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Paleogene marine bivalves of the deep-water Keasey Formation in Oregon, part IV: The anomalodesmatans

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Documentation of the Keasey bivalve fauna would not have been possible without the encouragement of the late Harold Vokes, who generously turned over the specimens and considerable research effort he originally invested in anticipation of publishing monographic treatments of mollusks of the Keasey Formation. For collecting assistance in the field, I am grateful to James C. Hickman and to the following undergraduate students from the 1979 invertebrate paleontology class at the University of Oregon: Janet Baldridge, Les Boyer, Scott Larson, Greg Miles, Gordy Miller, Diane Searcy, Gary Smith, and Barbara Zeller. Digital photography of specimens illustrated in color is the work of UCMP photographer and Associate Dave Strauss, and the exceptional quality of his morphological documentation of specimens is the most important single contribution to this monographic treatment. Micrographs of very small transparent shells were recorded digitally with the Hitachi S-r800 Field Emission Scanning Electron Microscope at the Biological Scanning Electron Microscope Facility of the University of Hawaii with advice and assistance from Tina Weatherby Carvalho. I am especially grateful to Casey Burns for contributing specimens from several important localities in the uppermost portion of the middle member of the formation. Other colleagues who collected and donated specimens now in the University of California Museum of Paleontology collections include Ellen Moore, Elizabeth Nesbitt, and David Taylor and Bruce Welton. Communications with Alan Niem have been helpful in understanding stratigraphic relationships in the Paleogene of northwestern Oregon. Curators, collection managers, and colleagues at the following institutions provided access to collections and/or assistance with loans: Burke Museum of Natural History and Culture (University of Washington), California Academy of Sciences, Natural History Museum of Los Angeles County, Oregon Museum of Science and Industry, Stanford University collections now housed at the California Academy of Sciences, University of Oregon Museum of Natural and Cultural History (Condon Collection), US National Museum of Natural History (Smithsonian Institution). I appreciate the helpful suggestions of reviewers Elizabeth Harper, Robert Prezant and Paul

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Abstract:

The late Eocene–early Oligocene Keasey Formation in Northwestern Oregon contains a unique fauna of deep-water (>200 m) marine bivalves preserved in sparsely fossiliferous massive tuffaceous siltstone as well as in several distinctive cold-seep limestone bodies and carbonate layers. The Keasey gastropod fauna has been described previously, but this treatment of the anomalodesmatan bivalves is the first systematic account for any portion of the bivalve fauna. Cenozoic evolutionary radiation and history of anomalodesmatans is less well known than their deep Paleozoic and Mesozoic history. Because internal relationships are not well resolved, ranked classification is not used above the family level, while recognizing that these rare and unusual bivalves do represent a monophyletic assemblage nested within the basal heterodonts. Six species in four anomalodesmatan families in the Keasey Formation shed new light on the Cenozoic history of the group as well as the Eocene appearance of precursors of the living deep-water fauna of the northeastern Pacific. The families represented are Pandoridae, Thraciidae, Periplomatidae, and Cuspidariidae. The new species are *Pandora eocapsella*, *Thracia keaseyensis*, *Cardiomya anaticepsella*, and *Cardiomya pavascotti*. *Aperiploma?* n. sp. is described in open nomenclature pending discovery of additional and more complete material. Although shells are frequently crushed and the exterior shell layers are often poorly preserved, the interior nacre is distinctive, well-preserved and useful for recognizing fragments in the field. Characteristic anomalodesmatan granules are well preserved on many specimens of the new thraciid, and the fine-grained matrix at some localities preserves shell features on external molds where no original shell material remains. High-resolution images of uncoated shell encourage greater attention to collection of fragments and imperfect specimens in the fine-grained deep-water facies on the active margin of the Pacific.

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Paleogene marine bivalves of the deep-water Keasey Formation in Oregon, part IV: The anomalodesmatans

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The late Eocene–early Oligocene Keasey Formation in Northwestern Oregon contains a unique fauna of deep-water (>200 m) marine bivalves preserved in sparsely fossiliferous massive tuffaceous siltstone as well as in several distinctive cold-seep limestone bodies and carbonate layers. The Keasey gastropod fauna has been described previously, but this treatment of the anomalodesmatan bivalves is the first systematic account for any portion of the bivalve fauna. Cenozoic evolutionary radiation and history of anomalodesmatans is less well known than their deep Paleozoic and Mesozoic history. Because internal relationships are not well resolved, ranked classification is not used above the family level, while recognizing that these rare and unusual bivalves do represent a monophyletic assemblage nested within the basal heterodonts. Six species in four anomalodesmatan families in the Keasey Formation shed new light on the Cenozoic history of the group as well as the Eocene appearance of precursors of the living deep-water fauna of the northeastern Pacific. The families represented are Pandoridae, Thraciidae, Periplomatidae, and Cuspidariidae. The new species are *Pandora eocapsella*, *Thracia keaseyensis*, *Cardiomya anaticepsella,* and *Cardiomya pavascotti*. *Aperiploma?* n. sp. is described in open nomenclature pending discovery of additional and more complete material. Although shells are frequently crushed and the exterior shell layers are often poorly preserved, the interior nacre is distinctive, well-preserved and useful for recognizing fragments in the field. Characteristic anomalodesmatan granules are well preserved on many specimens of the new thraciid, and the fine-grained matrix at some localities preserves shell features on external molds where no original shell material remains. High-resolution images of uncoated shell encourage greater attention to collection of fragments and imperfect specimens in the fine-grained deep-water facies on the active margin of the Pacific.

Keywords: Eocene, Oligocene, bathyal, nacre, biomineralization, active margin

INTRODUCTION

Of the four traditional major groupings of marine bivalves the anomalodesmatans, including those referred to as "septibranchs," are the least well known from the Cenozoic fossil record of the Eastern Pacific. The record of deep-water bivalves in tuffaceous siltstone beds of the late Eocene–early Oligocene Keasey Formation in Oregon is exceptional in its representation of six species in four anomalodesmatan families. Only one of the species is previously described. This is the first of four systematic treatments of the Keasey bivalve fauna. Although the anomalodesmatans would normally be the last group described in a traditional hard-copy taxonomic monograph, this presentation recognizes the new flexibility with which taxonomic data can be assembled and configured in an age of digital monography that should not be constrained by traditional taxonomic ordering. The four traditional bivalve "subclasses" Protobranchia Pelseneer, 1889, Pteriomorphia Beurlen, 1944, Heterodonta Neumayr, 1884, and Anomalodesmata, Dall, 1889 have been replaced by six major monophyletic lineages (Bieler et al. 2014). The Keasey bivalve monograph begins with the anomalodesmatan clade in part because less is known about both the living and fossil Cenozoic representatives. It will be followed by separate treatments of the protobranchs, pteriomorphs, and two clades of former heterodonts, the Archiheterodonta Giribet (Taylor et al. 2007) and Imparidentia Bieler et al., 2014.

Traditional classifications consistently recognize anomalodesmatans as a subclass of bivalves with deep origins (Early Ordovician), an abundant Paleozoic and Mesozoic fossil record, and a relatively poor record of Cenozoic evolutionary radiation. Life habit is reflected in an extraordinary diversity and disparity of conchological and anatomical features. Internal relationships of family groups are not resolved, in spite of modern attempts at both morphological and molecular phylogenies (Campbell et al. 1998, Harper et al. 2000, 2006, Giribet and Wheeler

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2002, Dreyer et al. 2003). Although the constituent taxa are under-sampled in molecular studies, they repeatedly emerge as a robustly supported monophyletic group nested within the heterodonts (Giribet and Wheeler 2002, Giribet and Distel 2003, Dreyer et al. 2003, Harper et al. 2006, Taylor et al. 2007). With the addition of new morphological characters, the most recent analysis (Bieler et al. 2014) increases internal resolution while recognizing the need for denser family-level sampling. Many of the living species are rare, occur in cold, deep water or in spatially-restricted habitats, and appear to have narrow geographic ranges. In contrast, Paleozoic and Mesozoic anamalodesmatans were more common and widespread in tropical shallow-water environments.

Anomalodesmatans have been characterized as "the rarest living bivalves—those without common names" (Runnegar 1974, p. 904), as "the most obscure subclass in the Bivalvia" (Yonge and Morton 1980, p. 284), as "some of the strangest and most specialised bivalves" (Prezant 1998, p. 397) and as a group with systematic relationships that have been "notoriously problematic to resolve" (Bieler and Mikkelsen 2006, p. 226). The constituent taxa have been "variously modified so as superficially to appear unrelated" (Morton 1977, p. 152). In spite of representing the culmination of bivalve evolution in terms of alternative inventions to circumvent their primitive limitations, they are seen as having "largely failed in competition with more 'generalist' bivalves" (Morton 1981, p. 35) and as being "very far from the peak of success" (Yonge and Morton 1980, p. 290).

It is therefore unfortunate that so many accounts of anomalodesmatans emphasize rarity in the modern fauna and exclude the fossil record. Treatments of nomenclaturally valid and available family-group names (Newell et al. 1969, Bouchet and Rocroi 2010) include 16 extinct families: 11 restricted to the Paleozoic, four to the Mesozoic and one to the Cenozoic (Miocene). There is considerable generic diversity and species diversity in some of the extinct families. Vokes (1967) lists 47 available genus-group names based on fossil species, and the systematic section in the Treatise on Invertebrate Paleontology (Newell et al. 1969) lists 80. Nine of the 15 extant families have origins in the Paleozoic or Mesozoic, and four have Paleogene origins.

One of the most striking features of the Keasey bivalve fauna is the high proportion of anomalodesmatans. The proportion also is high in modern deep-water faunas, and Hickman (1984) used this observation to develop a taxonomic structure method of bathymetric analysis free of the anti-evolutionary assumptions of inferring depth in fossil faunas from depth ranges of presumably equivalent living species. Cenozoic onset of subduction of the Farallon Plate beneath Washington and Oregon created deep-water basins along the Cascadia margin where interesting details of anomalodesmatan history are preserved in tuffaceous fine-grained sedimentary sequences (Hickman 2003).

