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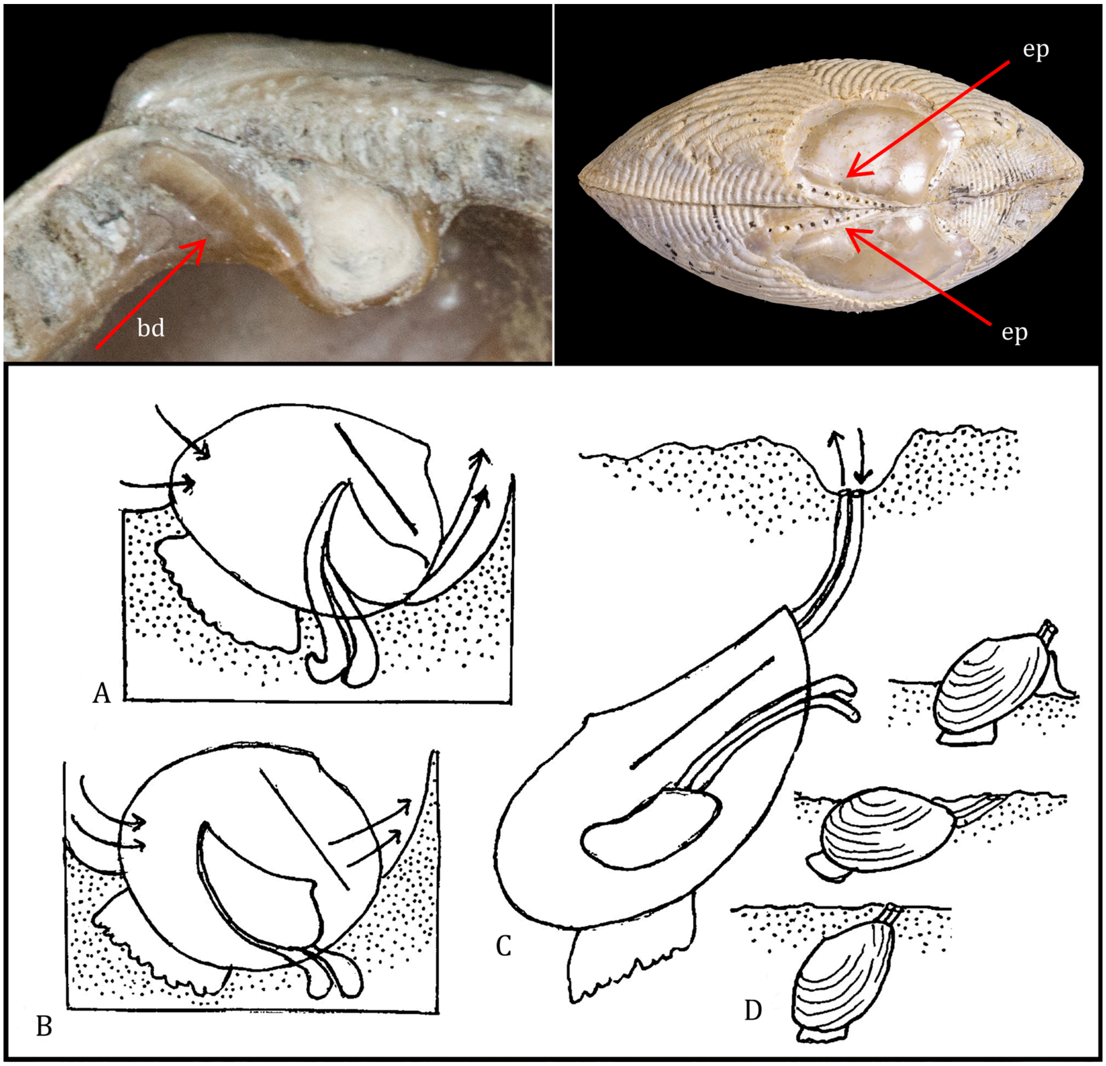

Carole S. Hickman (2025). Paleogene marine bivalves of the deep-water Keasey Formation in Oregon, Part IA: The protobranchs (Nuculidae, Sareptidae, Pristiglomidae).

Cover: Protobranch bivalves are abundant and diverse in the Keasey Formation and include previously unrecognized genera and new species. They preserve novel and rarely-observed shell features including a “bandgrubenzahn” (bd) and escutcheonal perforations (ep). Life habits and functional anatomy distinguish nuculoideans, which lack siphons (A, nuculanids and B, pristigomids) from siphonate nuculanoideans (C,D).

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Paleogene marine bivalves of the deep-water Keasey Formation in Oregon, Part IA: The protobranchs (Nuculidae, Sareptidae, Pristiglomidae)

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Systematic description and illustration of protobranch bivalves of the late Eocene–early Oligocene Keasey Formation in Oregon follows previous monographic treatments of the Keasey anomalodesmatans, heteroconchs and pteriomorphs. Of the three protobranch families documented here, this is the first recognition of Sareptidae and Pristiglomidae in the fossil record of the Northeastern Pacific and Cascadia Margin, as well as recognition of three undescribed species of Nuculidae. Small size and poor preservation contribute to previous failure to notice them in the field. New taxa include *Nucula* (*Nucula*) *cascadensis*, *Ennucula keaseyeyesis*, *Sarepta oregonensis*, *Sarepta nascif*, and *Pristigloma mistensis*. *Nucula (Nucula) n. sp*. is treated in open nomenclature pending discovery of additional material. *Acila* (*Truncacila*) *nehalemensis* is one of the most abundant and frequent bivalves in the formation. Because of the longstanding importance of the truncate acilas in Paleogene biostratigraphy, comparative accounts and illustrations are provided for three superposionally important species from the Eugene and Pittsburg Bluff formations in Oregon and the Twin River Formation in Washington. The Keasey Protobranch Association is an important component of the transitional *peri-seep biotope* at three distinctive Keasey methane seeps. The association also occurs throughout the formation at localities where protobranchs are preserved in fine-grained tuffaceous siltstones with gadilinid scaphopods and deposit-feeding taxa with living relatives adapted to dysoxia, diffuse methane seepage, and toxic geochemistry. Treatments include global biogeographic references and comparisons with similar taxa and molluscan assemblages, notably in the basins of southern New South Wales, South Australia, Western Australia, New Zealand, and Antarctica as well as active Western Pacific Margin settings in northern Japan and Far Eastern Russian Kuril Islands, Sakhalin Island, and Kamchatka Peninsula.

Keywords: taxodont dentition, nacre, Eocene-Oligocene transition, Cascadia Margin, methane seep, peri-seep biotope

INTRODUCTION

Systematic documentation of the protobranchs of the Keasey Formation is the final contribution in a four-part treatment of major subdivisions bivalves of the Cascadia Margin of North America—living in deep water during a dramatic interval of global cooling and regional tectonic reorganization. It is based on 55 years of research by the author and intermittent publications documenting the Keasey gastropods and deep-water mollusks on a broader temporal and biogeographic scale. This work includes comparisons and illustrations of closely related species in other Paleogene formations in Washington and Oregon, notably the Gries Ranch, Lincoln Creek, Eugene, Pittsburg Bluff, and Nestucca formations. It also includes illustrations of closely similar living species from the Northeastern Pacific.

Because of their Cambrian origins, long evolutionary history, and diversity within three recognized orders of Protobranchia, the Keasey Nuculida are presented herein, to be followed separately by Solemyida an Nuculanida. Persistent taxonomic controversy, alternative phylogenetic hypotheses, new characters and character sets on which alternative classifications have been recognized are reviewed within individual treatments. This approach accommodates expansion beyond taxonomy and systematics to include 6 secondary foci in which these Keasey taxa offer productive avenues for future research.

Temporal focus is on the Eocene doubthouse interval (53–33.5 Ma) and broader record of global climate deterioration from the tropical greenhouse state and thermal maximum of the Early Paleogene to establishment of permanent polar icecaps and modern icehouse conditions. ***Biostratigraphic focus*** is on deep-water protobranch lineages that have played a dominant role in designation of molluscan stages and zones and refining the superpositional control that has made them useful in regional

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age determination and correlation. ***Paleoecologic focus*** is on recurring assemblages and associations of genera and species that have been used to hypothesize, infer, and name communities and to reconstruct their basic trophic structure and functional dynamics. ***Paleobiogeographic focus*** repeatedly links Keasey taxa with similar taxa in high latitude Paleogene faunas of the Pacific Rim in the Northern Hemisphere and Southern Hemisphere faunas in Antarctica, Australia and New Zealand. ***Paleoceanographic focus*** is related primarily to Paleogene global cooling and evidence for development in the Pacific of a two-layered ocean with a deep cold-water mass as high latitude sea ice and polar ice caps began to form. The protobranch record is closely tied to reorganization of major current systems, tectonic events, and opening and deepening of gateways in the Southern Hemisphere during separation of Antarctica from Australia (Tasman Gateway) and South America (Drake Passage). ***Methane seep focus*** is a relatively recent development in the study of Paleogene mollusk faunas on convergent margins in the North Pacific. The late 20th Century discovery of mollusks metabolically fueled by chemosynthetic bacterial symbionts at hydrothermal vents (Corliss et al. 1979) and cold seeps (Paull et al. 1984) led rapidly to reinterpretation of unusual assemblages in the fossil record, especially in the Japanese archipelago and on the Cascadia Margin of North America. Three discrete cold seeps in the Keasey Formation, as well as evidence for widespread diffusive seepage and unique mollusk associations adjacent to Keasey seeps, are of special interest in the following treatment. The abundance and diversity of deposit-feeding protobranchs in the peri-seep biotope is consistent with hypothesized enriched productivity by chemosynthetic bacteria and protobranch adaptations to low oxygen and toxic geochemistry that exclude background fauna. For all of these secondary foci, literature references are provided in each taxonomic account.

A BRIEF PROTOBRANCH HISTORICAL PERSPECTIVE

The deep-sea protobranchs have a long history of investigations that combine biological and paleontological data. Although detailed review of that history is not relevant here, it is worth noting three episodes of excitement in the 1960s and ‘70s in which protobranchs assumed celebrity status. The first of these was a series of 30 cruises organized by Howard Sanders at the Woods Hole Oceanographic Institution to acquire and document deep-sea faunal assemblages and taxa from depths up to 5,000 meters along the now-legendary Gay Head-Bermuda Transect between Woods Hole and Bermuda (see Sanders et al. 1965). The second was the emergence of a discipline of “animal-sediment relationships” providing rigorous characterization of a deposit-feeding biotope (Rhoads and Young 1970; Levinton and Bambach 1975). The third was an intense multidisciplinary debate over the age, origin, and antiquity of the deep-sea fauna (Zenkevich and Birstein 1960). This was a period in which it was impossible for graduate students in biology, paleontology, and oceanography to escape classic studies featuring deposit-feeding protobranch bivalves.

MATERIALS AND METHODS

This following treatment is based primarily on collections by the author, supplemented by study of collections at the University of Oregon, Burke Museum of the University of Washington, University of California Museum of Paleontology, Stanford University, California Academy of Sciences, U.S. Geological Survey, and Smithsonian Institution. Type specimens for new taxa treated here along with hypotypes of previously described taxa are from collections by the author and deposited in UCMP, supplemented by USGS/Smithsonian material collected by the late Harold Ernest Vokes.

Institutional abbreviations, geographic terminology, and format for treatment of bivalve genera and species are the same as in the previous three parts (anomalodesmatns, heteroconchs, and pteriomorphs) of this four-part series (Hickman 2014, 2015, 2023). High-resolution focus stacked photographs by Dave Strauss document many features and details that have been overlooked or seldom illustrated in previous paleontological treatments. Color photography is adjusted as closely as possible to match specimens and includes detail that was obscured during a long history of ammonium chloride coating and black-and-white photography, retouching of photographs, and imprecise cut-outs of images of specimens preserved in matrix. As in the three previous Keasey bivalve treatments, literature citations are provided for authors and dates of taxa, which are frequently difficult to locate and consult in 19th Century literature that has not been scanned and is not available on line. For each of the Paleogene taxa in this treatment, morphologically close living counterparts are illustrated to document similarities as well as to highlight features of potential importance in future paleontological treatments.

THE KEASEY FORMATION

Exposures of the Keasey Formation in the Coast Range of northwestern Oregon and coeval strata in western Washington record a major molluscan faunal turnover at approximately 33.5 MA, coinciding major changes in ocean gateways, the Oi-1 isotopic excursion, and glaciations marking close of the doubthouse interval of climate change. On the Cascadia Margin faunal turnover also coincides with dramatic tectonostratigraphic change and inferred deepening of the calcite compensation depth.

However, at the time the formation was named and described by Schenck (1927) the tuffaceous siltstones and mudstones were known only from preliminary reconnaissance in a region of heavy rainfall, dense vegetation, few roads, no adequate maps, and deeply-weathered outcrops in stream banks. Difficulty measuring shallow dips in the nearly flat-lying and gently folded strata and slumping hindered basic assessment of stratigraphic relationships. Schenck (1928) also named and described the overlying Pittsburg Bluff Formation, but his primary reason for considering the Keasey to be older was that its molluscan fauna was "more Eocenic in character". Results of a century of refinement based on detailed mapping and field studies are summarized by Taylor et al. (2023) along with a summary of assessments of age, biostratigraphy, and correlation.

Perhaps the most important contributions to understanding the Keasey Formation and its fauna result from a revolution in modeling and tectonic understanding of the active Cascadia Margin and documentation of Paleogene events following early Eocene establishment of the Cascadia forearc subduction zone. These events focus on accretion of the large tectonostratigraphic terrane of Siletzia, subsequent abrupt westward shift of the subduction zone, and deposition of Keasey sediments in a landward retro-forearc basin on the overriding plate. The tectonic data and reconstructions are summarized by Taylor et al. (2023) while subduction dynamics and modeling continue as a fertile field of research.

The retro-forearc deposits are paleontologically significant to the following treatment of the Keasey protobranch bivalves as the sites of methane seepage, chemosymbiotic seep mollusk faunas, and peri-seep assemblages of opportunistic mollusks with adaptations that allow them to tolerate low oxygen and toxic sulfide and thrive nutritionally on chemoautotrophic microbial productivity (Hickman 2023).

SYSTEMATIC PALEONTOLOGY

The hybrid classification and order of treatment adopted here is based primarily on Bouchet and Rocroi (2010) and Carter and 50 others (2011). Ranking and new assessments of phylogenetic relationships (e.g., Lemer et al. 2019, Sato et al. 2020) are addressed where new molecular data provide resolution of previously chaotic taxonomic assessments. For morphological terms and vocabulary related to bivalves, both living and fossil, readers may consult the 209-page Illustrated Glossary of the Bivalvia by Carter and 21 others (2012).

Traditional categorical ranking is not philosophically intended to express phylogenetic relationships, nor is order of treatment strictly alphabetical or exclusively practical. Taxon treatments within ranks are usually alphabetical, with nominate taxa presented first but followed by a compromise ordering that integrates many different kinds of paleontological and neontological data that bear heavily on evolutionary and phylogenetic questions. Longstanding tradition is preserved where possible in a framework that minimizes repetition and identifies taxa and data lacunae that require new research effort.

As in the preceding taxonomic treatments of the Keasey gastropods and bivalves in this series, nomenclature is a continuing concern. Names, synonymies, differential diagnoses of new taxa, and descriptions are paired with discussions and comparative treatment of both fossil and living taxa in an effort to weigh both paleontological and functional anatomical data. The increasingly popular use of "accepted names" in global lists (e.g., Molluscabase, WoRMS, Paleobiology Database) is not considered appropriate to taxonomic practitioners and the consistent hypothetico-deductive practice of documentation in this series of systematic treatments of the Keasey mollusks. However, the stability and extraordinary benefits of these lists to users are not disputed.

