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A SILICIFIED LATE TRIASSIC (NORIAN) BIVALVE MOLLUSCAN FAUNA FROM THE ALEXANDER TERRANE, SOUTHEASTERN ALASKA

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ABSTRACT

A taxonomically rich and ecologically diverse silicified bivalve-dominated fauna is critically examined from the upper Norian Hound Island Volcanics of Kuiu Island, southeast Alaska. More than 1000 silicified bivalve specimens isolated by acid digestion of carbonate blocks yield a wealth of taphonomic, paleoecologic, paleogeographic, and taxonomic information. Petrographic analyses and scanning electron microscopy reveal specimens are preserved with silicification fabrics of quartzine-lutecite bladed masses and spherulitic chalcedony conserving fine details of original skeleton by both selective and complete replacement. Taphonomic indices indicate the fauna represents a parautochthonous storm-condensed assemblage of a shallow subtidal and relatively soft-bottom carbonate setting. Bivalves, ammonoids, conodonts, and the hydrozoan *Heterastridium* largely suggest a late Norian (*Gnomohalorites cordilleranus* ammonoid zone) age for the fauna.

The assemblage is taxonomically rich, containing 31 recognizable bivalve species (or equivalent taxa in open nomenclature) distributed amongst 11 orders, 17 superfamilies, 24 families, and 30 genera. Of the 31 taxa, 12 are incompletely known and left in open nomenclature and the following 11 are new: *Palaeonucula muffleri* n. sp., *Pinna keexkwaanensis* n. sp., *Plagiostoma scallanae* n. sp., *Entolium alaskanum* n. sp., *Filamussium walleri* n. sp., *Harpax articulatum* n. sp., *Erugonia boydi* n. sp., *Minetrigonia newtonae* n. sp., *Myophorigonia parva* n. sp., *Palaeopharus orchardi* n. sp., and *Tancredia norica* n. sp. The Erugoniidae n. fam. is proposed for smooth shelled trigonoideans with trigoniid-grade dentition but lacking marginal carina. The fine-scale preservation and large sample size revealed previously unrecognized morphologic details permitting revision of two bivalve families (Palaeopharidae Marwick, 1953 and Palaeocarditidae Chavan, 1969) and one genus (*Septocardia* Hall & Whitfield, 1877). The most diverse group is the Pteriomorpha with 16 species (51.6% of species and 69% of individuals), followed by the Heteroconchia with 12 species (38.7% of species and 28% of individuals) and Protobranchia with three species (9.7% of species and 2.8% of individuals). The assemblage is dominated by the pteriid *Cassianella cordillerana* McRoberts in McRoberts & Blodgett, 2002, which, taken with other reclining suspension-feeding species, accounts for 43.9% of individuals. Shallow infaunal burrowers comprise the second most common trophic group (27.6% of individuals), followed by epifaunal cementing forms (15.5% of individuals). The assemblage is dominated by endemic taxa, yet several species are known from other Norian faunas of the South American Cordillera and, to a lesser extent, North American terranes (Wrangell, Nixon Fork, and Wallowa). The biogeographic relationship with the Norian molluscan faunas of South America supports a southerly paleolatitude for the Alexander terrane with some biogeographic connection with other tropical terranes of eastern Panthalassa.

INTRODUCTION

The Late Triassic is generally regarded as a time in which reefs and other marine life flourished—the biotic recovery following the end-Permian mass extinction was largely complete and complex marine ecosystems are, at least locally, well established. The Triassic reorganization of benthic communities resulted in the replacement of brachiopod-stenolaematid-crinoid dominated faunas typical of the Paleozoic by a marine fauna of modern aspect dominated by bivalve and gastropod mollusks, bony fishes, gymnolaematid bryozoans, echinoids, and certain crustaceans, representing an increase in trophic variety ranging from deep infaunal suspension feeders to active nektonic carnivores (Sepkoski, 1981). The diversification and ecological restructuring that began in the Early Triassic has been dubbed the Marine Mesozoic Revolution (MMR), which has the central tenant that new adaptations and be-