The prismato-nacreous shell structure of many anomalodesmatans aids considerably in recognizing crushed and physically distorted fossil shells. In the fine-grained deep-water facies of the Pacific Coast Cenozoic, shells retain the interior nacreous layers even when the thin exterior layer of prismatic or homogeneous aragonite is wholly or partially exfoliated. Crushed specimens may retain a sufficient amount of the exterior layer to preserve a form of anomalodesmatan micro-ornament referred to alternatively as granules, spinules or spikes. Interest in these calcified elements in anomalodesmatans is intensified by recognition that they may form within the periostracum rather than in contact with the mantle epithelium and that homology is not easily determined (Checa and Harper 2010, Checa et al. 2012). As exceptions to the traditional model of shell calcification, some of these structures are more closely allied to an interesting but heterogeneous class of fabricational features resulting from remote biomineralization (Hickman 2013). Although comparative shell ultrastructure of the Keasey anomalodesmatans is beyond the scope of this treatment, remnant microstructure from Paleogene species could provide valuable historical perspective on anomalodesmatan calcification.

The six species in four anomalodesmatan families in the Keasey fauna establish a clearer picture of the temporal distribution of this group in the Cenozoic, and the Eocene appearance of precursors of the modern deep-water fauna of the northeastern Pacific. The families are not treated here in a formal classification, recognizing that anomalodesmatan internal relationships are unresolved in both morphological and molecular analyses.

KEASEY FORMATION BACKGROUND

Geographic location and stratigraphy

The setting of the Keasey Formation in the Nehalem River basin, on the east side of the Coast Range in northwestern Oregon, is well documented and includes maps of outcrop area and geology, including many fossil localities (e.g., Warren et al. 1945, Warren and Norbisrath 1946, Moore and Vokes 1953, Hickman 1969, 1976, 2003, Niem et al. 1994, Burns et al. 2005). Previous monographic work on the molluscan fauna includes a stratigraphic section for the three informal members (lower, middle and upper) of the formation and plots the stratigraphic distributions of more than 65 gastropod species (Hickman 1976, 2003). The thickness of the formation is approximately 7,000 m in the type area, but exposures are limited by dense vegetation and are primarily in roadcuts, stream beds and banks, an abandoned railroad grade and two abandoned quarries (Smithwick-Haydite, and Empire Lite Rock). Fresh exposures on new logging roads have yielded important material, but such exposures overgrow and rapidly disappear. The type section of the formation consists of a series of discontinuous outcrops of only the basal several hundred meters of the formation, although the molluscan fauna is highly distinctive.

Characterizations of the lithology have emphasized the tuffaceous nature of the clayey mudstone and massive siltstone facies, the paucity of fossils, and the number of similar near-shore massive fine-grained sequences in other Paleogene formations in the Pacific Northwest (e.g., **Hickman 1976**, **2003**).

The Keasey Formation lies unconformably on deep-water mudstone strata of the upper member (informal) of the Cowlitz Formation, which also was deposited early in the evolution of the active Cascadia margin but preceding the first appearance of distinctive cryophilic taxa. The Keasey is overlain by fine-grained transgressive, westward-prograding sandstones of the shallower and more richly fossiliferous Pittsburg Bluff Formation (**Moore 1976**). Very few species are common to both the Keasey and Pittsburg Bluff Formations (**Hickman 2003**). **Moore (1976)** provides an excellent annotated chronology of reports and interepretations of the Keasey and Pittsburg Bluff faunas between 1892–1975.

Depositional and tectonic setting

The earliest plate tectonic model described the Keasey Formation as an arc-trench gap sequence (**Hickman 1976**, p. 16–17) deposited adjacent to a young magmatic arc, a scenario supported by evidence for subsequent Paleogene and Neogene (westward) migration of the inferred trench and retrograde (eastward) migration of the volcanic arc to its current position. A large subsequent literature provides rigorous characterization of the sedimentary, volcanic, and tectonic framework for development of the forearc basins of the Pacific Northwest (**Niem et al. 1994**). Paleomagnetic data for the Keasey Formation indicate significant clockwise tectonic rotation, a recurring deformational feature of late Paleogene and Neogene formations in the Pacific Northwest that has been attributed to oblique subduction of the Juan de Fuca plate along the Cascadia Margin (**England and Wells 1991**).

Paleobathymetry and paleoecology

Paleontological evidence of bathyal depths for the Keasey Formation was established through analysis of the taxonomic structure of the mollusk fauna (**Hickman 1976**, **2003**), recognizing the same proportion of higher taxonomic groups and trophic groups that predominate in modern deep-water faunas. Six deep-water communities make their first appearance in the Pacific Northwest and were described primarily from the Keasey Formation (**Hickman 1976**). Four are bivalve-dominated: *Protobranch Communities, Mud Pecten Communities, Acesta Communities,* and *Thyasira-Lucinoma-Solemya Communities*.

The most striking paleoecological feature of the Keasey fauna is the combination of faunal and geologic evidence for chemosymbiosis and association of chemosymbiotic mollusks with cold-seep carbonate deposits (**Campbell and Bottjer 1993**, **Nesbitt et al. 1994**, **Niem et al. 1994**). Solemyid and thyasirid bivalves occur in direct association with autochthonous seep carbonate pods and lens-shaped bodies as well as in associations with carbonates that have been more difficult to interpret.

The most intensively-studied and enigmatic carbonate-associated fossil assemblage is the famous Crinoid Lagerstätte at Mist, Oregon. Here there is geochemical (isotopic) evidence that carbonates formed in a zone of archaeal methanogenesis (**Burns et al. 2005**). Although the isotopic evidence does not exclude the possibility of fluid migration during diagenesis, the shallow infaunal bivalves are indicative of low oxygen conditions. Two of the new anomalodesmatan species described in this paper are from the Mist locality.

Age and correlation

There is a long history of debate over the age of the Keasey Formation, its assignment in chronostratigraphic and biostratigraphic classifications, and the position of the Eocene-Oligocene boundary in marine Paleogene rocks of western North America (see **Hickman 1976** for a review). Although there are no absolute dates, paleomagnetic data (**Prothero and Hankins 2000**) are consistent with previous molluscan faunal estimates that it is late Eocene–early Oligocene, with the boundary situated near the top of the middle member but below the two most important and well-exposed outcrops in abandoned quarries near the top of the middle member.

It has not been possible to tie the magnetic chronology to absolute dates and the global time scale. Although the tuffaceous siltstones of the Keasey Formation contain thin ash layers and pumice clasts, the material is altered and not of adequate quality for $^{40}Ar/^{39}Ar$ dating (Paul Renne, personal communication 2014).

Record of the greenhouse-icehouse transition

The Keasey Formation records one of the major oceanic cooling events in Earth history. The marine record of this event was the subject of a Penrose Conference (Prothero 2003) exploring the relationship of taxonomic turnover to the negative oxygen and positive carbon isotopic excursions at 33.5 Ma. The transition from tropical Eocene marine faunas to cold-water Oligocene faunas has been recognized in the Northeastern Pacific for more than 100 years, although the timing of the transition has never been clear. Early studies of the Keasey molluscan fauna reported an abrupt crash in species diversity, although it is now clear that the change was an almost complete faunal turnover with only a small drop in diversity (Hickman 2003). The role of tectonic events on the Cascadia margin, development of deep near-shore basins, geochemically extreme settings, and heightened faunal exchange with Asia may be as important as global cooling in explaining the turnover fauna of the Keasey Formation.

PROJECT HISTORY, MATERIALS, AND METHODS

Specimen collection and chronology

The specimens in this study represent two major collecting efforts in the Keasey Formation: those of the late Harold E. Vokes and colleagues with the U.S. Geological Survey in the 1940s and '50s and subsequent field work by the author in the 1960s and '70s. These efforts have been augmented by contributions from colleagues, students and avocational paleontologists who have been attracted by the evidence for a global cooling event and major faunal turnover (Hickman 2003) and especially by recognition of chemosymbiotic bivalve associations and ancient cold seeps (Campbell and Bottjer 1993, Nesbitt et al. 1994, Campbell 1995).

United States Geological Survey (USGS) locality numbers were assigned to material from the two major collecting efforts, and equivalence between localities established where possible. General collections and type specimens are deposited either at the U.S. National Museum of Natural History (USNM) or in the University of California Museum of Paleontology (UCMP). In 1997 the USGS and Regents of the University of California negotiated legal transfer of all west coast collections in Menlo Park to the UCMP. Original USGS locality descriptions for specimens in the report can be obtained from the UCMP online database.

Many of the outcrops from the two major collecting efforts are overgrown and have disappeared, especially smaller exposures on logging roads. However, some of the most important classic localities in quarries, bluffs on the Nehalem River and Rock Creek, and several railroad and highway cuts have been revisited many times and are still accessible.

The most famous Keasey locality is the crinoid Lagerstätte in bluffs on the Nehalem River immediately south of the town of Mist, Oregon. Well-preserved crinoids, corals and echinoids occur in association with an undescribed molluscan assemblage (Warren et al.1945, Moore and Vokes 1953). Although the site was treated as a single fossil locality, detailed examination of the stratigraphy resulted in designation of seven informal units and documentation of their lateral and vertical extent (Burns et al. 2005). It is now possible to confirm from lithology that one of the anomalodesmatan species described in this report is from the main crinoid layer and a second, collected by Casey Burns, is from the distinctive, resistant upper calcareous layer (UCL).

The carbonates at Mist have attracted special interest because of multiple lines of evidence consistent with methane seepage and an environment conducive to chemosynthetic fixation of carbon (Burns et al. 2005).

Systematic treatment has proceeded over a similarly long period. Harold Vokes generously contributed the Keasey mollusks in his care, resulting first in monographic documentation of the Keasey gastropod fauna (Hickman 1976, 1980) followed by designation of six novel deep-water molluscan communities (Hickman 1984) and recognition of a major marine cooling event, abrupt faunal turnover, and geologic onset of subduction along the Cascadia Margin in Washington and Oregon (Hickman 2003). Preliminary efforts by Vokes and Hickman on the bivalves were never completed, although Smithsonian type numbers, preliminary manuscript names and identifications were assigned and photographic plates were prepared.