PROTOBRANCHIA Pelseneer, 1889

Protobranchs are diagnosed and recognized primarily by the shared taxodont hinge plate with numerous short interlocking teeth and sockets separated by a chondrophore or resilifer, a unique shell microstructure, a peculiar pericalyma larva and mode of larval development, respiratory pigments reflecting life in oxygen-poor habitats, and unique structural and functional features of the paired ctenidia, the paired labial palps with extensible sediment-gathering palp probocidies, and the enlarged and complexly looped hindgut related to deposit feeding in fine organic-rich sediments. Diagnostic features of the orders, superfamilies, families, subfamilies, and genera in the Keasey Formation are more easily defined in the following treatment, with citations of helpful literature. Although the emphasis is on morphological features that can be recognized in fossil specimens, anatomical and functional correlates are included where relevant to taxonomy and systematics as well as paleoecological and paleoenvironmental interpretation.

Labial palps and associated modifications of the protobranch digestive system for deposit feeding are of primary importance as key innovations underlying protobranch evolutionary radiation. Accordingly, results from increasingly detailed studies of living taxa most closely related to those in the Keasey Formation are emphasized in the treatments that follow.

The relevance of living deep-sea protobranchs resides in a particularly strong link in the rock record between the fossils and their preserved sedimentary milieu. Allen (1978) identified this link in the form of two selection pressures: performance in fine soft sediments and the paucity and refractory nature of food. Documentation of protobranch evolutionary radiation, success, and longevity demands fieldwork and close attention to the rocks.

Protobranchs are the most important elements in the Keasey bivalve fauna in terms of total number of species, *frequency* of occurrence (number of localities), and *abundance* (number of specimens at individual localities). Because they are small, inconspicuous and typically not well preserved, they are the least well-collected bivalves. For this reason, they are poorly represented in museum collections. However shell fragments often preserve diagnostic features that are not preserved in entire articulated specimens.

The ranked higher classification of protobranchs as a bivalve subclass by Bouchet and Rocroi (2010) is used here as a framework for treating living and fossil species under three orders (Nuculida, Nuculanida, and Solemyida) that have clear deep Paleozoic origins. At the same time, it recognizes that there are extinct Paleozoic genera and species that are uncomfortable in this framework, as well as in other available ranked classifications. A full review is not appropriate here, and protobranchs that do not fit clearly into a higher-ranking scheme can continue to be treated under a large number of valid and available superfamily- and family-group names.

Within each of the orders, treatment of Keasey taxa emphasizes diagnostic characters essential to recognition and differentiation, age determination, correlation, paleobiogeography, and paleoecology as well as providing a window on climate change during the Eocene doubthouse interval of global climate cooling (*sensu* Hickman 2021). They also contribute to a growing understanding of bivalve adaptations to dysoxia and life with sulfide and methane under cold-seep and peri-seep conditions.

Support for protobranch monophyly based on molecular analyses has become increasingly strong with expanded taxon sampling and number of markers (e.g., Sharma 2013, Bieler et al. 2013, 2014, Gonzales et al. 2015, Lemer et al. 2016, Combosch et al. 2017, Sato et al. 2020). Further reference to molecular analyses is beyond the scope of this treatment, except where new or refined morphological characters, such as protobranch shell microstructure (Sato et al. 2013, Sato and Sasaki 2015) have been integratively mapped onto molecular trees.

Protobranchia is here considered to have priority over Palaeotaxodonta Korobkov 1954, although that name remains available and useful in an informal sense until we achieve a better understanding of the diverse array of Early Paleozoic genera and species that have some form of taxodont dentition and lack distinct chondrophore or resilial pit. See Pojeta (1975) for outstanding photographic illustrations of hinge plates and uninterrupted gradidentate dentition. The evolutionary radiation of these unequivocal bivalves in the Early Ordovician led Pojeta (1971) to infer that palaeotaxodonts must have originated in the Cambrian, a view sustained by Allen (1978) in his review of evolutionary history of the living deep-sea taxa. However, there is a gap in the Cambrian record between the earliest bivalves (*Fordilla* Barrande, 1881 and *Pojetaia* Jell, 1980) and the Ordovician palaeotaxodonts. Both of these Cambrian genera are accepted as bivalves, although their relationship to each other and to the Ordovician palaeotaxodonts remains unresolved.

As noted above, the palaeotaxodont record includes considerable morphological diversity and features diagnostic of extinct family groups that do not fit comfortably into any existing classification scheme. Several decades of lively late 20th Century controversy and alternative interpretations of enigmatic early Paleozoic fossils, molluscan origins, relationships, and classification led to intensified field exploration and discoveries of new fossils. Readers interested in these debates, new discoveries, and a fundamental reorganization of early mollusk research at the dawn of the 21st Century may refer to Runnegar and Pojeta (1985), Pojeta and Runnegar (1985), Cope (2000), and the eight papers and references cited in a 2000 Symposium entitled "New Looks at Old Mollusks" [*American Malacological Bulletin* 15(2):115–2002].

The pattern of palaeotaxodont diversification is unusual, reaching a maximum of 30 genera in Middle and Late Ordovician seaways (Pojeta 1978). This explosive early Paleozoic diversification has been linked theoretically to a combination of early experiments and innovations in taxodont ligament, dentition, valve alignment, and adaptations for exploiting organic matter, not only in the sediment but also re-suspended particles in the water column (e.g., Cope and Babin 1999, Cope 2002). Furthermore, these early palaeotaxodonts were represented in deep- as well as shallow-water facies. Their initial radiation was followed by a long subsequent palaeotaxodont decline during the Paleozoic. Although the initial radiation included all the extant protobranch superfamilies (Waller 1990), they failed to diversify until after the end-Permian Mass extinction (Sharma et al. 2013). Conservative shell morphology and homeomorphy continue to plague attempts to reconstruct post-Paleozoic history of the extant clades, but it is clear that protobranchs underwent a secondary diversification in deep water on the active North Pacific rim. It is recorded particularly well in the Keasey Formation and coeval strata From Oregon to Alaska in the Northeastern Pacific and Japan and Kamchatka in the Northwestern Pacific during Paleogene global cooling.

Stratigraphic range—Cambrian or Lower Ordovician (Tremadocian)–Holocene.

NUCULIDA Dall, 1889
NUCULOIDEA J. E. Gray, 1824
NUCULIDAE J. E. Gray, 1824

Nuculids are typically small, with subovate to triangular shells that are anteriorly produced and posteriorly truncate, with prominent umbones, opisthogyrate beaks, and an exterior that is smooth or with subdued radial and/or commarginal striae. The interior ligament is contained in an oblique chondrophore and resilial pit that separates the anterior and posterior series of taxodont teeth on a well-developed hinge plate. The aragonitic shell consists of an outer prismatic layer and middle and inner nacreous layers. Crenulation of the ventral shell margin has been considered diagnostic, although it may be expressed only in the exterior prismatic shell margin where it may or may not interlock the valves or only as an interior crenulation of a nacreous layer that does not extend all the way to the shell margin. As a diagnostic feature, the nature of the crenulation must be specified and requires ontogenetic and microstructural documentation in order to be phylogenetically informative.

Soft-part anatomy of living nuculids is rich in features. Insights from detailed comparative documentation of deep-water species by John Allen and Howard Sanders during the second half of the 20th Century altered a prior history of taxonomy based primarily on shell features and incomplete assessments of fossil material lacking preservation of the hinge line, hinge plate, and shell interior.

Lack of siphons is recorded in the shell interior by an entire pallial line. The anterior inhalant respiratory current and posterior exhalant stream are correlated with a ctenidial axis that is oblique to hinge plate, in contrast to the posteriorly-elongate, siphonate nuculanids with a ctenidial axis parallel to the hinge plate and respiratory streams.

As small, shallow, semi-infaunal burrowers in fine, organic-rich sediment, nuculids have been targeted for studies of deposit feeding. Results include increasingly detailed characterizations of the labial palps and ctenidia (e.g., Schenck 1936, Stasek 1961, Sanders and Allen 1973) and their function in particle capture, sorting, selection, and rejection. Studies of gut looping document diverse solutions for coiling and accommodating a greatly elongated digestive system and increasing gut passage time for efficient digestion and absorption (Allen 1978). Alternative anatomical solutions that avoid enlarging the shell or changing conservative shell shapes are fascinating, but beyond recognition in fossil taxa.

Although conservative shell shapes prevail, miniaturization is a convergent evolutionary trend in nuculids. Small size also has attracted malacologists seeking insight into the biology and functional anatomy of the ancestral bivalve (e.g., Morton, 2012). Reduction of shell size may be correlated with anatomical reduction either by reducing cell number or cell size and may include reproductively significant decrease in egg number and size, hermaphroditism, as well as inbreeding and low rates of gene flow (Sanders and Allen 1973, Allen 1978). Miniaturized protobranchs are probably under-represented in paleontological accounts and museum collections because they are overlooked in the field.

One of the most important features differentiating nuculids and other protobranchs from all other bivalves is the unique pericalymma larva (Zardus and Morse 1988, Zardus and Martel 2001, Zardus 2025) and associated details of reproduction and development.

Physiological peculiarities of living nuculids and other deep-sea protobranchs continue to provide insight into their tolerance of dysoxic settings, including the relationship between low metabolic rates and unique oxygen metabolism as well as addressing major phylogenetic hypotheses.

The type species of *Nucula* is the source of molecular characterization of bivalve hemocyanin as the extracellular oxygen transport protein (Mangum et al.1987; Bergmann et al. 2007), an outgrowth of previous recognition that hemocyanin is the common respiratory pigment of protobranchs (see Zardus 2002 and references therein). Hemocyanin may be non-binding or variable in its binding ability, and investigations its function(s) and phylogenetic significance extend to questions of both protobranch and bivalve origins and monophyly. Although nuculoid ancestry of taxodont bivalves has been considered most likely (e.g., Waller 1998), the possibility of dual origin of taxodont dentition in the Early Paleozoic (Cox 1959) has prompted detailed morphological analyses that fail to provide strongly supported resolution. This work is noted here because of its relevance for evolutionary pathways that require integration of data from both living and fossil taxa.

Stratigraphic range—Cambrian or Lower Ordovician (Tremadocian)?–Holocene.

NUCULINAE J. E. Gray, 1824

Subfamily distinction is based on the shell microstructural feature of first order radial prisms in the middle nacreous layer of the shell, which are exposed terminally at the commissure as denticles or crenulation, originally noted by Van de Poel (1955). This microstructural feature is clearly observed in the two nuculids in the Keasey Formation, and the subfamily distinction adopted here follows its formalization by Maxwell (1988).

NUCULA Lamarck, 1799

Type species—By monotypy, *Arca nuculeus* Linnaeus, 1758. Holocene, North Atlantic.

Stratigraphic range—Lower Ordovician (Arenigian)–Holocene.

There are no close living analogs of the Keasey species of *Nucula*, but the crenulate ventral margin and ventral interior nacre are characteristic. Shells of the three Northeastern species are similarly small (<10 mm length), and *Nucula carlottensis* (Dall, 1897) from the Cascadia Margin of Washington State (SBMNH 36114), is illustrated here (Fig. 1A, B) to show the oblique chondrophore, taxodont dentition, radial and commarginal sculpture, and crenulation of the ventral margin.

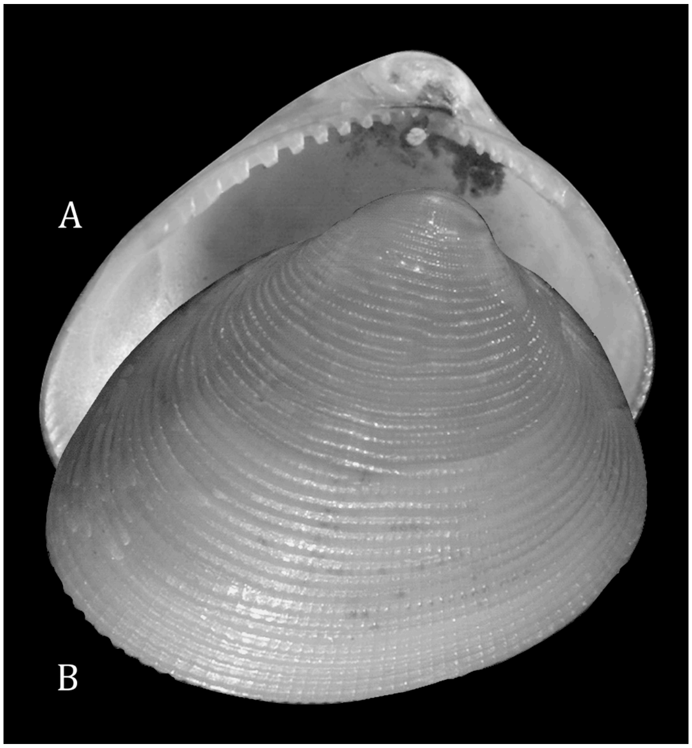

Figure 1A, B. *Nucula* (*Nucula*) *carlottensis* (Dall, 1897), a living deep-water species of *Nucula*, s.s. from the Northeastern Pacific Margin. **A.** right valve interior of double-valved specimen. **B.** Left valve exterior. SBMNH 36114. Length 4 mm.

Nucula (Nucula) cascadensis n. sp.

Fig. 2A–D

ZooBank LSID—urn:lsid:zoobank.org:pub:77B08747-F088-4A46-BA5A-5580FAF0EEB3

Diagnosis—Shell minute (length < 5 mm), subovate to subtrigonal, moderately inflated; outer aragonitic layer with 40–60 radial ribs, weak commarginal growth checks occurring on ventral 1/3 of valve; umbones broad, opisthogyrate; anterior dorsal margin convex, posterior dorsal margin short and nearly straight, dorsal margins merging gradually with ventral margin; lunule and escutcheon narrow, well delineated.

Discussion—This is a distinctive species preserving excellent detail of radial ribs in the thin outer prismatic layer (Fig. 2A, C) as well as underlying radial laths within the nacreous layers (Figs. 2A, C, D). In the best-preserved exterior layer several radial ribs become more prominent ventrally (Fig. 2A). Crenulation of the commissure results from marginal extension of radial laths in the prismatic layer (Fig. 2C). Finer structural laths within the nacreous layers (mnl, inl) are more numerous and do not correspond with radial structuring of the prismatic layer (opl)(Fig. 2A). The species is represented by five double-valved specimens, two of which are in matrix. Although the hinge plate and interior features are not available on any of the specimens, the new name is justified by the many exterior features distinguishing it from other living and fossil nuculids of the North Pacific margin. Because of its size it is easily overlooked in the field and is best recovered from bulk samples where it occurs with other small protobranchs, small gadilinid and dentaliid scaphopods, and mud pectens.

Etymology—Belonging to the Cascade region of the Pacific Northwest.

Material examined—five specimens.

Holotype—UCMP 110774, (articulated) length 5.7 mm, height 5,1 mm. Loc. UCMP IP7983 (formerly USGS 25026), illustrating lack of coincidence of radial ribs in exterior and interior shell layers and crenulation of the exterior shell ventral margin.

