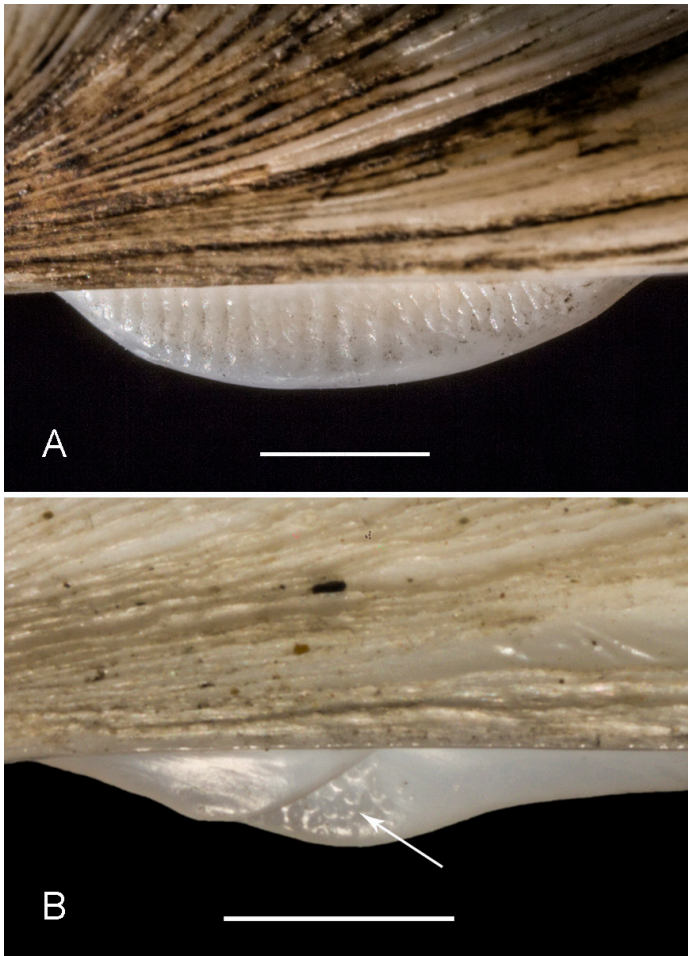
Fig. 16A–B. Mactrid micro-ornament on dorsal surface of lateral tooth. **A**. *Spisula solida* Linnaeus, 1758, UCMP RC144, with fine longitudinal ridges and grooves, scale bar = 2 mm. **B**. *Simomactra falcata* (A.A. Gould, 1850), UCMP RC2498, with fine pustules (arrow), scale bar = 1 mm.

hinge (Fig. 17A). The chondrophore does not project ventrally beyond the base of the hinge plate, and the anterior cardinal, although broken, is bifid and partially fused. The transversely elongate anterior lateral tooth partially disintegrated during additional preparation following initial photographic documentation, but the dorsal surface of the remaining fragment of the tooth preserves a finely-granular surface. The subtrigonal shell is nearly equilateral, with a rounded, slightly longer and more tapered anterior margin and a more broadly rounded posterior margin and dorsal slope set off by a shallow sulcus. The anterior dorsal margin is partially broken but the fine co-marginal growth increments on the shell indicate that it is shallowly concave.

A new name is not proposed at this time in view of the fragmentary nature of the specimen, but the details provided here will aid in recognizing material that might otherwise be overlooked in the field.

The Keasey shell is similar in outline to a shell illustrated by Schenck and Keen (1940, pl. 44, figs. 3, 4). It was originally described from the upper Miocene Briones Formation in California as *Spisula falcata brioniana* by Trask (1922). *Mactra falcata* A.A. Gould, 1851 is the type species of *Symmorphomactra* Dall, 1894, here considered a synonym of *Simomactra*.

Figured specimen—UCMP 110713.

Keasey Formation Locality—Upper portion of the middle member, Loc. UCMP IP7984 (=USGS 25031).

VENEROIDEA Rafinesque, 1815
VENERIDAE Rafinesque, 1815
PITARINAE Stewart, 1930

Stratigraphic range—Cretaceous–Holocene.