Specimen preparation

Field efforts by the author concentrated on collecting specimens in matrix and careful preparation of fragile material under a dissecting microscope using fine flexible needles, sable brushes and water only if the specimen was sufficiently well preserved. Crushed, cracked, and partial specimens received conservative treatment rather than risk destruction of significant features. For some localities, many individuals were inevitably broken in the process of manually breaking matrix apart, but fragments of shell and matrix were retained in anticipation that they might be useful in other research applications.

Photography and image processing

An early set of more than 100 photographs was produced in black and white from ammonium chloride-coated specimens mounted on a light box. Using the white background technique (Sakamoto 1970) negatives were re-exposed in a darkened room to burn in the background so that images could be printed on a white background without trimming with scissors or applying opaque medium to negatives. Many of the images originally recorded on film have been scanned for inclusion as figures. Several important specimens preserved as negative molds in fine-grained rock benefited from preparation of positive black latex impressions that were coated for photography.

Images of specimens from the later collecting efforts were prepared by UCMP photographer Dave Strauss using a Canon 5D Mark III digital camera, and either a Canon MP-E 65mm f/2.8 Macro lens or a Canon EF 100mm f/2.8L IS USM Macro lens. For most specimens, multiple images were recorded in a sequence of focal planes and 'focus-stacked' using Helicon Focus software to achieve necessary depth-of-field. Final images were adjusted using Adobe Camera Raw 8.6 within Photoshop CC in order to match image color to the actual specimen and to enhance contrast. Such adjustments were parametric (i.e., applied to the whole image). In no instance were features or details changed, moved, removed, obscured or introduced. Interpretation of features such as cracks, pitting, staining, adhering sedimentary grains, and exfoliation of shell layers are included in the text, but image data are available and open to reinterpretation by the reader. The original high-resolution images will be available through the UCMP online database and viewable using the "Zoom" option.

Conventions in taxonomy and systematics

Because internal relationships of anomalodesmatans are not well resolved, superfamily names are assigned only where there is strong support for monophyly, and informal names are employed for clades where uncertainty has been expressed in recent bivalve classifications (e.g., Bouchet and Rocroi 2010).

For new species, a diagnosis contains key distinguishing features followed by a description indicating any other noteworthy features. Noteworthy features of previously-described species are presented in the discussion, which is focused on making comparisons and distinctions from similar species. Measurements of length and height to the nearest 0.1 mm are given under type information for all figured types. In figure captions, the length is specified instead of a scale bar, both as a more informative measure and to avoid visual distraction from the images. Description of "material examined" includes *frequency* (occurrence at few or many localities) and *abundance* (occurrence as many or few specimens at a given locality) and range is given with respect to the three informal members of the Keasey Formation, following Hickman (1980). For each species, locality numbers are given by member. For all illustrated specimens, specimen number and locality number are given in the figure caption.

Author and date are provided for all taxa at first mention in the text, and full citations are included in the Literature Cited. Author and date are separated by a comma (in contrast to literature citations), as per Article 51 of the International Code of Zoological Nomenclature (1999) and the Official Lists and Indices (International Commission on Zoological Nomenclature 1987).

Synonymies are brief and focused on providing references to specific pages and figures within works. Full references to each work are provided in the Literature Cited.

SYSTEMATIC PALEONTOLOGY

EUHETERODONTA Giribet, 2008
ANOMALODESMATA Dall, 1889
(=PHOLADOMYOIDA Newell, 1965 +
SEPTIBRANCHIA Pelseneer, 1889)
PANDOROIDEA Rafinesque, 1815
PANDORIDAE Rafinesque, 1815

Pandorids are a neglected element in modern regional faunas, although documentation of their diversity in the Eastern Pacific (Coan et al. 2000, Valentich-Scott and Skoglund 2010, Coan and Valentich-Scott 2012) indicates a need for renewed global efforts. Taxonomy of living species is confused (Boss and Merrill 1965, Prezant 1998), although there are elegant studies of the behavior, unusual shell morphology and anatomy of shallow-water living species (Allen 1954, Allen and Allen 1955, Morton 1984, Thomas 1994). However, the literature contains misconceptions regarding bathymetyric and latitudinal distribution. The generalization that all species inhabit "sheltered sandy areas around extreme low tide levels" (Yonge and Morton 1980) and that the family is primarily a high-latitude cold-water group (Boss and Merrill 1965) are incorrect.

Misconceptions about bathymetyric range seem to originate with the classic studies of living animals of *Pandora inequivalvis* (Linnaeus, 1758) and *P. pinna* (Montagu, 1803) from low water in the Mediterranean (Allen 1954) and *P. filosa* (Carpenter, 1864) and *P. grandis* Dall, 1877 from low tide levels at the Friday Harbor Laboratories, Washington (Yonge and Morton 1980). However, subsequent studies of *P. filosa* at a lower latitude in Monterey Bay, California (Thomas 1994) were from live-collected specimens trawled between 55 and 80 m. The genus ranges from intertidal to abyssal depths

(Valentich-Scott and Skoglund 2010).

The high latitude generalization does not apply to the fauna of the Eastern Pacific. A recent treatment of six pandorid genera and 16 species in the Panamic Province (Valentich-Scott and Skoglund 2010) shows greater tropical diversity than the fauna of the northeastern Pacific, with only five species (Coan et al. 2000).

Regarding the fossil record of the group, pandorids are generally rare and poorly preserved (Prezant 1998). Although they are never abundant, their rarity in museum collections may result in part from failure to collect poorly-preserved specimens and fragments. However, shells are sufficiently distinctive, even when crushed or fragmental, that they should be recognized and collected. Although hinge features are not generally available for subgeneric assignment, the prismato-nacreous shell and the extremely compressed form, which is both inequivalve and inequilateral, is easily recognized in combination with the straight to convex posterior hinge margin, rounded anterior margin, and features of ornamentation. It is also the case that few specimens from the Pacific Coast Paleogene and Neogene strata have been figured. An exception is the superbly-illustrated account of the Pliocene molluscan fauna of the San Diego Formation (Hertlein and Grant 1972) in which there are eight illustrations of two pandorid species.

Vokes (1967) listed eight nomenclaturally valid genera, and Newell (1969) considered six of those names to be taxonomically valid, treating two of the eight available names as subjective synonyms. Valentich-Scott and Skoglund (2010) introduced a seventh name, although their genus *Coania* is known only from the type locality. Four of the seven have no recognized fossil record, and material from deep-water Paleogene strata in Washington and Oregon is here referred to *Pandora* s.l.

Stratigraphic range—Eocene to Holocene.

PANDORA Bruguière, 1797

Type species—By subsequent designation (Children, 1823), *Pandora rostrata* Lamarck, 1818 = *Solen inequivalvis* Linnaeus, 1758). Holocene, Mediterranean.

The controversy over the appropriate generic name, type species, type designation, and history of interpretations of the zoological code are discussed in detail by Boss and Merrill (1965).

In the northeastern Pacific, pandorids first appear in the late Eocene in the Eocene–Oligocene turnover faunas marking global cooling and onset of subduction and forearc volcanism on the Cascadia margin. There are four previously-described Paleogene species from the eastern Pacific margin. They are compared and distinguished by Hickman (1969, p. 72) in the description of *Pandora laevis* Hickman, 1969 from the Eugene Formation. The new Keasey species is distinguished from all four by the far anterior placement of the beaks and long, shallowly-arcuate posterio-dorsal margin. This is the lowest stratigraphic pandorid appearance in the Pacific Northwest, followed by *P. washingtonensis* Weaver, 1916, *P. laevis*, and *P. vanwinkleae* Tegland, 1933, although there is no implication that they represent an evolutionary series.

Stratigraphic range—Eocene to Holocene.

Pandora eocapsella n. sp.
Fig. 1A

Diagnosis—Shell strongly compressed and strongly inequilateral; right valve shallowly concave, fitting inside shallowly convex left valve and apparently overlapped by left valve along posterioventral margin; anteriodorsal margin short and straight, posteriodorsal margin long, shallowly arcuate and thickened along hingeline; no evidence in preserved shell material of radial ribbing or co-marginal striae.

Description—Exterior shell layer missing but inner layers of sheet nacre well preserved; hinge plate insufficiently preserved to describe hinge teeth except for a tubercular swelling of nacre in position where right cardinal would have been.

Discussion—Although the exterior shell layer is not preserved in any of the Paleogene species, specimens are typically double valved and preserve distinctive details of shell shape. Evidence of co-marginal and radial sculpture are preserved in the interior nacre. Previous figures of specimens coated with ammonium chloride mask the taphonomic features that make shells so distinctive. This is illustrated in new, uncoated images of the holotype of *P. acutirostrata* Clark, 1918 from the San Ramon Formation (Oligocene) of California (Fig. 1C) and the holotype of *P. vanwinkleae* Tegland from the Type Blakeley Formation (Oligocene) of Washington (Fig. 1B). The Blakeley specimen demonstrates clear preservation of both co-marginal ribs and wavy axials characteristic of *Pandorella* Conrad, 1863. Articulated Holocene specimens of high latitude pandorids commonly show extensive exfoliation of the thin exterior shell layer. Differing degrees of degradation and exfoliation on live collected shells of *Pandora trilineata* Say, 1822 from Massachusetts (Figs. 1D–F) illustrate how fossil shells can appear to be poorly preserved even if they have undergone little post-mortem alteration.

Etymology—*Eo* (Eocene, early) + *capsella* (a small box)

Material examined—The new species is known from a single specimen.