Paratypes—UCMP 110775 (interior, left valve in

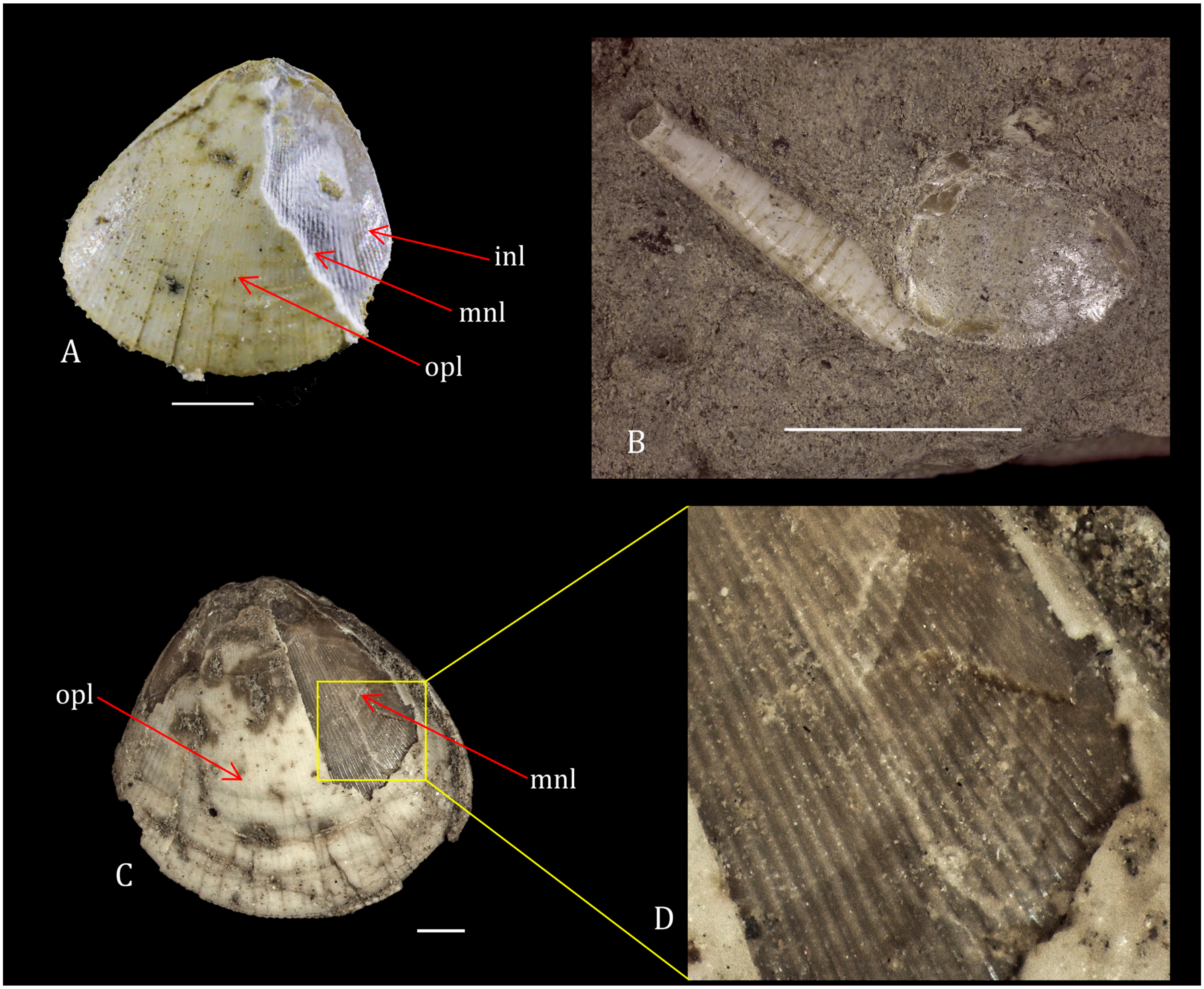

Figure 2A–C. *Nucula* (*Nucula*) *cascadensis* n. sp. **A.** Left valve, Paratype, USNM 561824, outer shell layer (opl) with radial ribs; middle nacreous (mnl) and inner nacreous (inl) shell layers with underlying radial laths. Scale bar=1 mm. **B.** Right valve, Paratype, UCMP 110775, in matrix with gadilinid scaphopod. Scale bar=5 mm. **C.** Right valve, Holotype, UCMP 110774 with opl and mhl shell layers. Scale bar=1 mm **D.** Detail of radial aragonite laths.

matrix with *Cadulus*) length 5.6 mm, height 4.1 mm). Loc. UCMP IP7983 (formerly USGS 25026), illustrating presence of oblique chondrophore and remains of anterior taxodont dentition. USNM 561824 (left valve exterior in matrix) length 4.3 mm, height 3.6 mm. Loc. USGS 15309, illustrating three different shell layers.

Type locality—UCMP IP7983, Columbia Co., Oregon.

Other localities—USGS 2717, 15309.

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

Nucula (Nucula) n. sp.
Fig. 3

Discussion—A single minute left valve in matrix, recovered from higher in the Keasey Formation at the classic Mist locality, differs in shape and ornamentation from *Nucula cascadensis*. It is insufficiently well preserved to warrant a new name and is differentiated and figured to aid in recognizing specimens that might otherwise be overlooked. The ventral shell margin is finely crenulate, as in *N. cascadensis*, but the shell sculpture differs in

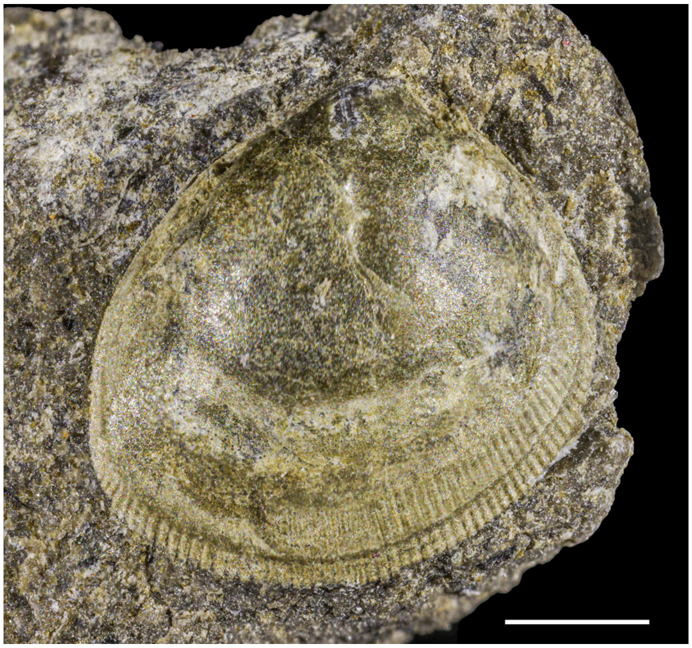

Figure 3. *Nucula* (*Nucula*) sp. Left valve exterior in matrix, UCMP 110776, with radial ribs, growth pause, and crenulated margin. Scale bar=1 mm.

having finer and more numerous radial ribs, a proportionately shorter anterior. Significance of the prominent submarginal growth check cannot be evaluated from the single available specimen.

The shell is strikingly similar in its minute size, shape, fine radial sculpture, and fine marginal crenulation to the living abyssal Easter Pacific *Nucula chrisocoma* Dall, 1908 (Paul Valentich-Scott, personal communication, 2025).

The Keasey specimen is associated with small nuculanids and yoldiids in a gray siltstone matrix that differs lithologically from that of the classic crinoid lagerstätte. The exposure at the previously undifferentiated Mist locality has been measured and sub-divided subsequently into seven informal units (Burns et al. 2005), containing other Mist protobrachs that must be treated as part of a composite fauna at this time.

Figured specimen—UCMP 110776. Left valve exterior in matrix, length 3.9 mm, height 4.1 mm. Loc. UCMP A1810.

Stratigraphic occurrence—Upper part of the middle member of the Keasey Formation.

NUCULOMINAE Maxwell, 1988

As noted above nuculids that lack marginal crenulation are tentatively treated here as natural group based on the microstructural absence of radial laths in the lenticular nacreous layer of the shell. Microstructural features provide paleontologists with an important tool for testing relationships and evolutionary hypotheses in deep time. Even in the event of silicified shells, remnant microstructure can be preserved, at the same time preserving other features better than heavily altered original shell. However, the lack of marginal crenulation has led to taxonomic difficulties in defining and recognizing genus groups and created controversy discussed below.

ENNUCULA Iredale, 1931

Type species—By original designation, *Nucula obliqua* Lamarck, 1819. Holocene, Australia.

Stratigraphic range—Upper Cretaceous–Holocene.

Nuculids with relatively smooth shells, that lack distinct radial ribs and interlocking ventral crenulations, and with an unusually narrow and obliquely-elongate chondrophore separating anterior and posterior tooth rows on the hinge plate, have been treated under a variety of genus-group names. Many authors have synonymized *Ennucula* with *Leionucula*, Quenstedt, 1930 to recognize a poorly defined cosmopolitan group of species that ranges from Upper Cretaceous to Holocene. Without detailed study of adequate shell material and examination of anatomical features of living taxa in this complex, *Ennucula* is used provisionally here as a form genus. The living type species along with a yoldiid and material of smooth-margined nuculids collected more recently from New Caledonia (Bergmans 1991) may aid in resolving the significance of marginal crenulation.

If the lack of a crenulate margin defines a natural group, it was cosmopolitan by the Late Cretaceous, ranging geographically from low latitudes in Australia and New Zealand to high latitudes in the North Pacific and Atlantic. In the northwestern Pacific they are documented from three Paleogene formations eastern Hokkaido, Japan by Honda (1989) and subsequent authors who have favored use of *Leionucula*. Cenozoic species from The Russian Far East (Sakhalin and Kamchatka) originally described in *Ennucula* also have been reassigned to *Leionucula* (Kafanov et al. 2001).

Following Iredale, *Ennucula* has been favored by paleontologists for both living and fossil species in Australia and New Zealand. Cotton (1961) figured two additional living species of *Ennucula*, illustrating the distinguishing features as the notably prominent oblique chondrophore and the reduced size of the anterior hinge teeth beneath the dorsal edge of the chondrophore. He also called attention to similar Australian species in the deep-water fossil record. Darragh (1985) subsequently considered *Ennucula* a key taxon in 17 informal assemblage zones in his detailed treatment of the molluscan biogeography and biostratigraphy of middle Paleocene to late Pliocene

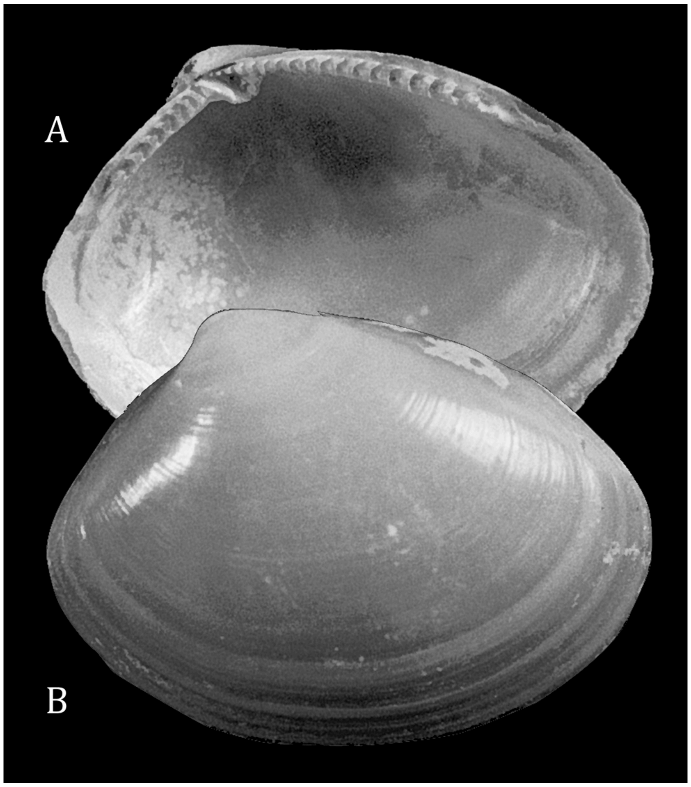

Figure 4. *Ennucula cardara* (Dall, 1916), Holotype of a living deep-water species of *Ennucula* from the Northeastern Pacific Margin. **A.** Left valve interior. **B.** Right valve exterior. USNM 265905. Length 16 mm.

basins of southern Australia. It is retained for six species in the most recent checklist of Australian marine Cenozoic Mollusca (Darragh 2024). *Ennucula* also has been retained by tradition in New Zealand (e.g. Powell 1979; Maxwell 1988, 1992; Beu and Maxwell 1990). However an early Paleocene species from New Zealand has been described as *Leionucula palaioanaxea* by Stilwell (1993), breaking with tradition to consider *Ennucula* a junior synonym. Zinsmeister (1984) also broke with tradition in describing two Eocene species from Antarctica. *Ennucula* remains in use for living nuculids with smooth margins from archipelagic Gondwanan fragments of the Scotia Arc and the southern Argentine Coast (e.g. Zelaya 2005, 2016) as well as species from southern Africa (Kilburn 1999). The most detailed comparative taxonomic treatment and illustration of living *Ennucula* includes 32 excellent images of the shells of six species from the temperate Southeastern Pacific from Northern Peru to Southern Chile (Valentich-Scott et al. 2020).

Although separation of *Ennucula* and *Leionucula* remains controversial there is a further knot in the taxonomic tangle: a third name *Nuculoma* Cossmann, 1907, based on a species from the Jurassic of northern Europe, also may be a senior synonym, and two additional genus-group names are available for smooth margined nuculids. The polylemma is not easily resolved, and the possibility of polyphyletic origin of the smooth-margined nuculids may simply represent multiple losses of the radial aragonitic laths that terminate to produce marginal crenulations. Well-preserved specimens of 6 distinctive nuculid species in the UCMP Cloez collection from the Paris Basin Eocene all have crenulate margins.

Ennucula is retained for the Keasey species described below and is consistent with its use for six living deep-water species from the temperate active margin of the northeastern Pacific (Coan et al. 2000) as well as species in the tropical eastern Pacific (Coan and Valentich-Scott 2012, and temperate southeastern Pacific (Valentich-Scott et al. 2020).

The holotype of the northeastern Pacific *Ennucula cardara* (Dall, 1916) (USNM 265905) is illustrated here (Fig. 4A, B) for comparison with the new Keasey species. Details of the hinge plate and long, narrow oblique chondorphore are strikingly similar.

Ennucula keaseyensis n. sp.

Fig. 5A–C

Nucula n. sp. Vokes n. sp. *in* Warren, Norbisrath and Grivetti (1945) (checklist)

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

ZooBank LSID—urn:lsid:zoobank.org:pub:77B08747-F088-4A46-BA5A-5580FAF0EEB3

Diagnosis—Shell moderately large for genus (length >10 mm); ovate-elongate, glossy, inequilateral with elongate anterior end; umbones low, opisthogyrate, situated in posterior quarter of length; paired valves moderately inflated, ratio of convexity to length approximately 40%; anterior margin convex, merging gradually with convex ventral margin; posterior margin short, nearly straight; escutcheon long and narrow, shallow, and delimited by shallow groove; valve surfaces with moderately strong, round-topped, faintly nodulose commarginal ribs with narrower shallow interspaces, no trace of radial ribs; ventral margin not crenulated; hinge plate arched, with prominent oblique-elongate chondrophore obscuring earliest and smallest anterior hinge teeth; hinge teeth chevron-shaped, short posterior row with estimated 10 teeth and long anterior row with estimated 25 teeth.