Pitarine bivalves, and venerids (the "Venus" clams) in general, are not common in deep-water molluscan communities, although they are both frequent and abundant in shallow and relatively warm-water faunas of the Eastern Pacific. Pitarines undergo a post-Eocene expansion in the Northeastern Pacific and are a conspicuous element in higher latitude faunas
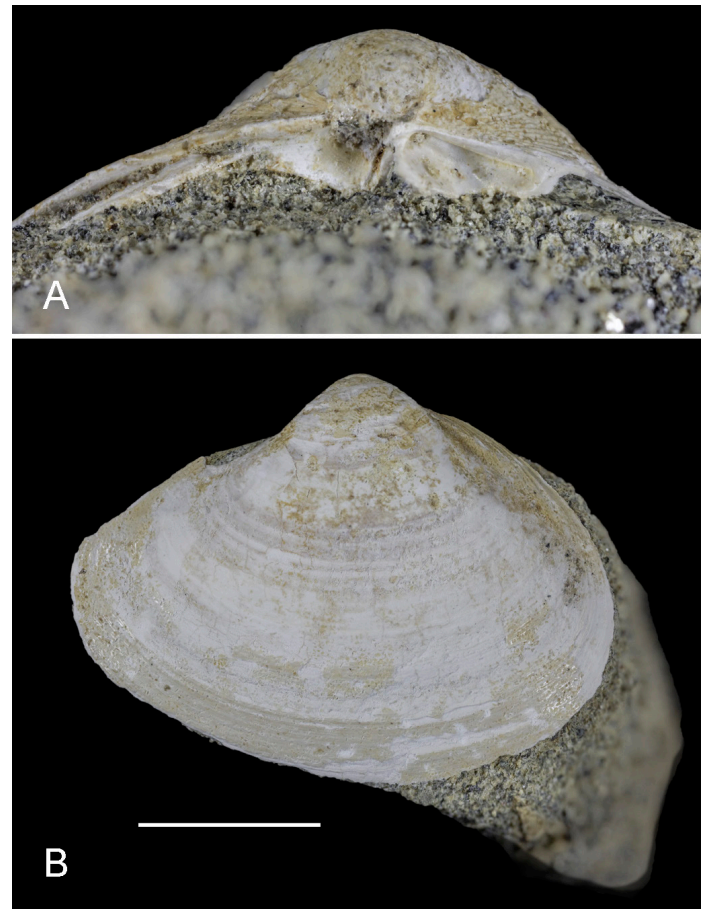

Figure 17A–B. *Simomactra* n. sp., UCMP 110713, Loc. UCMP IP7984. **A**. Detail of fragmentary hinge plate of left valve, **B**. Exterior of left valve. Scale bar = 5 mm.

from the Oligocene onward. The Pacific coast Eocene species have been treated primarily under *Pitar* Römer, 1857 or *Pitaria* Dall, 1902. The latter name was proposed as an emendation by Dall, who considered *Pitar* a vernacular name even though it was proposed with a Latin diagnosis. Stewart (1930, pp. 232–233) provides a lively account of the controversy in which authors attempted, unsuccessfully, to suppress "Pitar" as a "barbarism". The genus is represented in the living Northeastern Pacific fauna by a single species that is reported from as deep as 220 m (Coan et al. 2000). *Lamelliconcha* Dall, 1902 has been used for species with strong commarginal sculpture, but lacking the posterior spines of *Hysteroconcha* Dall, 1902.

LAMELLICONCHA Dall, 1902

Type species—By original designation, *Cytherea concinna* G.B. Sowerby I, 1835. Holocene, tropical Eastern Pacific.

Prominent commarginal sculpture distinguishes Eocene pitarines of the genus *Lameilliconcha* from those with smooth shells that are more appropriately placed in *Pitar* s.s. *Pitar dalli* Weaver, 1916 and *Lamelliconcha clarki* (Dickerson, 1917) co-occur abundantly in several Paleogene faunas, and detailed characterization an comparative illustrations provide consistent criteria for distinguishing the two (Hickman 1969).