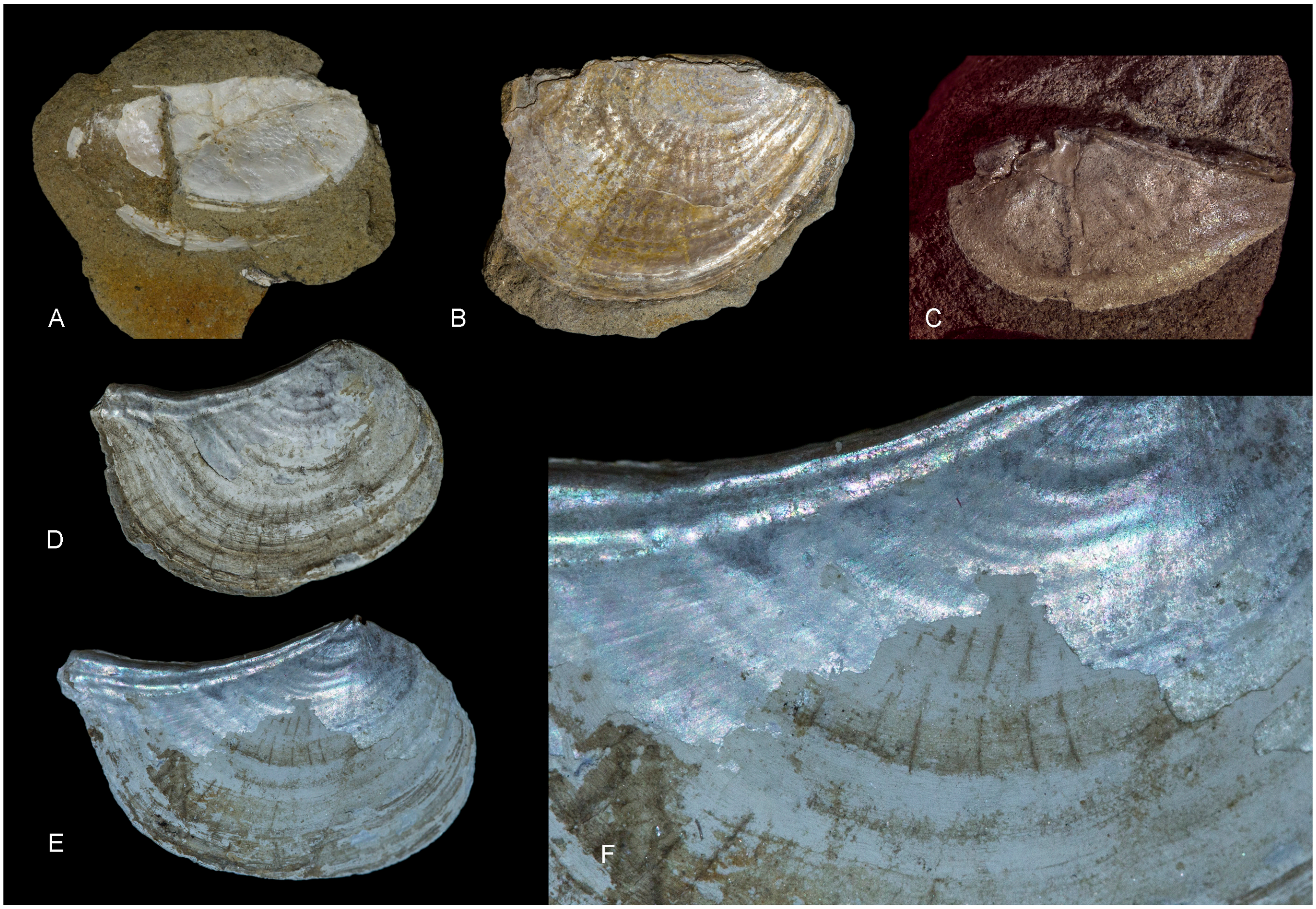

Figure 1A–F. Pandoridae, *Pandora*. **A.** *Pandora eocapsella* Hickman n. sp., holotype, UCMP 110671, Loc. UCMP IP7983 (=USGS 25026), length = 11.0 mm. **B.** *Pandora (Pandorella) vanwinkleae*, holotype, UCMP 32114, Loc. UCMP 681-, length (incomplete) = 31.6 mm. **C.** *Pandora acutirostrata,* holotype, UCMP 11111, Loc. UCMP 1132-, length = 13.6 mm. **D.** *Pandora trilineata*, UCMP 110679, double-valved live-collected specimen illustrating partial exfoliation of exterior shell layer, length = 23.2 mm. **E.** *P. trilineata*, UCMP 110680, right valve of double-valved specimen with extensive exfoliation of exterior shell layer, length = 22.3 mm. **F.** Detail of E showing boundary between thin exterior layer and thicker interior nacreous layers.

Holotype—UCMP 110671, right valve with margins of larger left valve visible, Length 11.0 mm, height 9.5 mm, Loc. UCMP IP7983 (=USGS 25026).

Keasey Formation occurrence—Lower member in association with protobranch bivalves.

THRACIIDAE Stoliczka, 1870 (1839)

Thraciidae, along with Laternulidae Hedley, 1918 and Periplomatidae Dall, 1895, traditionally have been classified in a superfamily Thracioidea (Newell 1965, Boss 1978, Yonge and Morton 1980, Morton 1981, 1982, 1985, Prezant 1998, Bieler et al. 2010). Cladistic analyses combining morphological and molecular sequence data initially suggested that these three families form a deep-branching monophyletic group (Harper et al. 2000). However, thraciids and periplomatids and laternulids also have been treated along with five other extant families under superfamily Pandoroidea (Newell 1969, Runnegar 1974). It is therefore significant that the first sequence data for a periplomatid (Bieler et al. 2014) add this family to a monophyletic “thraciid lineage.”

Living thraciid species are known primarily from shells, which display a great variety of external form and may be morphologically similar to some periplomatids. However, the granular homogeneous aragonite microstructure of the outer and inner shell layers of four species examined to date (Taylor et al. 1973, Sartori and Domaneschi 2005) clearly distinguish them from the prismato-nacreous shells of periplomatids. Eastern Pacific Cenozoic thraciid fossils all lack nacreous inner layers, apparently a derived condition because Runnegar (1974) reports that Mesozoic thraciids in collections at the Natural History

Museum (London) have nacreous shells. Eroded beaks of Cenozoic fossil specimens sometimes show a peculiar iridescence, although the microstructural basis has not been determined.

Thraciids are capable of deep burrowing and prolonged maintenance of siphonal tube connections to the sediment-water interface. Long, highly extensible siphons and mucus agglutination of the separate inhalant and exhalant siphonal tubes are hypothesized to facilitate deeper burrowing in some species (Yonge 1937). Detailed functional anatomy has been documented for two living thraciids (Morton 1995, Sartori and Domaneschi 2005). Animals removed from the sediment are slow to re-burrow, but capable of adjusting their position vertically if burrow openings are covered with sediment. Inequivalved species rest on the flatter left valve, with the more inflated valve uppermost and the commissural plane horizontal. This is consistent with the typical preservation of the Eastern Pacific fossil thraciids as double-valved specimens that lack alterations from post-mortem exposure or transport. The primary taphonomic characteristic is diagenetic crushing of the thin, brittle shells by compressional forces perpendicular to the commissural plane.

Stratigraphic range—Upper Triassic (Rhaetian) to Holocene.

THRACIA Blainville, 1824

Type species—By monotypy, *Mya pubescens* Pulteney, 1799. Holocene, North Sea.

The correct genus name, authorship, date, and interpretation of the type species and its designation have been controversial. This treatment follows the detailed account and conclusions of Coan (1990, p. 23–24).

Stratigraphic range—Jurassic to Holocene.

Thracia keaseyensis n. sp.

Figs. 2A–H

Thracia n. sp. Vokes in Warren et al. 1945 (checklist).
Thracia n. sp. Vokes in Warren and Norbisrath 1946, p. 227.
Thracia n. sp. Moore and Vokes 1953, p. 115, 118.

Diagnosis—Shell large for genus (up to 62.5 mm length x 41 mm width); strongly elongate-ovate; inequivalve but nearly equilateral; valves compressed, right valve more inflated; shell thin and fragile, typically articulated but usually diagenetically crushed or deformed; beaks opisthogyrate, left beak penetrating right and abraded right beak showing iridescence; sculpture of fine co-marginal growth lines and occasional irregular low undulations; surface granulation strongly developed posteriorly, with abundant granules aligned in co-marginal rows; ventral margin shallowly convex; anterior dorsal slope rounded and merging with evenly-rounded anterior end; posterior dorsal margin shallowly convex and posterior end broadly truncate; posterior dorsal slope set off by shallow radial sinus and ridge; ligament external, with well-developed nymph plates and deep ligament groove, hinge plate apparently edentulous but inadequately exposed.

Description—Shell size, extent of surface granulation and organization of granules variable; muscle scars and interior shell features unknown.

Discussion—*Thracia keaseyensis* is readily distinguished from *T. condoni* Dall, 1909 in the overlying Pittsburg Bluff Formation, Eugene Formation, and other coeval Oligocene formations by its more elongate form and prominent co-marginal surface granulation. *Thracia schencki* Tegland, 1933 from the younger Oligocene Blakeley Formation is smaller and also relatively shorter. *Thracia trapezoidea* Conrad, 1849, described from the Miocene Astroria Formation and still living in the North Pacific, also has surface granulation. However, it is more inflated and also less elongate. *Thracia dilleri* Dall, 1898, from the late Eocene Coaledo Formation in Oregon, is similar in outline and surface granulation, although it is inequilateral, with a more pronounced posterior end. Material of other Cenozoic thraciid species is inadequately preserved to permit meaningful comparison.

Etymology—For the geologic formation from which the species is described.

Material examined—The description is based on 28 almost complete double-valved specimens from 12 localities as well as crushed or fragmental specimens with diagnostic features such as the distinctive surface granulation. The species is restricted to the middle member where it is frequently associated with well-preserved double-valved specimens of *Nemocardium weaveri* (Anderson and Martin, 1914) and *Moerella* n. sp.

Holotype—USNM 561781, length 45.7 mm, height 29.7 mm, Loc. USGS 15282.

Paratypes—USNM 561782, length 43.6 mm, height 29.5 mm, Loc. USGS 15282; USNM 561783, length 45.3 mm height 22.5 mm, Loc. USGS 15267; UCMP 110672, length 39.3 mm, height 21.6 mm, Loc. UCMP IP1984 (=USGS 25031). (Measurements cannot be corrected for distortion, crushing, and broken margins.)