Discussion—Although not abundant, this species is distinguished by the combination of relatively large size and faintly nodulose commarginal ribs. Shell interiors are insufficiently exposed to characterize adductor muscle scars. Hinge plates are also too poorly exposed

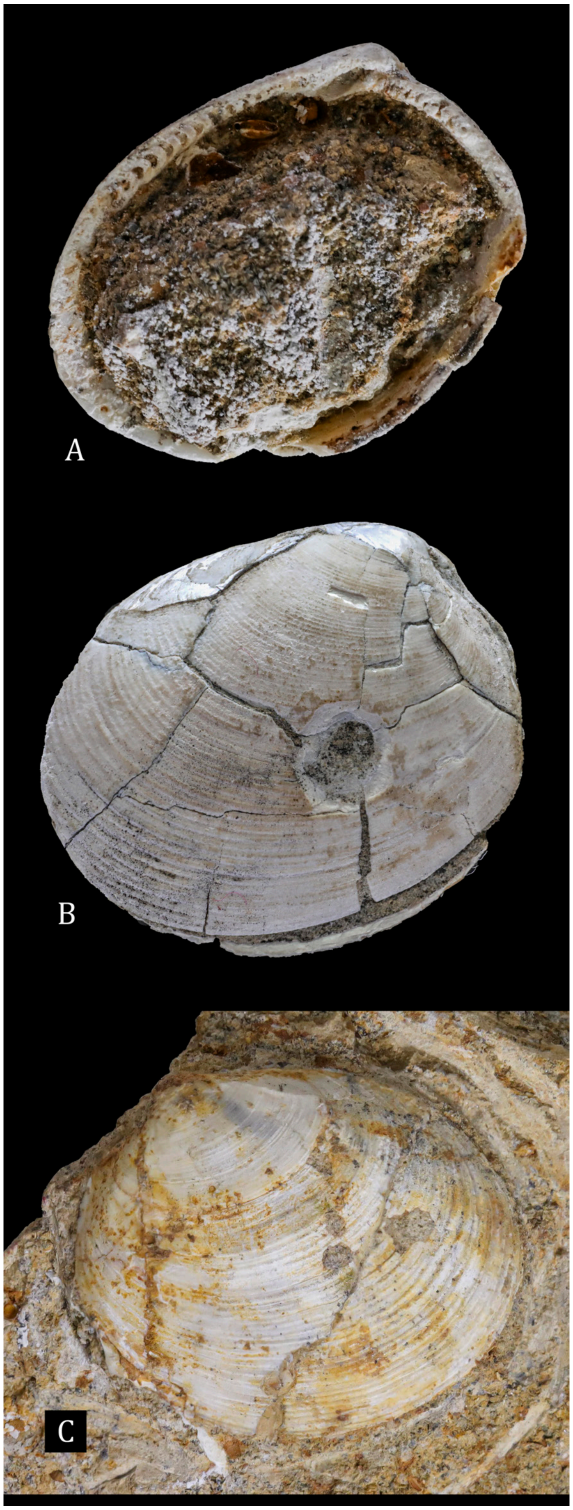

Figure 5. *Nucula* (*Ennucula*) *keaseyensis* n. sp. **A**. Holotype, right valve interior, hinge plate dentition, strongly oblique chondrophore, and non-crenulate ventral margin. USNM 561822, Loc. USGS 15318. Length 12.3 mm. **B**. Paratype, left valve exterior of double-valved naticid-drilled shell, concentric commarginal ribs, and non-crenulate ventral margins. USNM 561821, Loc. USGS 15279. Length 15.1 mm. **C**. Paratype, right valve in matrix. USNM 561832, Loc. USGS 15318. Length 11.7 mm.

to characterize in detail, but the holotype (Fig. 5A) illustrates the strongly-oblique chondrophore that obscures the small posterior hinge teeth in the anterior series and the difficulty in making accurate tooth counts. The species is best represented in the USGS collections from fresh highway and tunnel excavations in the 1940's and rare in subsequent collections from weathered outcrops. Larger size and lack of ventral marginal crenulations distinguish this species from two small-shelled Keasey *Nucula*. It differs from living Northeastern Pacific *Ennucula* species in its distinctive faintly nodular commarginal ribs.

Two additional Paleogene nuculids from the Cascadia Margin may be congeneric, but the condition of the ventral margin is not known. *Nucula (Leionucula) vokesi* Moore, 1976 from the overlying Pittsburg Bluff Formation is consistently less elongate, smaller, and smoother, lacking nodular swellings on the commarginal ribs. The hinge plate has fewer anterior and posterior teeth, although it shares a similarly oblique and strongly elongate chondrophore. *Nucula hannibali* Clark, 1925 from the Oligocene Blakeley Formation is also smaller and distinguished by fine radial ribbing. *Nucula (Ennucula) birchi* Keen, 1943 from the Miocene Round Mountain Silt and *Nucula postangulata* Clark, 1918 from the Oligocene San Ramon Formation are the only nuculid species from middle California that appear to lack marginal crenulations. Both are smaller (7 mm length) and also differ in lacking faintly nodular commarginal ribs.

Etymology—Named for the Keasey Formation, to which it is endemic at this time.

Material examined—19 specimens, including distorted and crushed shells that could not be measured.

Holotype—USNM 561822. length 12.3 mm, height 9.3 mm. Loc. USGS 15318.

Figured Paratypes—USNM 561821, (articulated, naticid drill hole in left valve) length 15.1 mm, height 11.7 mm, Loc. USGS 15279; USNM 561832, length 11.7 mm, height 9.4 mm, Loc. USGS 15318.

Unfigured Paratype—UCMP 110777, (incomplete articulated internal mold with shell fragments adhering to right and left valves, length 10.9 mm, height 11.1 mm, Loc. UCMP 7983 (=USGS 25026).

Type locality—USGS 15318 (=UCMP A5018) (middle member, Mist), Columbia Co., Oregon.

Other localities—Lower Member: USGS 15306, 15307, UCMP IP7983; Middle Member: USGS 15268 15279, 15280, 15282, 15283, 15318, 15508; Upper Member: USGS 15315, 15578.

Stratigraphic range and age—Restricted to the Paleogene *Bathybembix columbiana* molluscan zone of

Armentrout (1973) and the *Acila nehalemensis* biozone of Schenck (1936).

ACILA H. and A. Adams, 1858

Type species—By subsequent designation (Stoliczka 1871) *Nucula divaricata*, Hinds, 1843. Holocene, East China Sea, Japan Sea, Korea, Yellow Sea.

Species of *Acila* are easily recognized by their diagnostic divaricate, chevron-like sculpture. The genus group is most diverse and abundant in cold, deep water, where individuals are shallowly buried and often gregarious in fine sand, silt, and mud substrates. The depth range of the type species is 50–350 meters. Fossils frequently occur in assemblages on the margins of cold seeps. *Acila* s.s. is characteristically rostrate, with a posterior sulcus and indentation of the ventral shell margin. Living and fossil members of the genus group have been studied intensively by Schenck (1934, 1935, 1936, 1943).

Schenck's 1936 monograph has made *Acila* one of the best-known marine molluscan genera in the fossil record of Western North America. The truncate Cretaceous and Paleogene species from the Cascadia Margin have been treated consistently in separate clade from the younger rostrate forms of *Acila* s.s. that became more abundant in the Miocene.

Stratigraphic range—Lower Cretaceous (Aptian)–Holocene.

TRUNCACILA Grant and Gale, 1931 ex Schenck ms

Type species—By original designation, *Nucula castrensis* Hinds, 1843. Holocene, Northeastern Pacific.

The type species of *Truncaclia* is well represented in Museum collections. It is reported only from the Holocene in Alaska, British Columbia, Washington, and Oregon, but it is present from Miocene–Holocene in Northern California and Miocene–Holocene in Middle and Southern California (Moore 1983). The animals form dense populations, and specimens in lots of live-collected double-valved shells the UCMP collection show the exterior sculpture less well than fossil specimens due to brown periostracum and residual sediment.

Based on anatomical and functional study of more than 100 living specimens, Stasek (1961) documented a complex method of deposit feeding at the sediment-water interface in which particles are gathered, sorted, and rejected or selected for ingestion via a close functional association of (1) large, highly-extensible labial palps, (2) ciliated tracts on the labial palps, and (3) enlarged frontal cilia on the ctenidia. In all three methods of obtaining food, the substrate is the source of particles. However, the relative importance of direct capture from the substrate vs capture from inhalant currents is not clear. Also unclear is the relative importance of processing modes. It is a complicated system that may differ within species according to substrate conditions as well as between species. The paleontological significance of the work of Stasek is a cautionary correction to the earlier studies (e.g., Yonge 1939) concluding that labial palp deposit feeding was the ancestral mode of bivalve nutrition. Inhalant currents and ciliated ctenidial tracts capable of selecting or rejecting resuspended fine particles are part of nuculid deposit feeding. However, the system is highly evolved, and there is no theoretical reason why labial palps had to be present in the first nuculid, an Ordovician–Devonian genus with undisputed and diagnostic nuculid shell characters.

Truncacila is clearly differentiated from the rostrate species (*Acila* s.s.) by the prominent posterior truncation of the shell. The opisthogyrate beaks are situated posteriorly, immediately above the posterior truncation. An interior view of a hypotype of the living type species, UCMP 110768 (length 15.2 m, height 15.5 mm) is

Figure 6. *Acila* (*Truncacila*) *castrensis* (Hinds, 1843), interior view of left valve of the living type species of *Truncacila* from the Northeastern Pacific Margin. Hypotype, UCMP 110768 with pronounced posterior truncation, short posterior and long anterior tooth rows, and strongly oblique chondrophore with bordering large chondrophore tooth (bandgrubenzahn). Exterior shell sculpture obscured by dense periostracum, not illustrated. Length 15.2 mm.

illustrated here (Fig. 6) for comparison with the Keasey species.

Truncacila is well represented in Cretaceous rocks of Late Aptian through Maastrichtian age on the Northeastern Pacific Margin between the Queen Charlotte Islands, British Columbia and Baja California, Mexico. The record of nominate species is elegantly reviewed and illustrated by Squires and Saul (2006). Shallower and warmer settings of the Cretaceous record are in marked contrast to the increasingly cold Paleogene record of *Acila* from slope depths on the Cascadia Margin.

Stratigraphic range—Lower Cretaceous (Aptian)–Holocene.

Acila (Truncacila) nehalemensis G D. Hanna, 1924

Figs. 7A–D, 8A–D

Nucula (Acila) cordata Dall (1898). p. 573, not *Nucula cordata* Goldfuss (1838).

Nucula (Acila) cordata Dall, Dall (1909). p. 103.

Acila nehalemesis G D. Hanna (1924). p. 155.

Acila (Truncacila) nehalemensis G D.Hanna, Schenck (1934). p. 43.

Acila (Truncacila) nehalemensis G D. Hanna, Schenck (1935). p. 5.

Acila (Truncacila) nehalemensis G D. Hanna, Schenck (1936). pp. 57–63; figs. 1, 5–8, 10–12.

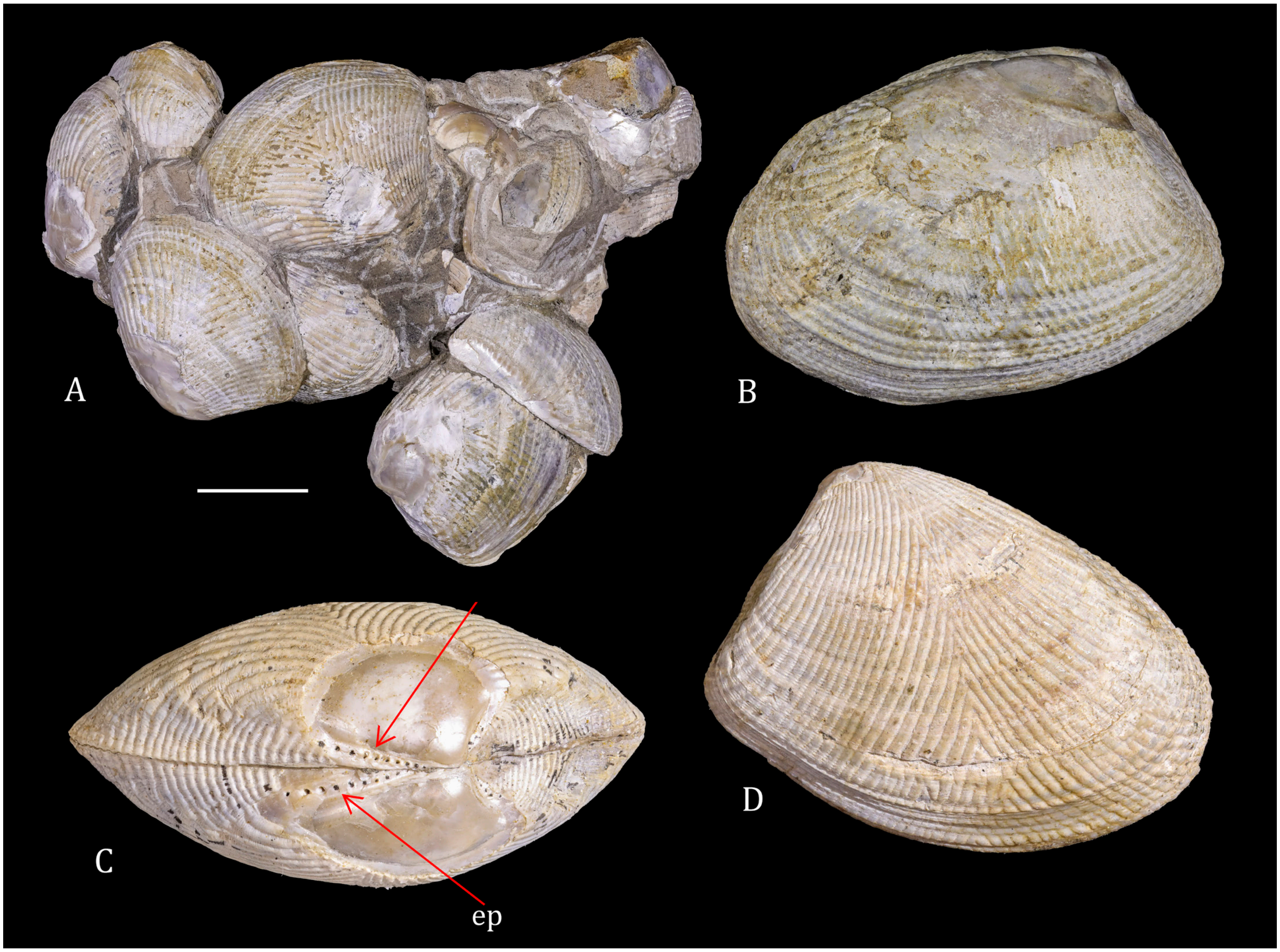

Figure 7A–D. *Acila* (*Truncacila*) *nehalemensis* hypotypes from fresh Keasey exposures, illustrating modes of preservation and diagnostic exterior shell features. **A**. Nodular concretion with many articulated shells; USNM 561837, loc. USGS 15602. Scale bar=1 cm. **B**. Left valve exterior of articulated hypotype with umbonal corrosion and concentration of ventral commarginal growth pauses; USNM561835, loc. USGS 15280. Length 31.3 mm. **C**. Dorsal view of articulated shell with umbonal corrosion and escutcheonal shell perforations (ep, red arrows); USNM 561834, loc. USGS 15280. Length 29.9 mm. **D**. Right valve exterior of articulated hypotype with ventral concentration of growth pauses and secondary bifurcation of radial ribs; USNM 561836, loc. USGSS 15282. Length 25.6 mm.