Lamelliconcha clarki (Dickerson, 1917)
Fig. 18A–C

Pitaria clarki Dickerson, 1917, p. 169, pl. 28, figs. 4a, 4b, 4c.
Pitaria clarki Dickerson, Van Winkle 1918. p. 75
Pitaria (Lamelliconcha) clarki Dickerson, Tegland 1929. p. 279, pl. 22, figs. 1–4.
Pitar (Lamelliconcha) clarki (Dickerson), Clark and Anderson 1938, p. 947, pl. 2, figs. 1–4.
Pitar (Lamelliconcha) clarki (Dickerson), Effinger 1938, p. 371.
Pitar (Lamelliconcha) clarki (Dickerson), Weaver 1942, pl. 42, figs. 1–9.
Pitar (Lamelliconcha) clarki (Dickerson), Keen and Bentson 1944, p. 100.
Pitar (Lamelliconcha) clarki (Dickerson), Durham 1944, pp. 115, 117, 119, 129, 149.
Pitar clarki (Dickerson), Vokes in Warren et al. 1945. Checklist
Pitar (Lamelliconcha) clarki (Dickerson), Moore and Vokes 1953, pp. 115, 119.
Pitar (Lamelliconcha) clarki (Dickerson), Hickman 1969. pp. 47, 50. Pl. 4, figs. 1–4.
Pitar (Lamelliconcha) clarki (Dickerson), Armentrout 1973. pp. 437–438, figs. 1–3.

Pitar (Lamelliconcha) clarki (Dickerson), Moore 1976, p. 28.

Discussion—This species is rare in the type area of the Keasey Formation, although it has been collected at seven different localities. All the specimens are incomplete and poorly preserved, but they retain original shell material with the commarginal sculpture characteristic of *Lamelliconcha*. Specimens are abundant in a shallower Keasey (?) facies farther south in the Salem area at Looney Butte. One of 19 double-valved specimens collected by Parke Snavely and Harold Vokes at Looney Butte is illustrated here (Fig. 18B). All of the Looney Butte specimens are articulated, but they are taphonomically compressed and distorted. The species was described from the partially coeval Gries Ranch Beds in southwestern Washington, and Dickerson's (1917) original illustrations of both the shell exterior and the hinge features provide good detail. An enlargement of the right hinge of a Gries Ranch specimen collected subsequently by the author is illustrated here (Fig. 18C) to call attention to the robust, anterior lateral tooth, which is perpendicular to the cardinal teeth and situated near the umbones.

Additional supplemental description of this species, is based on 62 specimens from the Eugene Formation (Hickman 1969), although considerable variation in shell shape (some of it an artifact of preservation) leads to difficulty identifying specimens that are distorted or preserved only as internal molds.

Material examined—Eleven specimens from the type area.

Type information—Hypotypes UCMP 110710, length 29.9 mm, height (incomplete) 18.9 mm, Loc. UCMP IP7984 (middle member); UCMP 110711, length (incomplete) 43.6 mm, height (incomplete) 41.3 mm, Loc. UCMP IP2289 (Gries Ranch Beds); UCMP 110712 (fragment with right hinge teeth), UCMP IP25709 (Unnamed Keasey-equivalent beds at Looney Butte).

Keasey Formation localities—USGS 15263, 15265 (lower member); USGS 15267, 15274, 15284, 15285, 15508, UCMP IP7984 (=USGS 25031) (middle member).

Keasey-equivalent localities—UCMP IP2289 (Gries Ranch Beds); UCMP IP25709 (Looney Butte);