Keasey Formation localities—Type locality: USGS 15282 (middle member). Other Localities: USGS 15267, 15274, 15276, 15277, 15281, 15283, 15284, 15285, 15508, 15525, 25031 (middle member).

PERIPLOMATIDAE Dall, 1895

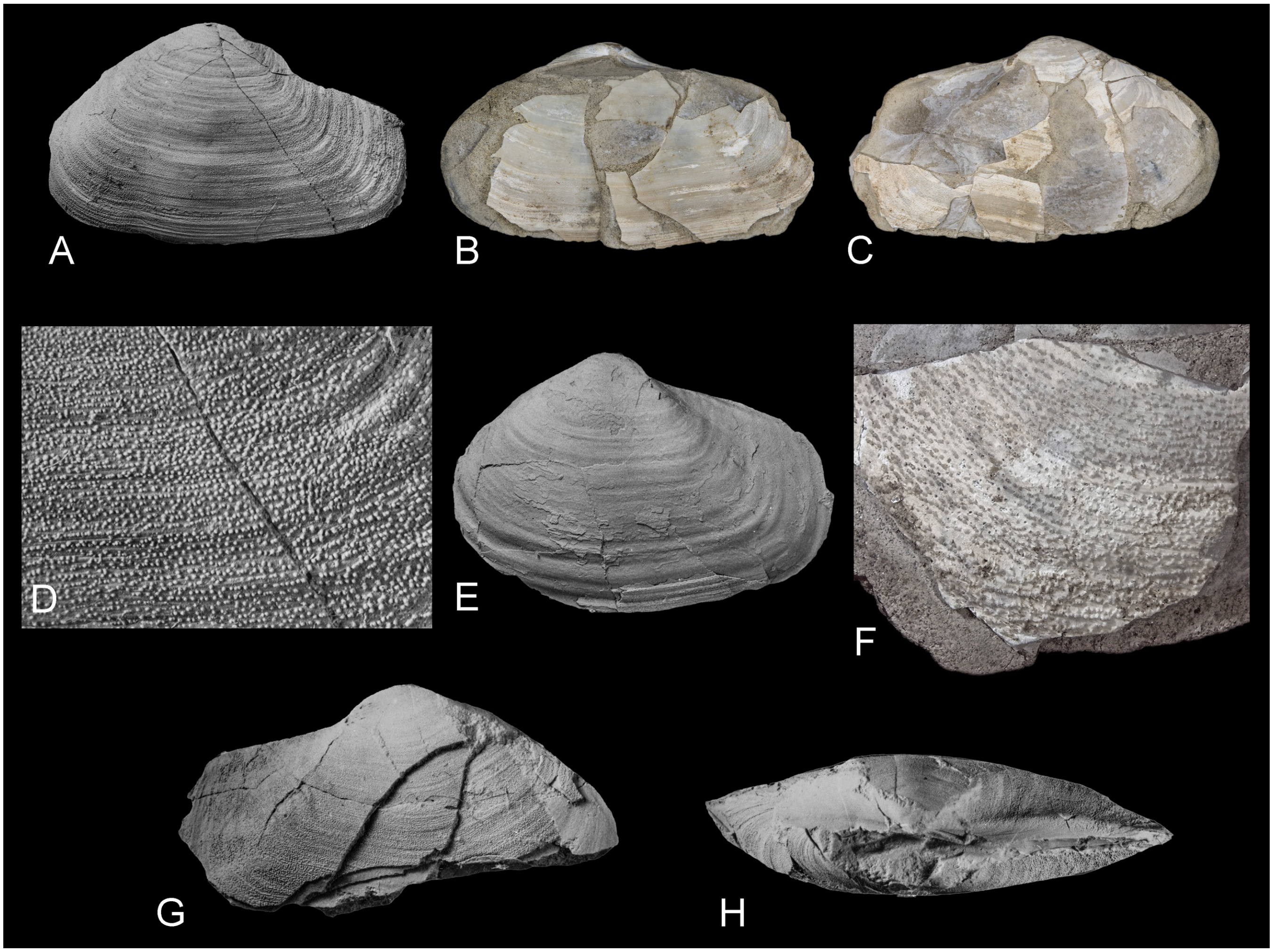

Figure 2A–H. Thraciidae, *Thracia keaseyensis* Hickman n. sp. **A.** Holotype, USNM 561781, Loc. USGS 15282, articulated, left valve, length = 45.7 mm. **B.** Paratype, UCMP 110672, Loc. UCMP IP7984 (=USGS 25031), articulated, left valve, length = 39.3 mm. **C.** Right valve of B. **D.** Detail of granular surface of holotype. **E.** Paratype, USNM 561782, Loc. USGS 15282, articulated, left valve, length = 43.6 mm. **F.** Detail of granules on surface of C (paratype). **G.** Paratype, USNM 561783, Loc. USGS 15267, double valved, crushed and partially incomplete left valve, length 45.3 mm. **H.** Dorsal view of G (paratype).

As noted under Thraciidae, periplomatids also have Mesozoic origins. Although they are never abundant as fossils, crushed and diagenetically altered specimens are easily recognized by a combination of inner sheet nacre and retained co-marginal undulations. The paucity of fossil periplomatid specimens in southern South America has been attributed to a combination of habitat specialization and non-preservation of the fragile shell (Griffin and Pastorino 2006). Considering the Cenozoic record in northwestern North America, especially in the fine-grained deep-water facies, I conclude that low population density is most likely responsible for paucity of fossils of a species that is rare at many localities. In addition, crushed specimens are difficult to collect intact and require special care when encountered in the field.

Stratigraphic range—Upper Jurassic (Tithonian) to Holocene.

APERIPLOMA Habe, 1952

Type species—By original designation, *Anatina lena* Conrad, 1831. Holocene, western Atlantic.

Nomenclatural confusion regarding the type species of *Cochlodesma* Couthouy, 1839 resulted in misapplication of this name to the Pacific Coast Cenozoic species. Although the nomenclaturally correct name is now *Aperiploma* Habe, 1952, the type species continues to be *Anatina lena*, a species that has been freed from synonymy with the eastern Atlantic *Mya praetenuis* Pulteney, 1799, the type of *Cochlodesma*. Vokes (1956) traces the history leading to this rectification of nomenclature. *Aperiploma* continued to be incorrectly synonymized with *Cochlodesma* by some authors who remained caught in the "taxonomic tangle" (e.g., Bernard 1989) that requires no further discussion here.

Specimens are frequent in occurrence in cool to cold high latitude faunas of the Pacific Coast Cenozoic, but they are never well preserved and never abundant at any one locality. Shells are typically articulated or partially disarticulated, but they are usually crushed and lacking in any of the very thin outer shell layer. However, the interior layers of nacre preserve the undulating concentric sculpture typical of the genus, and the heavily calcified and buttressed opisthodetic spoon-shaped chondrophore is often the most diagnostic feature of a crushed specimen. Individuals are seldom well enough preserved to be separated from the matrix, which may contribute to collection bias in the field. Specimens in matrix may preserve the original outline of individuals from which original shell material has exfoliated.

Marincovich (1983, p.109) states that at least 32 North Pacific Cenozoic species have been described under *Periploma*. Most of these are from the northwestern Pacific. Assignments to subgenera and species comparisons of the Asiatic Cenozoic taxa will be essential to reconstructing the high-latitude cold-water history of the group.

Stratigraphic range—Eocene to Holocene.

Aperiploma bainbridgensis (Clark, 1925)

Figs. 3A–E, G

Cochlodesma bainbridgensis Clark, 1925, p. 86; pl. 13, figs. 3, 4.

Cochlodesma bainbridgensis Clark, Tegland 1933, p. 112; pl. 6, figs. 3, 4.

Cochlodesma bainbridgensis Clark, Weaver 1942, p. 117, pl. 25, fig. 1, pl. 29, fig. 2.

Cochlodesma bainbridgensis Clark, Durham 1944, p. 141.

Cochlodesma bainbridgensis Clark, Moore 1976, p. 53, Pl. 16, figs. 6–11.

Discussion—Twelve specimens from eight localities in the lower and middle members of the Keasey Formation are assigned to this species. Allocation to *Aperiploma* is clear based on the combination of thin fragile shell, interior nacre, irregularly-spaced and weak concentric sculpture, absence of surface granules or pustules, opisthogyrous beaks, fissured umbones, and distinctive opisthodetic chondrophore attached to the shell by a prominent supporting buttress. Variability in outline and proportions of the Keasey specimens is at least in part a consequence of deformation, but the shells were inequivalve, with a nearly flat left valve slightly more convex right valve (Fig. 3D). Moore (1976) noted a similar difficulty in characterizing the outline of specimens from the overlying Pittsburg Bluff Formation. The shell is ovate in outline and nearly equilateral, with an acutely-rounded to sub-truncate posterior margin and more broadly-rounded anterior margin.

Although Grant and Gale (1931, p. 255) did not illustrate *C. bainbridgensis*, they suggested that it be referred to *Cyathodonta* Conrad, 1849. However, specimens from the Eocene and Oligocene of the Pacific Northwest all have weaker and non-undulating sculpture as well as lacking the "minute, very closely arranged, granulated radiating ribs" described by Conrad (1849, p. 156) in the type species, *C. undulata*. *Cyathodonta* is also posteriorly truncate and lacks the characteristic buttressing ridge that supports the chondrophore in *Aperiploma*. The chondrophore of a topotype of *C. bainbridgensis* from the Blakeley Formation (Tegland, 1933, pl. 6 fig. 3) is refigured here (Fig. 3F).

This is the earliest reported occurrence of the species and the earliest unequivocal occurrence of the genus in the Cenozoic of the Eastern Pacific.

Material examined—Fourteen specimens from the Keasey Formation and specimens from younger Paleogene formations noted below.