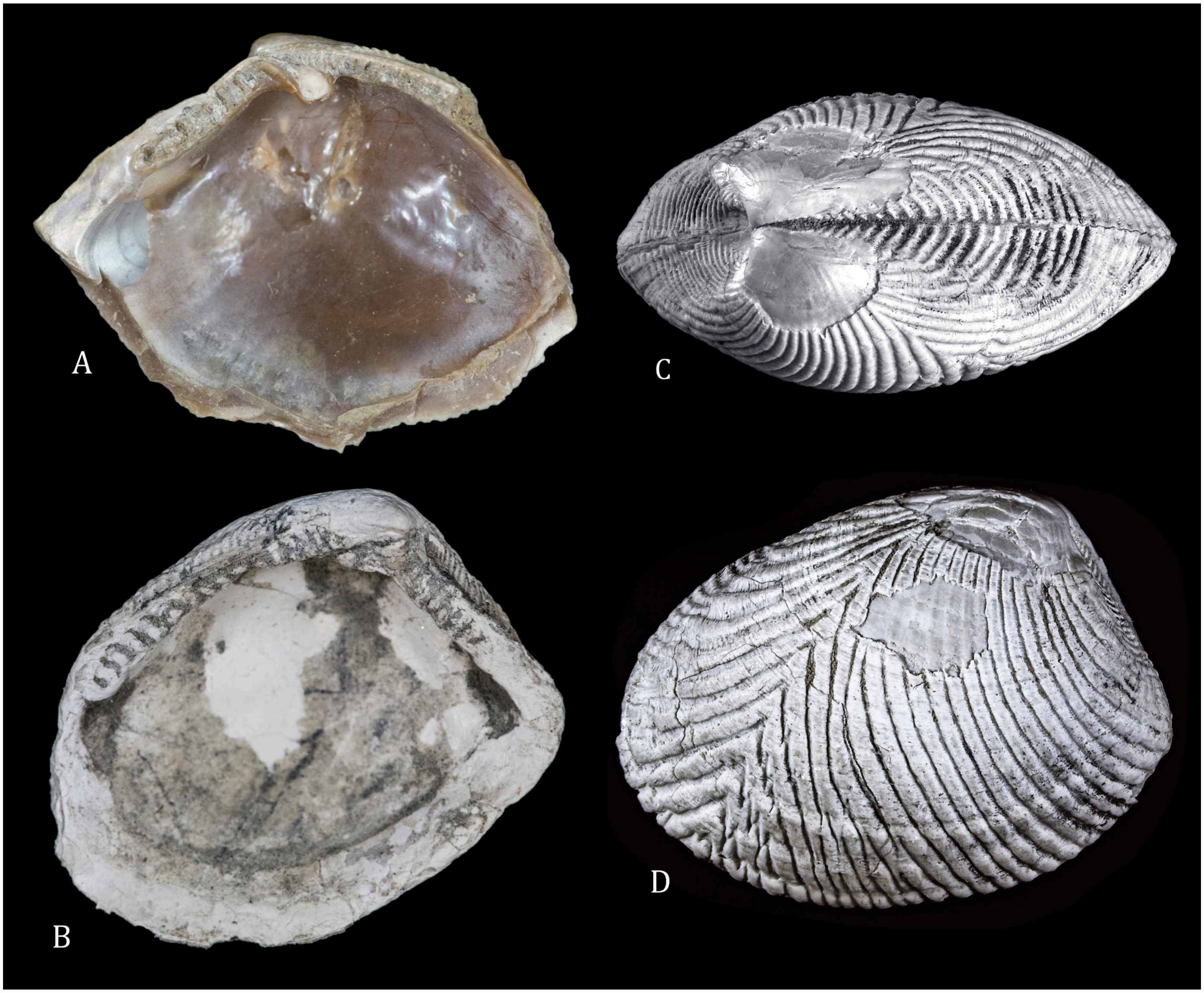

Figure **8A–D**. *Acila* (*Truncacila*) *nehalemensis* hypotypes from weathered outcrops with disarticulated shells and diagnostic interior features. **A.** Left valve interior with hinge plate, oblique chondrophore and bordering large chondrophore tooth (bandgrubenzahn) separating anterior and posterior tooth rows. UCMP 110765, loc. IP2297. Length 23.6 mm. **B.** Right valve interior with hinge plate, adductor muscle scars and entire pallial line. UCMP 110766, loc. IP2297. **C.** Dorsal view of articulated shell with corroded umbones. UCMP 110767, loc. IP7984. Length 17.5 mm. **D**. Left valve view of **C** (UCMP 110767) with umbonal corrosion, ventral growth pauses, and ventral secondary bifurcation of radial ribs.

Acila (Truncacila) nehalemensis G D. Hanna, Weaver (1937). p. 105.

Acila (Truncacila) nehalemensis G D. Hanna, Weaver (1943). p. 24; pl. 6, fig. 9.

Acila (Truncacila) nehalemensis G D. Hanna, Vokes, in Warren et al. (1945). checklist.

Acila nehalemensis G D. Hanna, Warren and Norbisrath (1946). p. 227.

Acila nehalemensis G D. Hanna, R.C. Moore and Vokes (1953). pp. 115, 118, 119.

Acila (Truncacila) nehalemensis G D. Hanna, Hickman(1969). pp. 24–25, pl. 1, figs. 1–3.

Acila (Truncacila) nehalemensis G D. Hanna, Armentrout (1973). pl. VIII, fig. 5

Acila (Truncacila) nehalemensis G D. Hanna, Burns et al. (2005). pp. 6, 9, 12, 13, 15, 18, fig. 8A.

Amended diagnosis and description—Schenck's detailed treatments of this species need no elaboration other than to note the prominent extension of radial ribs on the escutcheon (Figs. 7C, 8B); corrosion of the exterior aragonitic layer on the beaks and umbones during life, exposing the thick interior nacre (Figs. 7B, C; 8B, D), including escutcheonal "perforations" that represent the dorsal ends of hinge teeth (Fig. 7C, red arrows); the interior preservation of previously undocumented details of the hinge teeth, oblique chondrophore and the adjacent large chondrophore tooth (bandgrubenzahn of Quenstedt (1930) on the hinge plate of the left valve (Fig. 8A); and faint ventral crenulation of interior nacre, which does not extend to the margin (Fig. 8A). The exterior concentration at the ventral margin of commarginal growth pauses (Figs. 7B, D; 8D) along with a secondary ventral bifurcation of radial ribs (Figs. 7D, 8D) are a consistent features on large specimens.

Discussion—A proterotype of this species (USNM 107450) was figured by Dall (1898) but not described. Dall's name was preoccupied, but Hanna's (1924) rectification of nomenclature and new name did not provide a diagnosis or figure. Schenck (1934) published the first descriptions of Dall's primary type material, followed by a more detailed account (Schenck 1936) that serves as a combined diagnosis and description based on the primary types plus new material (Stanford and CAS hypotypes) from what he considered the type locality or "near the type locality" at Mist (=UCMP A5018). The well-preserved hypotypes figured here are from exposures in fresh roadcuts and two formerly active quarries that were not available to Schenck.

The escutcheonal perforations of the thick inner nacreous layer (Fig. 7C) are remarkable as a previously un-noted feature in Cenozoic acilas. Their interpretation as bases of dental sockets merits additional comment. There are literature references to shell perforations along the margins of both the escutcheon and lunule of fossil nuculoid bivalves as early as the Ordovician (McAlester 1963) and Pennsylvanian (Driscoll 1966) as well as the Cenozoic (Sorgenfrei 1936, Trueman 1952).They have been variously interpreted as the bottoms of tooth sockets that have perforated mantle secretory tissue or as points of muscle insertion of an external ligament.

Schenck included a separate table of measurements of length, height, thickness, umbonal angle, angle of bifurcation, and ratio of height to length. However, detailed descriptive features and measurements do not separate it from other species of *Acila (Truncacila)*, and many of his descriptive terms differ from those in current usage as defined and illustrated by Carter et al. (2012).

In addition to Dall's *Nucula (Acila) cordata* (a preoccupied name), there are additional Dall references to earlier 19th century nuculid names (also preoccupied) proposed by Timothy Abbott Conrad and William More Gabb. Resolution of this taxonomic morass is beyond the scope of this treatment.

Many citations of the author of this species—G Dallas ("Doc") Hanna of the California Academy of Sciences—incorrectly place a period after the "G". It is correctly attributed above and in the Literature Cited. Dall's 1898 specimen USNM 107459 is the holotype of the species.

Material examined—More than 100 articulated and well-preserved specimens were studied in addition to observations of collected material that included disarticulated whole valves, well-preserved fragments, molds, concentrations of articulated specimens in nodular concretions and bedding-plane concentrations on rock slabs. Variation in preservation provides an unusually clear picture of many important features and variation in their expression. There is little or no evidence of significant post-mortem (biostratinomic) alteration by exposure or transport. Fragmentation occurs primarily at weathered outcrop surfaces and during collection.

Figured hypotypes—USNM 561834, length 29.9 mm, height 21.1 mm, Loc. USGS 15280 (articulated); 561835, length 31.3 mm, height 24.2 mm, Loc. USGS 15280 (articulated); 561836, length 25.6 mm, height 17.7 mm, Loc. USGS 15282 (left valve); 561837, Loc. USGS 15602 (concretion with many specimens); UCMP 110765, length 23.6 mm, height 18.1 mm, Loc. UCMP IP23031 (incomplete right valve); 110766, length 23.1 mm, height 18.7 mm, Loc. UCMP IP2297 (right valve); 110767, length 17.5 mm, height 14.1 mm, Loc. UCMP IP7984 (articulated); UWBM 97632 length of large slab approximately. 30 cm.

Keasey Localities—Lower member: USGS 2717, 15263, 15265, 15307, 15308, 15309, 15584; UCMP IP7983, 2286, 2536, 2537. Middle member: USGS 15267, 15268, 15274, 15275, 15279, 15280, 15281, 15282, 15283, 15384, 15285, 15313, 15316, 15318, 15508, 15517, 15602, 2712, 2723, 5390; UCMP A5018, 2538, 2539, 2541, 2543, 2544, 2545, 7984. Upper member: USGS 15315. UCMP IP2540.

Other Occurrences—In Oregon this species also occurs in the lowermost (Keasey equivalent) beds of the Eugene Formation and at Holmes Gap, northwest of Salem in Polk County. In southwestern Washington it has been collected at many outcrops on the Willapa River near the community of Holcomb along with typical Keasey species, including *Bathybembix Columbiana* (Dall, 1909). The Willapa River section has been variously treated as "lower Keasey equivalent beds" (Hickman 1980), Lincoln Creek Formation (e.g., Armentrout 1973), Keasey Formation (e.g., Squires and Goedert 1991), and "Keasey beds" (e.g., Nesbitt et al. 1994). The fauna is typical of the type section of the Keasey Formation, and the Willapa River section has been treated by this author as Washington Keasey throughout monographic treatments of the Keasey gastropods and bivalves.

Stratigraphic range and age—Restricted to the Paleogene *Bathybembix columbiana* molluscan zone of Armentrout, 1973. This species figures prominently in a long history of stratigraphic classification on the Cascadia margin of Oregon and Washington. The *Acila nehalemensis* biozone is stratigraphically lowest of the three *Acila* biozone species of Schenck (1936), followed by *A. shumardi* Dall, 1909 and *A. gettysburgensis* Reagan, 1909. Schenck's three superpositionally distinct biozones have rough equivalents or correlates in the regional (Oregon and Washington) rock-stratigraphic, time-stratigraphic, and biostratigaphic classifications of many authors (e.g., Arnold and Hannibal 1913, Weaver 1916, Durham 1944, Weaver et al. 1944, Armentrout 1973, 1975, 1981, Armentrout et al. 1983). These are increasingly well correlated with international chronostratigraphic ages and California benthic foraminiferal stages (Nesbitt 2018).

In view of the significance of the acilas in Cenozoic biostratigraphy on the Cascadia Margin, comparative treatments of two superpositionally important Paleogene species from the Eugene and Pittsburg Bluff Formations in Northwestern Oregon are included below.

Acila (Truncacila) minima (Hickman, 1969)

Fig. 9A–D

Acila (Truncacila) nehalemensis minima Hickman (1969). pp. 25–26; pl. 1, figs. 1–3.

Discussion—Originally described as a subspecies of *Acila (Truncacila) nehalemensis*, the consistently small shells are recognized here as a distinctive species, with many of the same features of large adult shells of the Keasey species. They typically occur on bedding planes as articulated and single whole valves (<10 mm in length) along with larger shells of Eugene mollusks that do not occur in the Keasey Formation. They do not represent size-sorted concentrations of juveniles. A siltstone slab noted in the original description (Hickman, 1969, p. 26) as containing 59 specimens could not be relocated in collections at the University of Oregon (Edward Davis, written communication 2024). A smaller mini-slab from UCMP collections is figured here, illustrating the distinctive association of bivalve and gastropod taxa (Fig. 9C).

The holotype, refigured here (Fig. 9A), illustrates the same ventral concentration of commarginal ridges and secondary divarication of radial ribs that occur only in large specimens of *Acila (Truncacila) nehalemensis*. They have fewer and wider radial ribs and interspaces than *Acila (Truncacila) shumardi* (Dall, 1898) in younger strata of the Pittsburg Bluff Formation and the upper portion of the Eugene Formation. A distinguishing feature not noted in the original description is crenulation of the ventral margin of the commissure, expressed in the microstructure of both inner and outer nacreous shell layers (Fig. 9D).

The distinctive stratigraphic succession of these three species is noteworthy because it interpolates a third taxon as a biostratigraphic tool for correlating Paleogene strata of the Cascadia Margin. The Miocene *Acila (Acila) gettysburgensis* (Reagan, 1909) is not treated here, but further biostratigraphic resolution, including the Miocene–Holocene type species of *Truncacila* merits future attention. The provincial Neogene record is well documented by Moore (1963).

No attempt is made here to re-evaluate *Acila (Truncacila) decisa* (Conrad, 1855). Described by Conrad as *Nucula (Acila) decisa*, the name correctly applied to a large complex of Paleocene and earlier Eocene small-shelled acilas (<10 mm length) in mudstone and siltstone facies in central and southern California. Schenck (1936, pp. 53–56) provides a long synonymy and discussion of the names, authors, localities, and formations ranging from Washington state to San Diego, California. Moore (1983) reviews the California occurrences and broader range into Alaska and Kamchatka. Small double-valved specimens of *Acila (Truncacila) decisa* have been reported from earlier Eocene localities in the Coaledo Formation at Coos Bay and the Spencer Formation west of Eugene. Coaledo and Spencer specimens collected by the author are insufficiently well preserved for detailed comparison with Eugene specimens of *A. minima*. A lot of more than 33 articulated Coaledo shells range in length from 4 to 10.5 mm. They lack the ventral concentration commarginal growth pauses, and valves are less inflated and more variable in shape. Although they show evidence of taphonomic distortion and flattening, compressional forces were insufficient to crack any of the shells.