Occurrence elsewhere—In Oregon this species occurs stratigraphically higher in the overlying Pittsburg Bluff Formation, although not at the type locality and not reported by Moore (1976), the Eugene Formation (Hickman 1969), and younger un-named beds near Clatskanie, Oregon (personal observation). In Washington it occurs in Keasey-equivalent strata in the Lincoln Creek Formation (Armentrout 1973) and in the Quimper Sandstone on the Olympic Peninsula (Durham 1944). Referral by Weaver (1942 pp. 184, 636) of
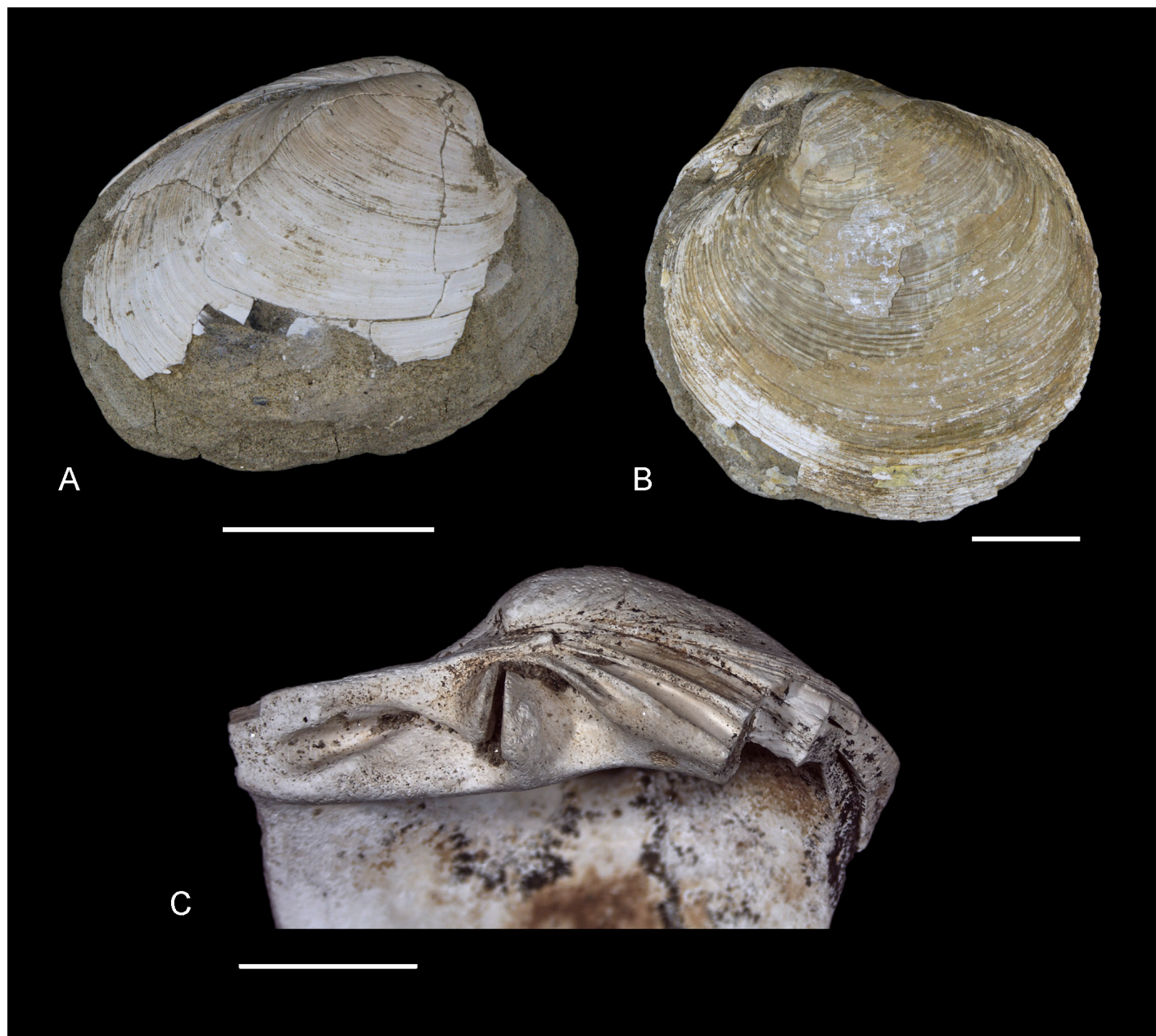
Figure 18A–C. *Lamelliconcha clarki* (Dickerson, 1917). **A.** Hypotype, UCMP 110710, Loc. UCMP IP7984, Keasey Formation, right valve view, scale bar = 1 cm. **B.** Hypotype, UCMP 110711, Loc. UCMP IP2289, Looney Butte beds, left valve view, scale bar = 1 cm. **C.** Hypotype, UCMP 110712, Loc. UCMP IP25709, Gries Ranch beds, right hinge plate, scale bar = 5 mm.

L. clarki to the older Eocene Cowlitz Formation fauna in Washington is in error. In California, the species is present on the eastern margin of the Sacramento Valley in the Wheatland Formation, which is similar to the Keasey in its tuffaceous character. Suggestion of a possible late Eocene age for the Wheatland by Clark and Anderson (1938) was discounted by Almgren and Schlax (1957), who presented evidence that it is part of the post-Eocene feature known as the "Markley Gorge" fill.

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