Hypotypes—USNM 561793, length 26.4 mm, height 18.6 mm, Loc. USGS 15318; UCMP 110673, length 21.5 mm, height 19.5 mm, Loc. UCMP IP1432 (=USGS M3865); UCMP 110674, length 22.0 mm, height 19.5 mm, Loc. UCMP IP1432 (=USGS M3865); UCMP 110675, length 20.6 mm, height 15.5 mm, Loc. UCMP IP1431 (=USGS M3862); UCMP 110676, length 14.9 mm, height 10.5, Loc. UCMP IP7983 (=USGS 25026). Unfigured hypotype: USNM 561794, length 10.7 mm, height 8.2 mm, Loc. USGS 15318.

Keasey Formation localities—USGS 15309, UCMP IP7983 (lower member); USGS 2713, 15279, 15314, 15318, UCMP IP7984 (middle member); USGS M3862, M3865 (middle member).

Other occurrences—Lincoln Creek Formation, Twin River Formation, and Blakeley Formation (Washington); Pittsburg Bluff Formation and Alsea Formation (Oregon). The species is also reported from the Poul Creek and Stepovak Formations in the Gulf of Alaska (Burk 1965) but specimens were not examined in the course of this study. Collections from strata of probable middle Eocene age at USGS locality 15289 contain fragments that have an outline and ornamentation suggestive of *Aperiploma*. The fragments are in a shale lens within the Tillamook Volcanic Series in the Oregon Coast Range and are overlain by strata containing a late Eocene Cowlitz fauna.

Four of the five California Cenozoic species described under *Periploma* Schumacher, 1817 are inadequately

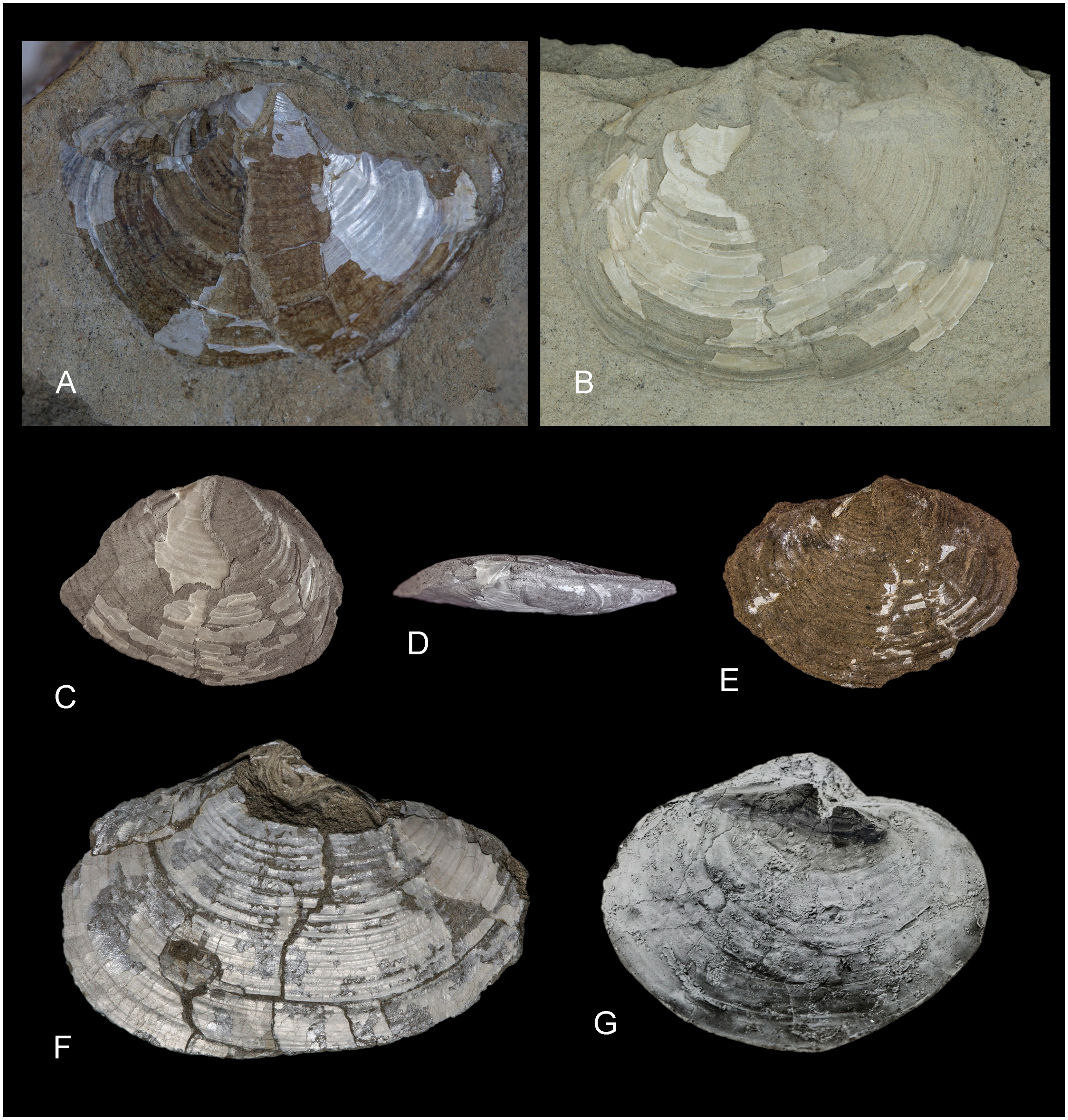

Figure 3A–G. *Aperiploma bainbridgensis*. **A.** Left valve of double-valved Keasey hypotype in matrix, UCMP 110673, Loc. UCMP IP1432 (=USGS M3865), length = 21.5 mm. **B.** Right valve of double-valved Keasey hypotype in matrix, UCMP 110674, Loc. UCMP IP1432 (=USGS M3865), length = 22.0 mm. **C.** Right valve of double-valved Keasey hypotype, UCMP 110675, Loc. UCMP IP1431 (=USGS M3862), length (incomplete) = 20.6 mm. **D.** Dorsal view of C. **E.** Right valve of double-valved Keasey hypotype, UCMP 110676, Loc. UCMP IP 7983 (=USGS 25026), length = 14.9 mm. **F.** Left valve of Blakeley Formation double-valved topotype prepared to show chondrophore in right valve, UCMP 32125, Loc. UCMP 681-, length = 32.0 mm. **G.** Latex cast of interior of left valve of Keasey hypotype showing part of chondrophore, USNM 561793, Loc. USGS 15318, length = 26.4 mm.

preserved to confirm their generic or familial assignment. Specimens of a fifth species, *Periploma cryphia* Woodring, 1938 (and subspecies *P. cryphia stenopa* Woodring, 1938), from the deep-water facies of the Pliocene Repetto Formation in the Los Angeles Basin, preserve the distinctive chondrophore buttress. They are similar to Keasey specimens in compressional crushing of the shells and exfoliation of the thin exterior layer, and Woodring (p. 56) noted their similarity to specimens from the Blakeley Formation in Washington. However, there are no other records of *A. bainbridgensis* from the Neogene, and there is nothing similar in the living fauna of the eastern Pacific. Although shell morphology may be conservative, there is no basis for suspecting evolutionary stasis.

Aperiploma? n. sp.
Figs. 4A–C

Discussion—A large, flat, fragmental specimen 70 mm across preserves distinctive *Aperiploma*-like concentric undulations in interior nacre with unique reflection and refraction of light as colors that range from gold in some angles of illumination (Fig. 4A) to green, blue and purple in others (Fig. 4B,C). Generic assignment is tentative, and formal species description is unwarranted at this time. Illustrations of the nacre may aid in recognition of additional material that might otherwise be overlooked in the field.

Figured specimen—UCMP 110677.

Keasey Formation locality—Upper part of the middle member, Loc. UCMP IP16000. The specimen is embedded in a slab of calcareous siltstone from the upper carbonate layer (UCL of Burns et al. 2005) at the Mist locality and was donated by Casey Burns.

SEPTIBRANCHIA Pelseneer, 1889
CUSPIDARIOIDEA Dall, 1886
CUSPIDARIIDAE Dall, 1886

Living cuspidariids are most diverse, abundant and well-documented in the deep sea, especially at abyssal and hadal depths (Knudsen 1970, 1979). Their origins and relationships are unresolved. The oldest records of rostrate bivalves assigned to Cuspidariidae place the origins of the family in shallow, brackish water in the Triassic (Ladinian) (Morris 1967, Sepkoski 1992). However, re-examination of shell morphology and microstructure shows that the early Mesozoic forms are actually corbulids (myoid heterodonts) (Harper et al. 2002) and that fossil rostrate taxa must be treated with caution. The earliest unequivocal evidence of cuspidariid shell musculature is in the Late Cretaceous (Maastrichtian) (Runnegar 1974 text-fig. 9, p. 924).

Cuspidariid features of greatest interest to biologists are the absence of gills, the unique muscular septum, adaptations for prey capture, and modifications of the digestive system for carnivory (Yonge 1928, Bernard 1974, Knudsen 1979, Alan and Morgan 1981, Reid and Reid 1974, Reid 1977, Morton 1987). The family has a cosmopolitan distribution, although it is especially well documented from high latitudes in the southern hemisphere (Prezant 1998, Marshall 2002).

Fossil cuspidariids are rare in Cenozoic faunas of the northeastern Pacific and have a peculiar taxonomic and stratigraphic distribution. Ten species, including the new Keasey species, are all in the genus *Cardiomya* A. Adams, 1864 and all occur in rocks of middle and late Eocene age. Eighteen species in eight genera are reported in the living northeastern Pacific fauna (Coan et al. 2000). Restriction of many of the living species to abyssal and hadal depths places them out of the normal preserved record of bathyal and shallower marine sedimentary settings. However, the absence from Neogene strata in the northeastern Pacific is puzzling.

The lack of an onshore fossil record of most of cuspidariid diversity is consistent with the hypothesis that this group has undergone a major evolutionary radiation in the deep sea and is not derived by onshore-offshore migration over geologic time of a shallow-water evolutionary radiation. However, shallow-water cuspidariids are reported from Upper Cretaceous and Eocene faunas in Texas (Garvie 2013), and incursions of the group into shallower settings also occur in the modern fauna of the Panamic Province (Coan and Valentich-Scott 2012).

Stratigraphic range—Upper Cretaceous to Holocene.