A closer comparison can be made with a younger small-shelled species, *Acila muta* Clark, 1918, described from the San Ramon Sandstone in Contra Costa County, California. The shell is truncate, lacks a rostral sinus, and shares secondary bifurcation of radial ribs and growth checks near the ventral margin. Shell shape is less elongate and more ovate. The San Ramon species is not easily correlated with small truncate species from the Cascadia Margin, although Schenck (1936) considered it of probable late Oligocene age. The younger age is supported by account of specimens identified as *A. muta* from a

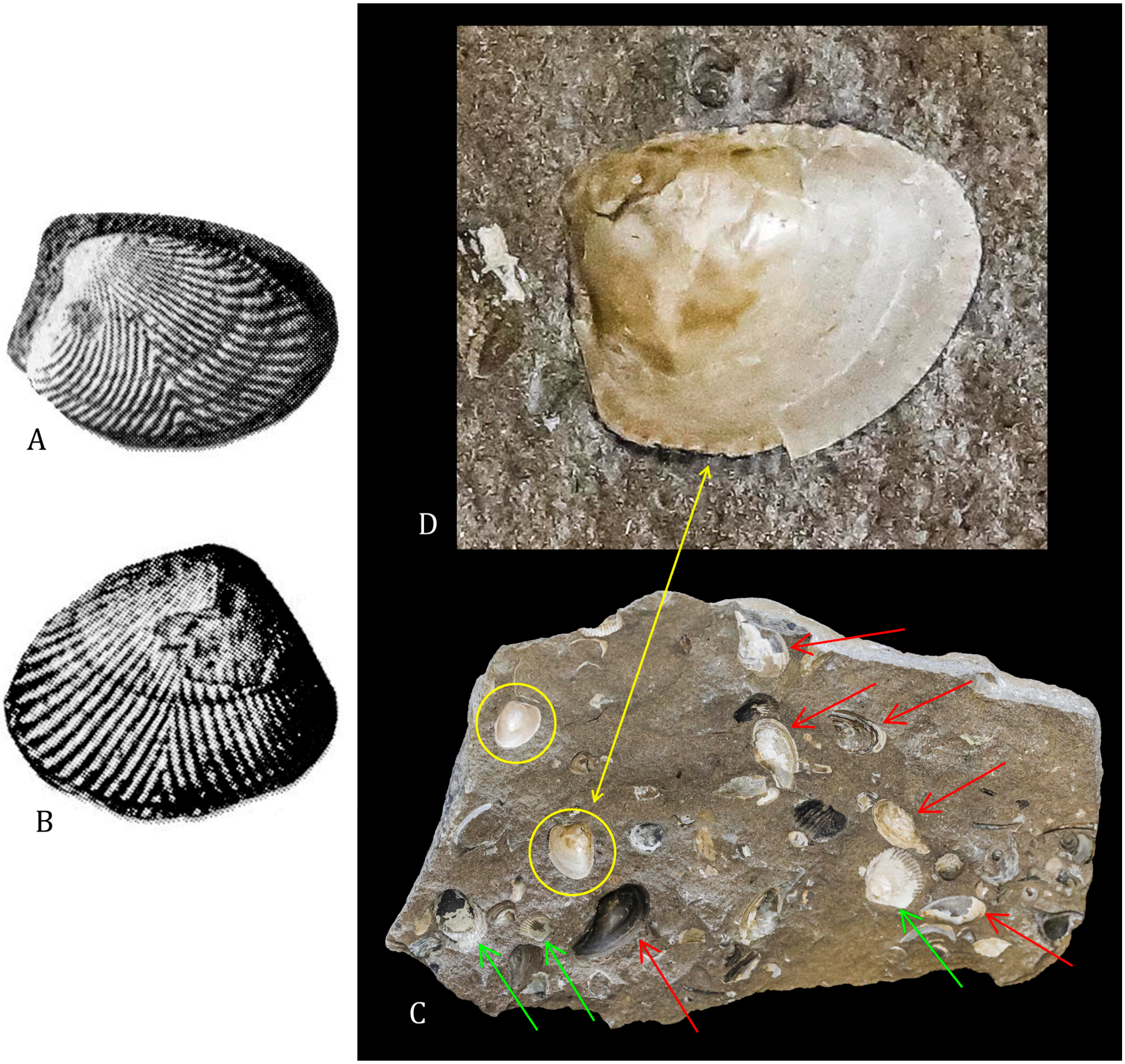

Figure 9A–D. *Acila* (*Truncacila*) *minima* from the Eugene Formation, originally described as a minute-shelled, successionally younger, subspecies of *Acila* (*Truncacila*) *nehalemensis*. **A.** Refigured holotype (right valve), UO 27169, UO Loc. 2531. Length 10.5 mm. **B.** Refigured paratype (left valve). UO 271170, UO loc. 2531. Length 8 mm. **C.** Small slab (length 10 cm) with two hypotypes (yellow circles) from the Eugene Formation, UCMP 110769 (lower circle), length 9 mm, and UCMP 110770 (upper circle), length 8 mm, with typical associated nuculanids (red arrows) and a small *Parvicardium* (green arrows), Loc. IP25765. D. Enlarged view of hypotype UCMP 110769 with interior crenulation of nacre and broken radial laths.

mixed assemblage of reworked shells in an unnamed conglomerate and sandstone in the upper member of the Twin River Formation Addicott (1976a). His illustration, reproduced here (Fig. 10), also shows clear evidence of secondary bifurcation and growth pauses near the ventral margin, consistent with inference that it is an adult and not a small juvenile. The presence of a giant limid bivalve in this assemblage suggests a deep-water site of deposition, and the presence of a lucinid bivalve adds a cold seep signature.

Figured Hypotypes—UCMP 110769, length 9.0 mm, height 8.0 mm, (interior, left valve in matrix);

UCMP 110770, length 8.1 mm, height 6.1 mm, (interior right valve in matrix). Both on slab from Loc. UCMP IP25765.

Material examined—More than 100 articulated

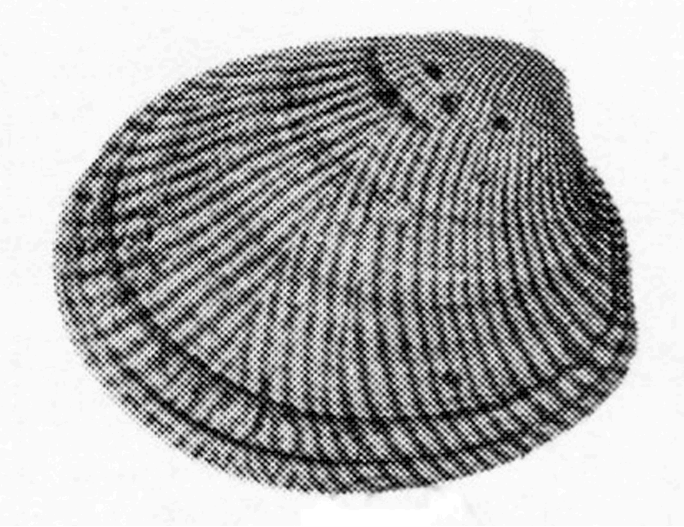

Figure 10. *Acila* (*Truncacila*) *muta* from the Twin River Formation, refigured from Addicott (1976), hypotype USNM 219821, loc. USGS M4682. Length 11 mm.

shells and shells in mixed faunal assemblages on slabs collected by the author and USGS Menlo Park material (now in the UCMP Invertebrate Paleontology collection).

Localities—UO27169 (type locality), UO27171, 27172, 27173, 27174, 27175, 27176; Loc. UCMP IP25765).

Stratigraphic range and age—Restricted to an unnamed regional biozone between the Paleogene *Acila nehalemesis* and *Acila shumardi* biozones of Schenck (1936, p. 42) all of which are superpositionally below the Neogene *Acila gettysburgensis* biozone. As defined by Schenck, biozones are lithostratigraphic units—rocks formed "during the total existence of a species, indicated by absolute range". As a working hypothesis, the intercalation of an *Acila minima* biozone suggests that the poorly documented contact between the Keasey and Pittsburg Bluff is nonconformable.

Acila (Truncacila) shumardi (Dall, 1909)

Fig. 11A–D

Nucula (Acila) decisa Conrad, Dall (1898). p 573.
Acila (Acila) decisa Conrad, Dall (1900). pl. 40; figs. 1,3.
Nucula (Acila) shumardi Dall 1909. p. 103.
Nucula (Acila) shumardi Dall, Clark (1925). p. 75; pl. 8, fig. 11.
Nucula (Acila) shumardi Dall, Tegland (1933). p. 107; pl. 5, fig. 10.
Acila (Truncacila) shumardi Dall, Schenck (1936). pp 64–67; pl. 4, figs. 5–7, 9; pl. 6, figs. 1–11.
Acila (Truncacila) shumardi Dall, Weaver (1943). pp. 25–26; pl. 7, figs. 5–7, 11; pl. 8, figs. 2,5.
Acila (Truncacila) shumardi Dall, Hickman (1969). pp. 26–27; pl. 1, figs. 6,7,10.
Acila (Truncacila) shumardi Dall, Moore (1976), pp., 42–43; pl. 8, figs 1–9, 11, 12, 14, 15, 18.

Figure 11. *Acila* (*Truncacila*) *shumardi* hypotypes from the Pittsburg Bluff Formation. **A.** Left valve exterior with fine, closely-spaced radial ribs, UCMP 110773, Loc. IP 256649. Length 22.6 mm. **B.** Right valve interior with strongly oblique chondrophore separating anterior and posterior tooth rows and faintly crenulate ventral margin, UCMP 110772, Loc. IP 25910. Length 23.3 mm. **C.** Dorsal view of articulated shell, UCMP 110771, Loc. IP 25910. Length 23.9 mm.

Discussion—The detailed treatment of this species by Schenck (1936) included re-description of the type material, a supplementary description of many well-preserved specimens from the type locality in the Pittsburg Bluff Formation, and 15 figures. Moore (1963) refigured the holotype, and specimens from additional localities along with a description of variation in features that aid in distinguishing it from all other truncate acilas. Whereas Schenck did not have adequate material to describe the shell interior, Moore emphasized description of exposed hinge plates. However, *A. shumardi* is most clearly distinguished from *A. nehalemensis* by the finer radial ribs and narrower interspaces. The two species are of similar adult size, similarly inflated, and specimens are typically articulated. It is figured here to illustrate the more finer, more subdued sculpture (Fig. 11A, C), the lunule and escutcheon in dorsal view as well as a similar corrosion exterior shell of beaks that exposes the underlying the underlying nacre (Fig. 11C) and the interior of a left valve (Fig. 11B) to illustrate the presence of the large chondrophore tooth (bandgrubenzahn) bordering the posterior margin of the strongly oblique chondrophore and resilial pit.

Material examined—Many specimens from the Pittsburg Bluff Formation and uppermost Eugene Formation have been examined in the course of this and earlier studies, and those collected by the author were deposited in the University of Oregon Condon Collection and Natural History Museum. During the preparation of this monograph more that 100 specimens from USGS Menlo Park localities (now in the UCMP Invertebrate Paleontology collection) were examined, including the three hypotypes are illustrated here . Some of the USGS lots contain entire disarticulated valves preserving otherwise poorly known features of the hinge plate and shell interior.

Figured hypotypes—UCMP 110771, length 23.9 mm, height 18.6 mm, Loc. UCMP IP25910 (articulated). UCMP 110772, length 23.3 mm, height 19.2 mm. Loc. UCMP IP25649 (left valve). UCMP 110773, length 22.6 mm, height 19.0 mm. Loc. UCMP IP25649 (right valve).

Stratigraphic range and age—Restricted to the Paleogene (lower Oligocene) *Acila shumardi* biozone of Schenck (1936).

SAREPTIDAE Stoliczka, 1870

SAREPTA A. Adams, 1860

Type species—By original designation, *Sarepta speciosa* A. Adams, 1860. Holocene, Japan.

Stratigraphic range—Upper Cretaceous (Maastrichtian)? Paleocene—Holocene.

Very small, non-crenulate, non-nacreous, sub-ovate, equilateral to slightly inequilateral shells with evenly rounded anterior and posterior margins and absence of distinctive exterior sculpture have been difficult distinguish as Nuculoid or Nuculanoid without knowledge of anatomy Allen 1992). Miniaturization and loss of nacre, as recurring themes in deep-sea protobranch evolution, compound the difficulty of taxonomic placement. The genus *Sarepta* has eluded consistent allocation within the protobranchs, having been placed within the nuculoids (e.g., Ockelmann and Warén 1998, Bouchet and Rocroi 2010), nuculanoids (e.g., Cotton 1961, Puri 1969, Knudsen 1970, Allen and Hanna 1986, Maxwell 1988, Reid 1998), and separately as sareptoids (e.g., Huber 2010, Sharma et al. 2013, Sato et al. 2020). Combined analyses based on molecular and shell microstructural data are consistent with recognition of a separate sareptoid clade (Sato et al. 2020) but the later authors suggested the need for anatomical data and inclusion of additional potential species of *Sarepta*.

Minute bivalve shells of two new species in the Keasey fauna represent the first recognition of *Sarepta* in the fossil record of the Northeastern Pacific and are treated here as nuculoids based in part on their similarity to Paleogene species from southern Australian margin. The Australian specimens are typically better preserved, with a record from localities in the Otway Basin, St Vincent Basin, Bremer Basin, and Southern Carnarvon Basin (Darragh 1985, Darragh and Kendrick 2000, 2008). An additional species from Perth Basin, Western Australia (Stilwell 2005) extends the geographic record to the west Australian margin.

The living Australian species described as *Sarepta tellinaeformis* Hedley, 1901 provides a strong anatomical and functional argument for treating sareptids as nuculoids and is here considered a probable synonym of the type species. It is figured by Cotton (1961) in four excellent drawings (Fig. 13) of the shell interior, including an elongate-oblique chondrophore and a pallial line that lacks a sinus. The presence of siphons and a corresponding pallial sinus is a hallmark of the nuculanoids with their deeper infaunal mode of life. Siphons are absent in the shallow-burrowing and miniaturized epipsammic nuculoids. A further anatomical distinction of the nuculoids from nuculanoids is the relationship of the gill axis to water flow. The cetenidial axis is inclined to the hinge line and perpendicular to the anterior inhalant current in nuculoids and parallel to the hinge line and posterior inhalant-to-exhalant siphonate flow in nuculanoids (Sanders and Allen 1973, fig. 22).

The two new minute-shelled Keasey protobranchs are assigned to *Sarepta* and described below along with a third microprotobranch assigned to *Pristigloma* Dall, 1900 in the Pristiglomidae Sanders and Allen, 1973. The higher classification of these distinctive new Keasey protobranchs is disputable without better-preserved specimens and morphological support. However, the three species present an opportunity for new discoveries in the field and the need to resist the traditional lure of well-preserved trophy specimens of the larger-shelled Keasey mollusks.

In the meantime there is a fundamental nomenclatural roadblock to classification of slightly elongate species of *Sarepta* in the traditional nuculanoidean family Yoldiidae Dall, 1908. Because Sareptidae has priority over Yoldiidae, the family has been characterized in the literature not by the genus *Sarepta* but by well known large-shelled, rostrate and siphonate living species of *Yoldia* (e.g., Reid 1998).

Sarepta oregonensis n. sp.

Fig. 12A–C

ZooBank LSID—urn:lsid:zoobank.org:pub:77B08747-F088-4A46-BA5A-5580FAF0EEB3

Diagnosis—Shell small (<10 mm), moderately inflated; outline elongate-ovate, nearly equilateral; dorsal margins equally declivous; anterior dorsal margin with shallow, narrowly-elongate poorly-demarcated escutcheon, posterior dorsal margin lacking lunule; umbones low. beaks small, pointed, opisthogyrate, slightly anterior to midline; anterior margin evenly rounded, posterior margin more narrowly rounded but not rostrate; ventral margin shallowly convex, not crenulate; surface smooth and glossy with low sculpture of rounded, evenly spaced commarginal undulations; hinge plate and interior not preserved in available material.

Discussion—Three specimens assigned here to *Sarepta* are all from the classic Mist crinoid locality and constitute the first report of the genus from the Cenozoic fossil record of the Northeastern Pacific. The holotype (Fig. 12A) and one of the paratypes (Fig. 12B) are from a siltstone faces above the main crinoid layer at the type locality, and a second smaller paratype (Fig. 12C) is from the main crinoid layer and associated with crinoid remains.