CARDIOMYA A. Adams, 1864

Type species—By monotypy, *Neaera gouldiana* Hinds, 1843. Holocene, Japanese Seas.

Features of the hingeline and anatomy are required for allocation to some of the cuspidariid genera, but *Cardiomya* has been used consistently for both fossil and living inflated rostrate species with strong radial ribbing on the shell. The ribbing differentiates them from similarly shaped rostrate shells of *Cuspidaria* Nardo, 1840 and other genera that are smooth or have only co-marginal striae or ribs.

Some of the Pacific Coast Cenozoic species were originally described under *Cuspidaria* (or *Neaera* Gray in Griffith and Pidgeon 1833, an earlier name preoccupied by a dipteran insect genus). It is fortunate that the Cenozoic species all have radial ribbing and cannot be confused with the smooth shells of *Cuspidaria* or smooth-shelled

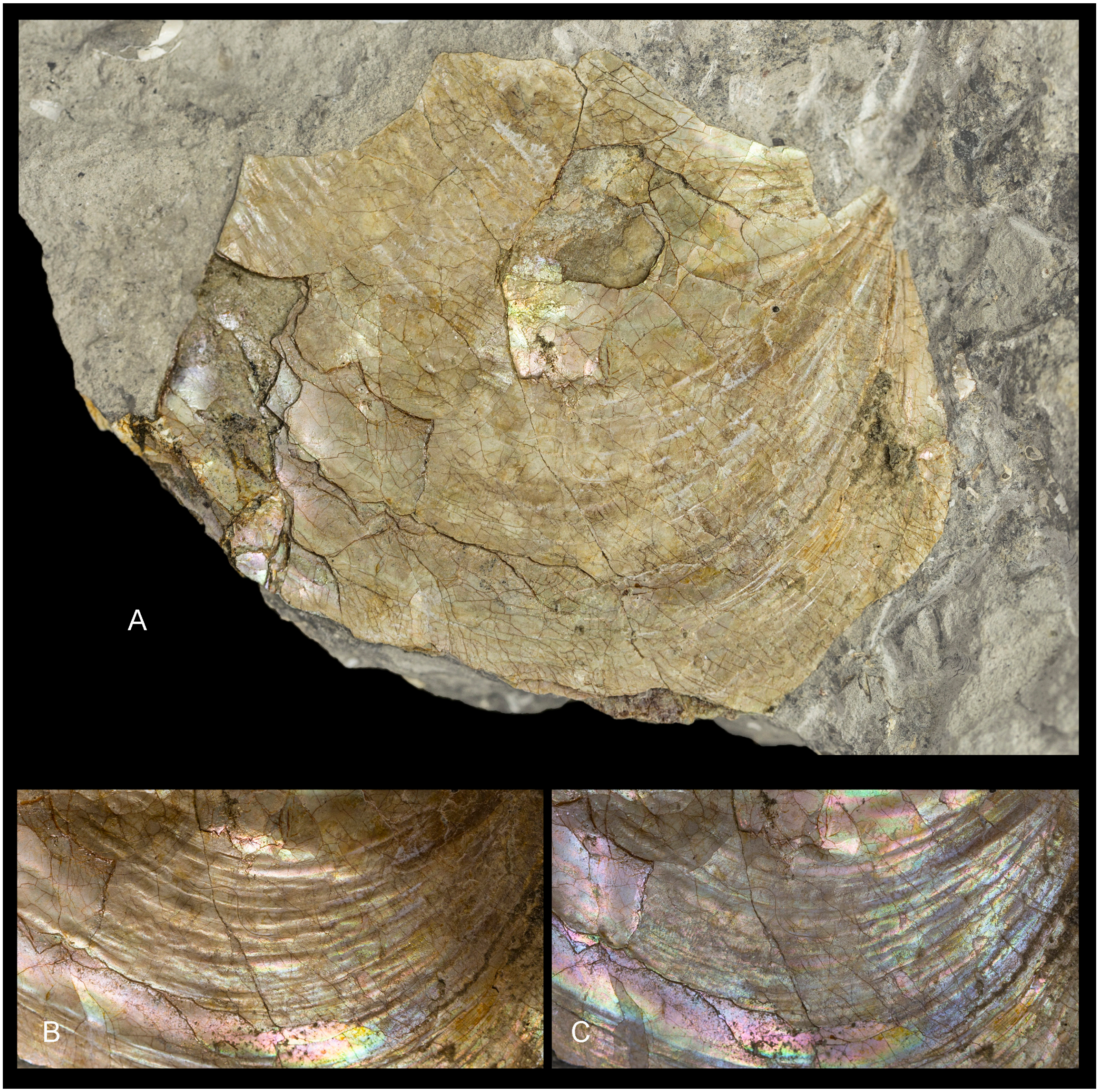

Figure 4A–C. *Aperiploma*? Hickman n. sp. **A.** Incomplete right valve in matrix with multiple exfoliating inner nacreous layers, UCMP 110677, Loc. UCMP IP16000, length of shell fragment = 67.3 mm. **B, C.** Details of identical areas from A to show refraction patterns under different lighting.

species assigned to *Neaera* under its tangled history of misspellings (Stewart 1930, p. 307–308, Petit and Coan 2008, p. 228).

Species of *Cardiomya* in the Pacific Coast Eocene have been distinguished initially by the presence or absence of radial ribbing on the rostrum. Second-order features include relative length and width of the rostrum, the number and comparative strength of radial ribs on the disc, presence or absence of "inter-ribs" on the disc, and the shape, strength and number of ribs on the rostrum.

Although the shells are thin and fragile, the shallow infaunal life habit appears to have conferred some advantage in preservation by rapid burial. Fossil specimens are typically double-valved and are not crushed, although the valves may be partially separated.

Stratigraphic range—Cretaceous to Holocene.

Cardiomya anaticepsella n. sp.

Figs. 5A–D

Cardiomya n. sp. Vokes in **Warren et al. 1945**. (checklist)

Diagnosis—Shell of normal size for genus (length to 10 mm), with ovate, inflated disc and long, smooth, straight, compressed, posterior rostrum. Disc with 18 to 20 well-developed rounded radial ribs. Radial ribs on anterior disc finer than those on posterior segment. Coarser posterior ribs with wider interspaces with occasional finer interrib. Umbones situated posterior to midlength of inflated portion of valve, approximately at 1/3 total shell length. Interior and hinge features unknown.

Discussion—Shells of this species are thin but are not crushed as in the other Keasey anomalodesmatan taxa. They are readily distinguished from the other anomalodesmatans by the rostrate shell form, smaller size, lack of nacre (as in *Pandora* and *Aperiploma*) or granules on the surface of the shell (as in *Thracia*).

The only other Paleogene *Cardiomya* from the Pacific Northwest, *C. comstockensis* **Turner, 1938**, has fewer radial ribs on the expanded disc and has radial ribbing on the rostrum, which is also proportionally shorter and broader. Species from the California Eocene that differ in having radial ribbing on the rostrum include three species from the Rose Canyon Shale originally described under *Cuspidaria*: *C. russeli* (**M.A. Hanna, 1927**), *C. israelskya* (**M.A. Hanna, 1927**), and *C. vorbei* (**M.A. Hanna, 1927**), as well as *C. silverensis* **Vokes, 1939** from the Domengine Formation. *Cardiomya domenginica* **Vokes, 1939** lacks

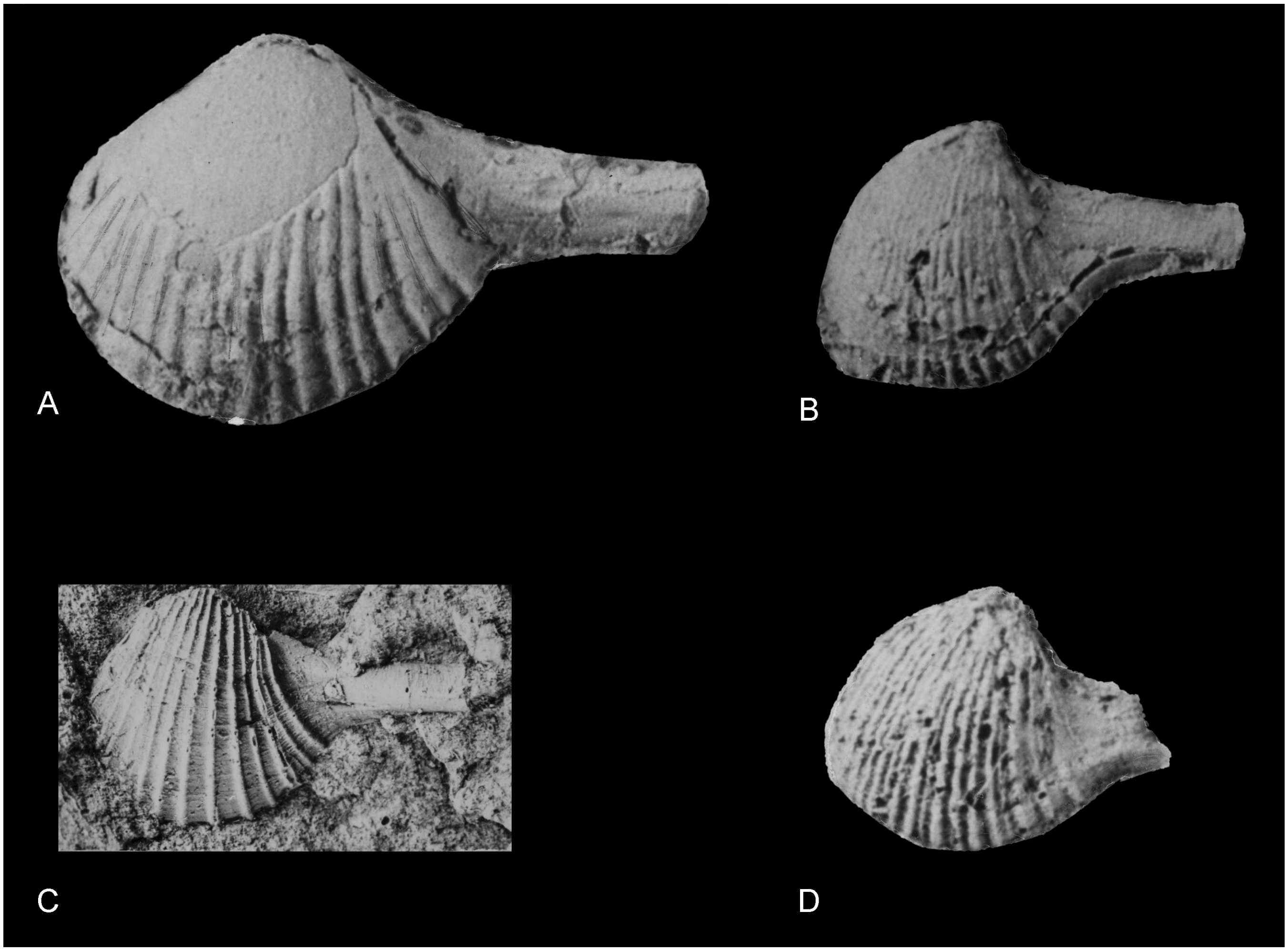

Figure 5A–D. *Cardiomya anaticepsella* Hickman n. sp. **A.** Holotype, UNSM 16196, Loc. USGS 15318, left valve, length = 10.5 mm. **B.** Paratype, USNM 561795, Loc. USGS 15318, slightly crushed left valve, length = 7.8 mm. **C.** Paratype, USNM 561797a, Loc. USGS 15318, latex cast of internal mold of left valve, length = 5.8 mm. **D.** Paratype, USNM 561797b, Loc. USGS 15318 (counterpart of USNM 561797a), latex cast of external mold.

ribbing on the rostrum but is unique in a disc ornamentation of numerous very fine radial threads. *Cardiomya hannibali* (Dickerson, 1914) from the Martinez Formation of northern California is distinguished by a disc divided into a smooth anterior portion and a posterior portion with four radial ribs and a rostrum bearing a single sharp thread extending from the beak to the distal end. Type specimens of all of the above species are in the UC Museum of Paleontology type collection, facilitating comparisons.

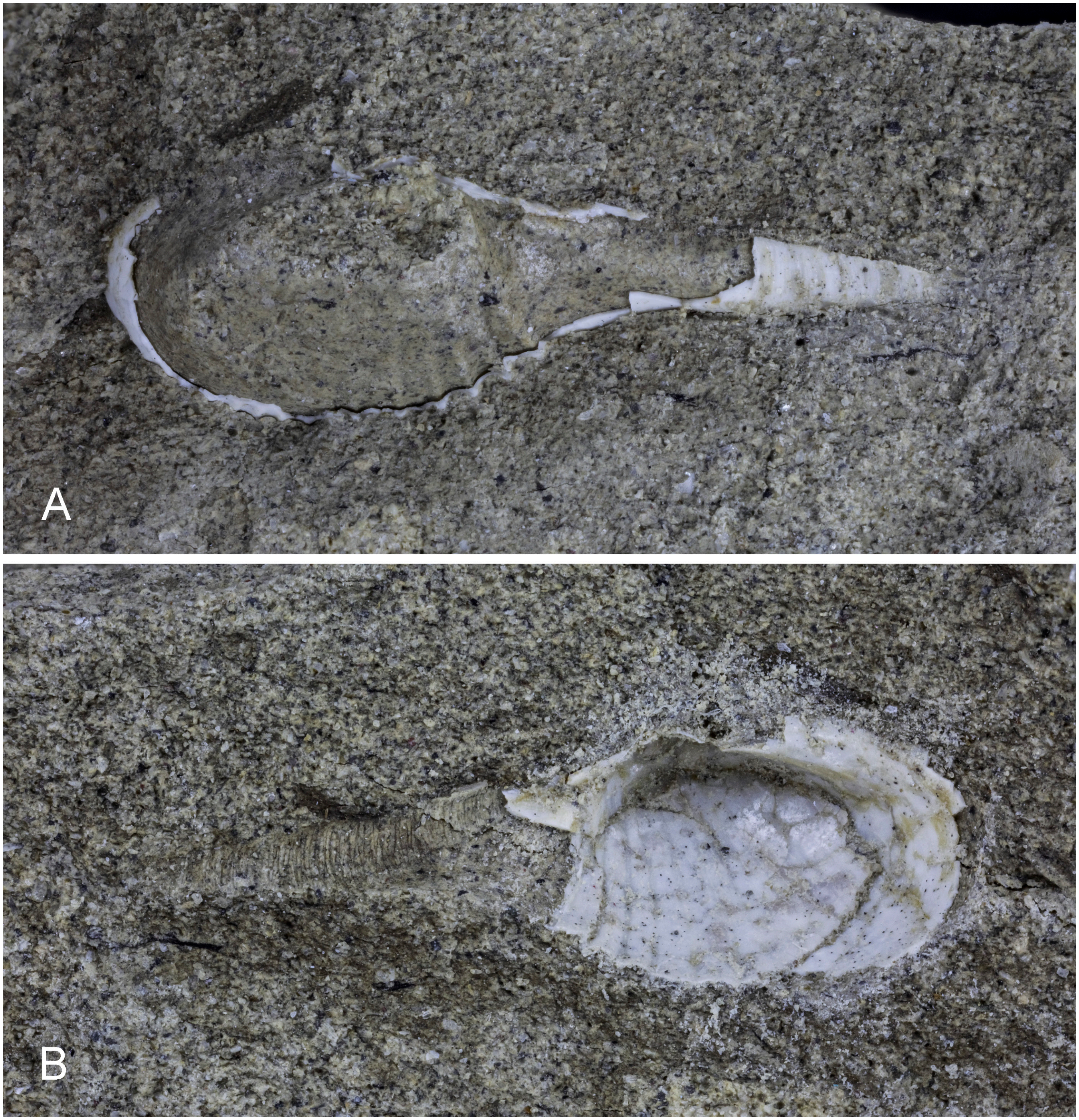

Figure 6A–B. *Cardiomya pavascotti* Hickman n. sp. Holotype, UCMP 110678, Loc. UCMP IP7983 (=USGS 25026), part and counterpart of left valve in matrix. **A.** Internal mold with some adhering original shell in exterior view, length=7.7 mm. **B.** External mold with growth lines on rostrum and some adhering shell material in interior view with anterior muscle scar, length=7.7 mm.

Preservation of this species is primarily as external and internal molds, and illustrations are primarily from latex casts coated with ammonium chloride.

Etymology—The name refers to the superficial resemblance of the shell outline to a miniature duck head and is the name that Harold Vokes attached to intended USNM type specimens.

Material examined—Diagnosis is based on 11 specimens. Seven of the specimens are from the main crinoid-bearing layer at the Mist locality.

Holotype—USNM 561796, left valve, length 10.5 mm, height 5.2 mm, Loc. USGS 15263.

Paratypes—USNM 561796, left valve, length 5.8 mm, height 3.8 mm, Loc. USGS 15263; USNM 561795, left valve, length 7.8 mm, height 4.6 mm, Loc. USGS 15318.

Keasey Formation localities—Type Locality: USGS 15263 (lower member). Other localities: USGS 15309 (lower member), USGS 15318 (middle member).

Cardiomya pavascotti n. sp.
Figs. 6A–B

Diagnosis—Shell strongly inequilateral, with exceptionally long, narrow and straight posterior rostrum with numerous very fine co-marginal striae; disc ovate-elongate, strongly inflated and with coarse radial ribs where exterior shell is preserved; five posterior ribs stronger than anterior ribs; anterior margin broadly rounded; ventral margin scalloped by ribs extending beyond rib interspaces.

Description—Shell poorly preserved, but interior of left valve (Fig. 6B) preserving circular anterior muscle scar and impressions of three strongest posterior radial ribs on disc; hinge plate insufficiently preserved to describe hinge teeth.

Discussion—This striking species is represented by a part and counterpart of the left valve of a single specimen from the lower member of the Keasey Formation. Shell adhering to the rostrum on the external mold (Fig. 6A) appears to be smooth, but numerous fine growth lines are distinctly preserved in the matrix (Fig. 6B). Interspaces between the strongest radial ribs are two times the width of the ribs. This lower Keasey species is readily distinguished from *Cardiomya anticepsella* n. sp. from the upper portion of the middle member by the narrower and more elongate posterior rostrum.

Etymology—Named in honor of Paul Valentich-Scott in recognition of his contributions to knowledge of the Holocene anomalodesmatan fauna of the Eastern Pacific.

Holotype—UCMP 110678, length 7.7 mm, height (approximate) 2.9 mm.

Keasey Formation type locality—Lower Member, Loc. UCMP 7983 (=USGS 25026).

ACKNOWLEDGEMENTS

Documentation of the Keasey bivalve fauna would not have been possible without the encouragement of the late Harold Vokes, who generously turned over the specimens and considerable research effort he originally invested in anticipation of publishing monographic treatments of mollusks of the Keasey Formation. For collecting assistance in the field, I am grateful to James C. Hickman and to the following undergraduate students from the 1979 invertebrate paleontology class at the University of Oregon: Janet Baldridge, Les Boyer, Scott Larson, Greg Miles, Gordy Miller, Diane Searcy, Gary Smith, and Barbara Zeller.

Digital photography of specimens illustrated in color is the work of UCMP photographer and Associate Dave Strauss, and the exceptional quality of his morphological documentation of specimens is the most important single contribution to this monographic treatment.

Micrographs of very small transparent shells were recorded digitally with the Hitachi S-r800 Field Emission Scanning Electron Microscope at the Biological Scanning Electron Microscope Facility of the University of Hawaii with advice and assistance from Tina Weatherby Carvalho.

I am especially grateful to Casey Burns for contributing specimens from several important localities in the uppermost portion of the middle member of the formation. Other colleagues who collected and donated specimens now in the University of California Museum of Paleontology collections include Ellen Moore, Elizabeth Nesbitt, and David Taylor and Bruce Welton. Communications with Alan Niem have been helpful in understanding stratigraphic relationships in the Paleogene of northwestern Oregon.

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