Etymology—The name recognizes the geographic provenance of the first Cenozoic report and species description of a fossil sereptid from Northeastern Pacific.

Type locality—UCMP IP16000. At the Mist crinoid locality, IP16000 is in the bluff stratigraphically above the main crinoid layer in a calcareous siltstone facies originally described by Burns et al. (2005). Although the holotype (UCMP 110778) and one of the paratypes (UCMP 110779) are from the siltstone facies, an additional paratype (USNM 561808) is part of an earlier collection from the main crinoid layer (USGS 15318). It was recognized by Harold Vokes as an undescribed species of Sarepta. Although Moore and Vokes (1953) did not list it as part of the invetebrate fauna associated with the crinoids, Vokes assigned a USNM type number to the specimen.

Material examined—Three specimens in matrix.

Holotype—UCMP 110778. (articulated and removed from matrix, after photography and archived along with original matrix with cast of the exterior of the left valve). Length 5.5 mm, height 4.2 mm, Loc. UCMP IP16000 (siltstone facies above main crinoid layer**)**.

Figured paratypes—UCMP 110779**.** Right valve exterior in matrix, length 6.9 mm, height 4.5 mm, Loc. UCMP IP16000. USNM 561808. USNM 156809, length 2.4 mm,

Figure 12. *Sarepta oregonensis* n. sp. **A.** Articulated holotype photographed in matrix prior to removal, UCMP 110778, loc. IP16000 (bivalve/cold-water coral tuffaceous siltstone layer at Mist crinoid locality and cold seep). Scale bar=5 mm. **B.** Paratype UCMP 110779, loc. IP16000 (bivalve/cold-water coral tuffaceous siltstone layer). Scale bar=5 mm. **C.** Paratype USNM 561808, loc. USGS 15318 (Mist crinoid layer). Scale bar=1 mm.

height 1.7 mm, Loc. USGS 15318 (main crinoid layer).

Unfigured paratype—USNM 561809. Length 2.4 mm, height 1.7 mm.

Stratigraphic occurrence—Known only from the type locality in the upper part of the middle member of the Keasey Formation.

Sarepta nascif n. sp.

Fig. 13A, B

ZooBank LSID—urn:lsid:zoobank.org:pub:77B08747-F088-4A46-BA5A-5580FAF0EEB3

Diagnosis—Shell small (<10 mm), thin, fragile, shallowly inflated, equilateral; outline ovate to elongate-ovate; dorsal margins very shallowly concave to nearly straight, merging gradually with rounded anterior and posterior margins; ventral margin convex; surface with numerous commarginal threads alternating with narrow, deeply-incised interspaces; hinge plate and shell interior not exposed.

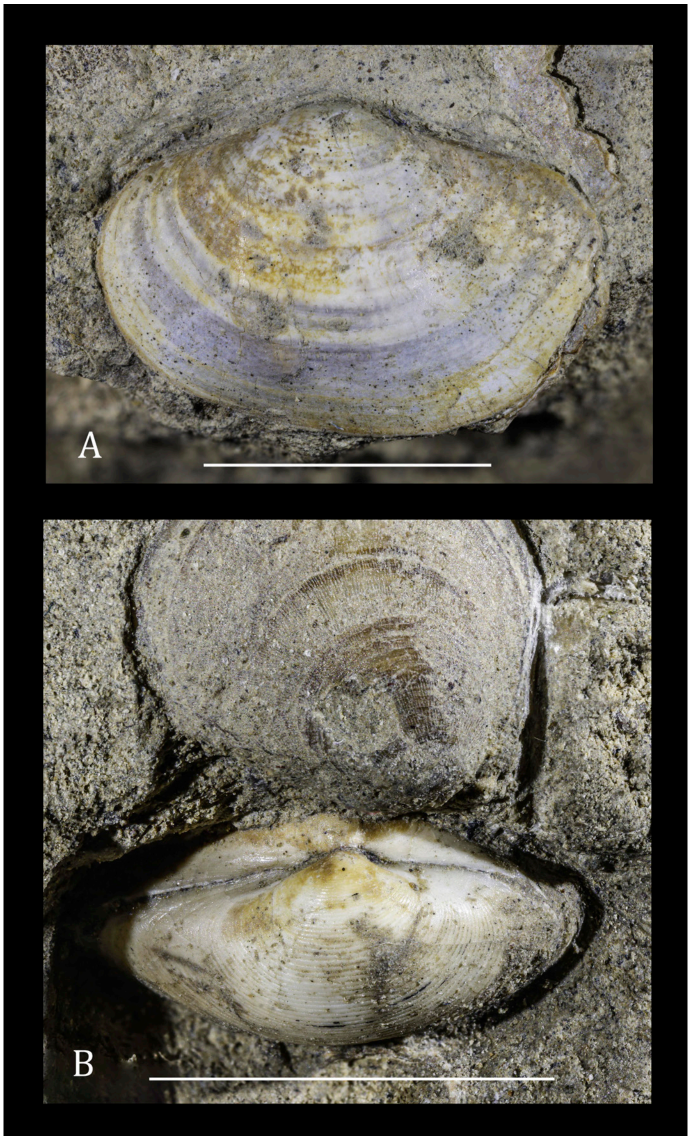

Figure 13. *Sarepta nascif* n. sp. A. Holotype, exterior, left valve in matrix, UCMP 110780, loc. IP2537 length 7.9 mm, scale bar=5mm B. Paratype, dorsal view of articulated shell in matrix, UCMP 110781, loc. IP2537, length 6.6 mm; adjacent to shell of *Delectopecten kieli* Hickman, 2023. Scale bars=5 mm.

Discussion—This distinctive species is distinguished from *S. oregonensis* by its thinner, less inflated, more fragile shell and finer commarginal sculpture. Although only two specimens have been designated as types, many incomplete shells and fragments were recovered from disaggregated matrix containing a diverse faunal assemblage dominated by *Delectopecten kieli* Hickman, 2023, echinoid spines, and fish scales and shark teeth along with *Acila nehalemensis*, nuculanid bivalves yet to be described, and a diverse fauna of rarer gastropods, including *Turrinosyrinx nodifera* Hickman, 1976 and *Conus weltoni* Hickman, 1980, species that also are restricted to the lower member of the Keasey Formation. A sample of protobranchs from the type locality, including many poorly preserved tentatively identified specimens of the sareptid, is illustrated in Figure 14.

Etymology—Named in recognition of grant support for fieldwork from the U.S. National Science Foundation.

Type locality—UCMP IP2537 and a closely adjacent outcrop at UCMP IP2536.

Material examined—In addition to the holotype and paratype specimens in matrix many incomplete shells and fragments as noted above.

Holotype—UCMP 110780, left valve exterior in matrix, length 7.9 mm, height 6.9 mm. loc. UCMP IP2537.

Paratype—UCMP 110781, dorsal portion of articulated shell in matrix, length 6.6 mm, height not measurable, loc. UCMP IP2537.

Stratigraphic occurrence—Known only from the type locality in the lower member of the Keasey Formation.

PRISTIGLOMDAE Sanders and Allen, 1973
PRISTIGLOMINAE Sanders and Allen, 1973
PRISTIGLOMA Dall, 1900
(*nom. nov. pro*. *Glomus* Jeffreys, 1876, non Gistel, 1848)

Type species—By monotypy, *Pristigloma nitens* Jeffreys, 1876, Holocene, North Atlantic, widespread and represented in the living northeastern Pacific deep-water fauna.

Stratigraphic range—Upper Cretaceous (Maastrichtian)–Holocene.

Although pristiglomid anatomy is complex, the shell is

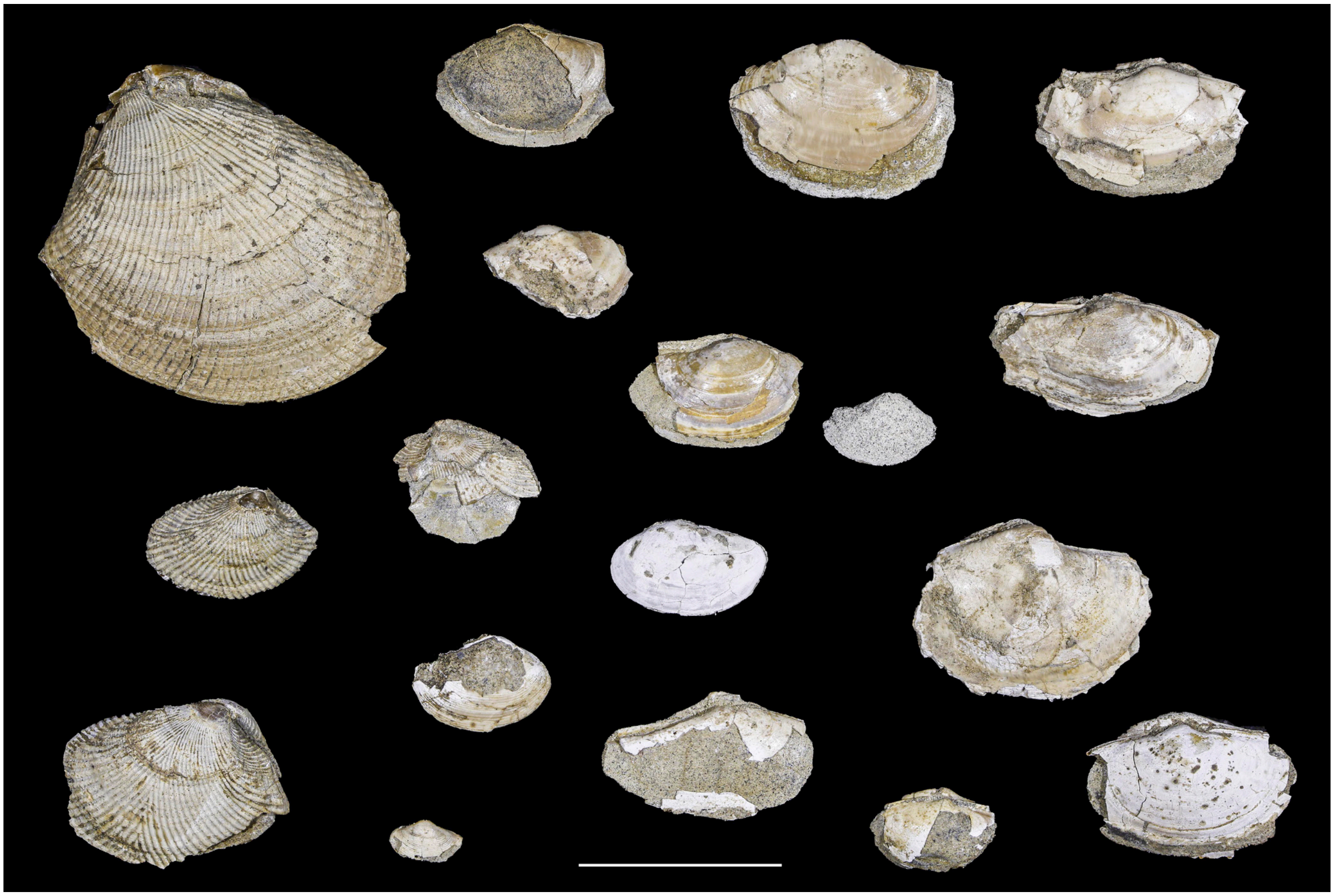

Figure 14. A typical sample poorly-preserved but abundant nuculid, sareptid, and nuculanid bivalves extracted from matrix at UCMP IP2537, where *Sarepta nascif* is associated with easily recognized small *Acila* (*Truncacila*) *nehalemensis*. Scale bar = 1 cm.

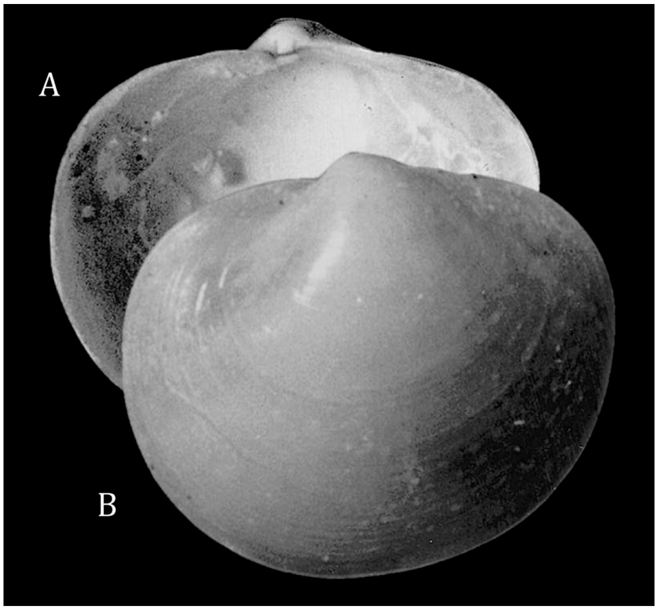

Figure 15. *Pristigloma nitens* (Jeffreys, 1876), a specimen of the living type species of *Pristigloma* from deep water off the Coast of Vancouver Island, British Columbia, illustrating smooth, thin, fragile shell and ovate shape. **A**. right valve interior of double-valved specimen. **B**. Left valve exterior. LACM 68-249. Length 3 mm.

remarkably lacking in distinctive features. Lack of nacre (Sato and Sasaki 2015) may be a result of evolutionary loss. A specimen of the living type species of *Pristigloma* from deep water off the coast of Vancouver Island, British Columbia (Fig. 15) illustrates the ovate shape that typically distinguishes pristiglomids from sareptids. Treatment of *Pristigloma* in the Treatise of Invertebrate Paleontology (Puri 1969) recognized the genus as “Recent” and “cosmopolitan” and did not include an illustration. Recognition in the fossil record is long overdue.

The minute, smooth, thin, non-nacreous shells of *Pristigloma* and Pristiglomidae are distinguished from those of the similarly miniaturized shells of *Sarepta* and Sareptidae primarily by their weak inflation more ovate shape. Recognition of the shells of both families as protobranchs can be confirmed only by presence of a hinge plate with taxodont dentition. It is therefore not surprising that this is also the first report of both families in the fossil record of the Northeastern Pacific margin. Small size increases the probability of being overlooked in the field. However, major anatomical differences in living specimens enabled Sanders and Allen (1973) to describe pristiglomids as a distinct family. Allen (1992) subsequently hypothesized evolution of pristiglomids and nuculids as sister taxa within Nuculoidea subsequent to the split of nuculoids and nuculanoids, based on detailed documentation of patterns of gut looping in deep-water protobranchs Rhind and Allen (1992). The two families have become increasingly separated based on molecular phylogenetic analyses (Sato et al. 2020). Pristiglomids and sareptids are treated here as nuculoids rather than as non-rostrate nuculanoids, while recognizing that controversy persists. They can, of course, be treated under separate superfamily names to circumvent the question of relationships.

Jeffreys (1876) recognized the distinctive minute ovate shell outline more than a century ago. However, these miniaturized bivalves, initially referred to as “glomids”, did not capture widespread attention until the first anatomical documentation of live-collected material from abyssal depths on the Gay Head-Bermuda transect. Sanders and Allen (1973) reported that miniaturization was achieved by reducing cell size. This was contrary to traditional expectation of fitting a functional animal into a minute shell by reducing cell number and/or eliminating structural complexity. Furthermore, the pristiglomid anterior to posterior water flow and its relationship to the gill axis led Sanders and Allen to characterize these bivalves as nuculacean “in all respects”—ovate and lacking nuculanacean mantle fusion, retaining posterior to anterior flow across a transversely oriented gill, and not requiring paired posterior siphons and a rostrate shell shape. The absence of a pallial sinus should be the best evidence of nuculacean affinity, although the pallial line is seldom visible in literature illustrations or on specimens of these fragile shells.

Pristigloma mistensis n. sp.

Fig.16A–C

ZooBank LSID—urn:lsid:zoobank.org:pub:77B08747-F088-4A46-BA5A-5580FAF0EEB3

Diagnosis—Shell minute, ovate, weakly inflated, and equilateral, with evenly convex dorsal and ventral margin; umbones weakly prosogyrate and slightly anterior to midline; sculpture absent or not preserved; lunule and escutcheon absent, anterior hinge plate with five oblique peg-like to slightly chevron-shaped teeth; posterior hinge plate longer, with impressions of seven teeth preserved; central portion of hinge line indistinct, with possible small ligament pit separating anterior and posterior teeth.

Discussion—Although the holotype is an imperfectly preserved cast of the interior of a right valve with no remaining shell material, different forms of illustration

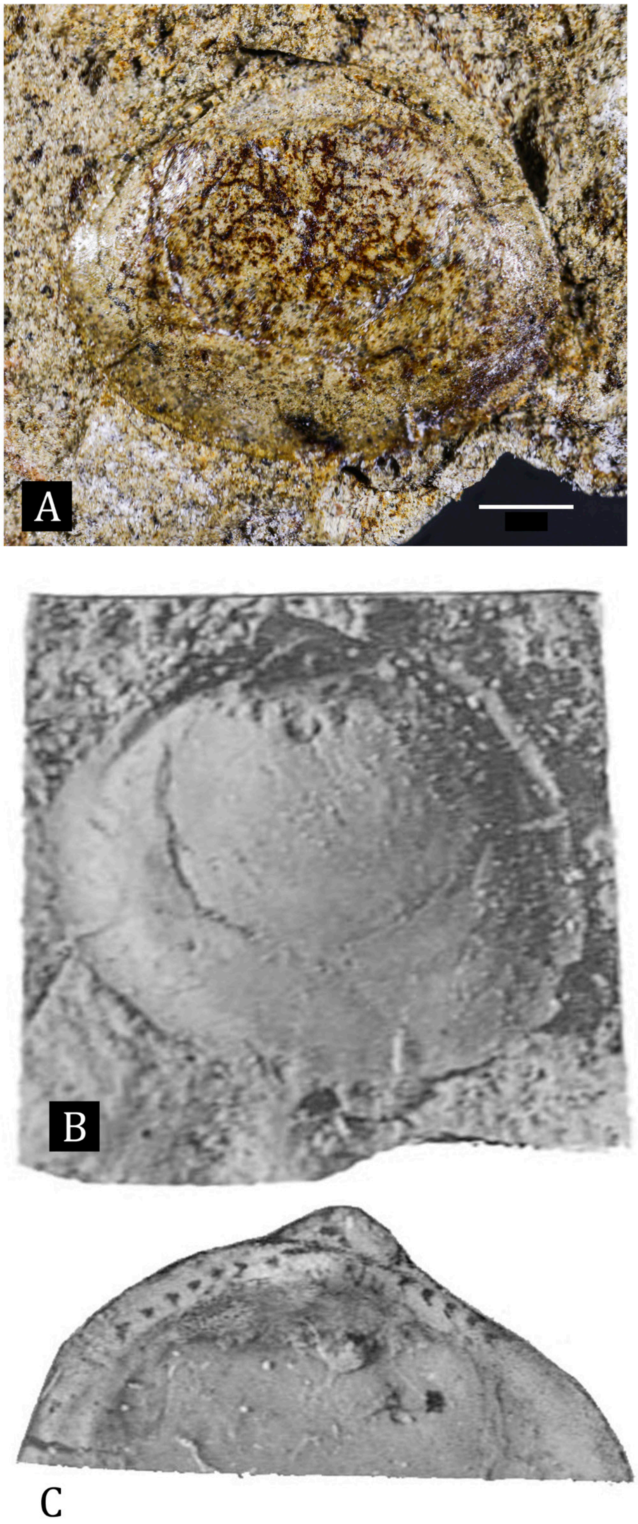

Figure 16. *Pristigloma mistensis* n. sp. Three alternative images recording different features of the Holotype, USNM 561809. Length 4.9 mm. **A**, Color image of uncoated natural mold of left valve interior in matrix. Scale bar=1 mm. **B.** Image of natural mold coated with ammonium chloride. **C.** Ammonium chloride coated latex pull of dorsal area of natural mold with prosogyrate beak and hinge plate with posterior and anterior dentition.

have been combined to provide additional information. Figure16A is a color image of the specimen in matrix. It is difficult to interpret but conveys the best view of how the specimen actually appears. An earlier photograph of the specimen after coating with ammonium chloride Fig. 16B) conveys a better picture of the smooth surface of the valve, but lacks some of the hinge plate detail visible in the uncoated specimen. A latex pull from the specimen, also coated with ammonium chloride (Fig. 16C) yields the best representation of the hinge teeth.

This is the first report of a fossil pristiglomid from the Northeastern Pacific. However, relatively well-preserved ovate shells of a minute protobranch bivalve from Japanese deep-water Paleogene Katsuhira Formation on Hokkaido are described and illustrated by Amano and Jenkins (2017). They tentatively identify the material as *Pristigloma*? *sachalinensis* (Salinkova, 1987), a species described from the Cretaceous (Maastrichtian) of Sakhalin as *"Sarepta" sachalinensis*. The lack of a pallial sinus in the Paleogene fossils supports nuculacean affinity but is insufficient to distinguish non-siphonate sareptids and pristiglomids.

Etymology—named for the classic crinoid locality, cold seep, and river bluff outcrops of the Nehalem River at Mist, Oregon.

Type locality—USGS 15318 (Mist, crinoid layer), Columbia Co., Oregon

Material examined—one specimen**.**

Holotype—USNM 561809, length 4.9 mm, height 4.0 mm. Cast of interior of right valve, no original shell material remaining.

Stratigraphic occurrence—Known only from the type locality in the upper part of the middle member of the Keasey Formation.

CONCLUDING REMARKS

The preceding systematic treatment of nuculoid protobranch bivalves includes description, illustration, and comparisons of thirteen species in three families, including five new Keasey species. As basal bivalves, the protobranchs have a long geologic history dating from the Cambrian or Lower Ordovician. Unequivocal nuculids appear in the Lower Ordovician, and sareptids and pristiglomids appear in the Upper Cretaceous (Maastrichtian).

The classification adopted here unites Nuculidae, Sareptidae, and Pristiglomidae under Nuculoidea, It is controversial primarily because molecular data favor classifying Sareptidae and Pristiglomidae under Nuculanoidea. The alternative topology recognizes the morphological and anatomical significance of non-rostrate shell form and absence of a pallial sinus. These shell features indicate non-siphonate anatomy in which orientation of the gill axis is functionally consistent with an anterior inhalant and posterior exhalent respiratory current and ecologically indicative of shallow burial at the sediment-water interface.

New species of *Sarepta* and *Pristigloma* described and illustrated here are the first representatives of these families in the fossil record of the Northeastern Pacific Margin. Although the new names are based on few specimens, they highlight the value of attention in the field to small shells and fragments that are commonly overlooked.

Deposit-feeding protobranchs are the most frequent, abundant, and diverse element in the bivalve fauna of the Keasey Formation. They occur in an active margin tectonic setting in which subduction and formation of the young Cascadia forearc resulted in deep water and tuffaceous siltstone and mudstone deposition close to shore. This coincided climatically with the doubthouse transition from a tropical greenhouse to modern temperate icehouse conditions and faunal turnover. To a greater extent than anomalodesmatan, heteroconch and pteriomorph bivalves, the protobranchs are specialized for life with low oxygen and high sulfide and preadapted for the appearance of distinctive cold seep environments. Three discrete late Eocene cold seeps in the Keasey formation are characterized by a central carbonate rich core with chemosymbiotic mollusks with methanotrophic bacterial symbionts, a peripheral zone of deposit feeding mollusks that are tolerant of sulfide and low oxygen and able to exploit a chemosymbiotically-rich sedimentary food source, and a "normal" background fauna that may reflect diffuse or periodic methane seepage. The Keasey Formation is the exemplar of the transitional peri-seep biotope (Hickman, 2023; Taylor et al. 2023) between seep and background biotopes.

Variation in preservation occurs at many localities. A large densely-fossiliferous slab (University of Washington Burke Museum 97632) from the upper siltstone unit and peri-seep biotope at the classic mist crinoid locality (Figure 17) illustrates a diversity of information. Original shell material (red arrows) and exterior molds (white arrows) of *Acila nehalemensis* preserve different aspects of divaricate ribs and a specimen of the cold-water coral *Flabellum hertleini*) (yellow arrow) provides additional evidence of diffuse methane seepage.

Biogeographically the most similar Paleogene protobranch faunas are from marginal marine basins of South and Western Australia, New Zealand, and Antarctica. There are also close similarities to Paleogene protobranchs from active margin settings in northern Japan (Hokkaido) and Far Eastern Russia (Kuril Islands, Sakhalin Island, and Kamchatka Peninsula) separating the Sea of Okhotsk from the North Pacific. Uplift of the

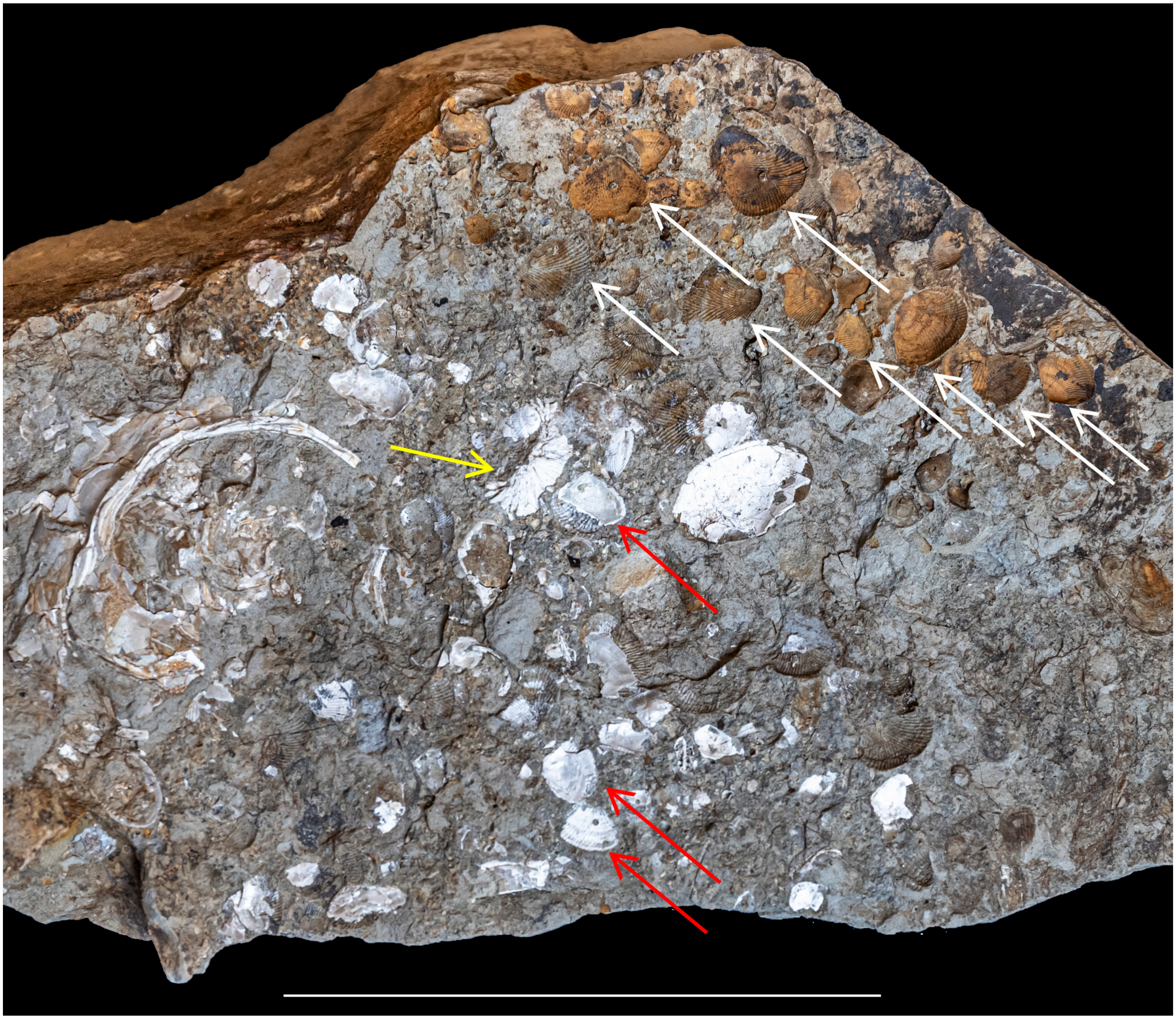

Figure 17. A large, densely-fossiliferous, partially-weathered slab (UWBM 97632) from the upper siltstone layer at the (composite) Mist locality (UCMP loc. A5018) illustrating the richness of information in Keasey peri-seep biotope exposures, including unweathered nacreous *Acila nehalemensis* shells (red arrows), entire weathered shells lacking nacre (white arrows), and the associated cold-seep coral *Flabelluim hertleni* (yellow arrow). Scale bar=10 cm.

East Asian continental margin exposed a remarkable Upper Cretaceous and Cenozoic deep-water tectono-sedimentary record with hundreds of new molluscan taxa that were described by Russian scientists during a period in the 20th Century when specimens remained inaccessible and published literature and illustrations were difficult to obtain. Accordingly, the annotated checklists and bibliographies of Cenozoic marine bivalves (Kafanov et al. 2000, 2001) are extremely valuable resources.

The rostrate Nuculanoidean protobranchs in the Keasey Formation are similarly frequent, abundant, and diverse. They also are part of the peri-seep biotope. The final Keasey bivalve manuscript (in preparation) will document the nuculanoids along with two chemosymbiotic solemyid protobranchs that are restricted to the seep biotope.

ACKNOWLEDGMENTS

Many individuals have contributed their expertise, field and technical assistance, suggestions and encouragement over the past 50 years of research on the Keasey molluscan fauna and are acknowledged in the nine previous papers cited herein. This monograph is dedicated to Harold Vokes in special recognition of his encouragement and use of the USGS and Smithsonian protobranch specimens he collected.

I am indebted to the many colleagues who have contributed to my understanding of the Paleogene protobranch component of the Keasey fauna treated herein. For comparative regional perspectives I acknowledge Alan Beu, Phil Maxwell, and Bruce Marshall (New Zealand); Tom Darragh and George Kendrick. (Australia); Alexander Kafanov, Kenshiro Ogasawara, and Lou Marincovich (Japan, the Russian Far East, and Alaska); David Jablonski and Paul Valentich Scott (North America and the Northeastern Pacific, bivalve taxonomy and systematics); Eugene Coan (encyclopedic knowledge of the literature), Brian Morton (protobranch functional morphology and anatomy); John Pojeta, Jr. (the Paleozoic Fossil Record, bivalve origins and early history).

M. Patricia Morse and John Zardus have been inspirational in sharing their contributions of new data, perspectives and contagious enthusiasm for living protobranchs. I credit Howard Sanders and Bob Hessler for the origin of my enthusiasm for the revolution in sampling and thinking about the age, origin, and evolution of the deep-sea fauna.

Liz Nesbitt and Dave Taylor played a major role in fieldwork on the Keasey methane seeps. Along with Kathy Campbell they contributed to recognition of distinctive recurring assemblages of seep-associated protobranchs in the formation.

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