haviors within certain invertebrate groups, such as bivalve and gastropod mollusks, may in part have been driven by a concomitant increase in durophagous predators and escalating predator-prey interactions (Vermeij, 1987). Within the contextual framework of the MMR, the Triassic is an important time during which bivalves numerically dominated shallow level-bottom benthic marine communities (Fraiser & Bottjer, 2007) and several major bivalve clades either originated or diversified. A most informative example is the oysters, a group of cementing bivalves that originated in the Middle Triassic (Hautmann & Haggdorn, 2013) and whose cementing life-habit may have been an adaptive defense strategy against durophagous predators (Harper, 2004). By Late Triassic time, bivalve dominated faunas occur throughout the Arctic, Tethys, and Panthalassan seas, and are known from an increasing number of well-preserved and well-documented

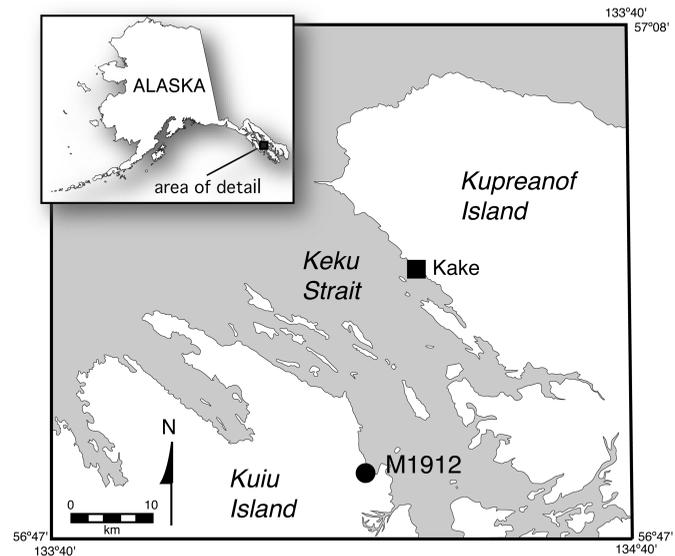
fossil assemblages (*e.g.*, Fürsich & Wendt, 1977; Newton *et al.*, 1987; Hautmann, 2001b).

This present study focuses on an exceptionally well-preserved silicified bivalve fauna from the upper Norian at Gill Harbor in the Keku Strait area of southeastern Alaska. The significance of the Gill Harbor fauna lies not only in its being one of the most diverse late Norian shallow-water tropical bivalve faunas known, but also that it provides critical taxonomic linkages between temporally positioned, well-known early Norian and Rhaetian faunas. Additionally, the fine-scale silicification replacement fabrics of these bivalves permits the recognition of exquisite morphologic detail allowing for a better understanding of named species (many of which were poorly known or based on incomplete specimens) and reassessment of new genera and higher taxa for which morphologic data were scarce. The aim of this research, therefore, is to fully document this taxonomically rich and ecologically diverse bivalve-dominated assemblage within the context of diversifying bivalve clades and use this to better understand the paleoecologic structure and paleogeographic significance of this tropical Late Triassic marine fauna.

GEOLOGIC AND STRATIGRAPHIC SETTING

The main fossil locality at Gill Harbor occurs within the intertidal zone at latitude N 56° 52.621'; longitude W 133° 56.016' on the eastern shore of Kuiu Island approximately 16 kilometers SSW of Kake Alaska (Text-fig. 1). Strata at this locality are assigned to the Hound Island Volcanics, a lithostratigraphic unit within the Hyde Group originally named by Muffler (1967) for nearly 600 meters of strata exposed along the coast of Hound Island in the center of Keku Strait. At its type locality, the Hound Island Volcanics is comprised mostly of basaltic lavas, including pillow basalt, volcanoclastic breccia, tuff, and conglomerate, with minor amounts of sandstone and thin-bedded limestone. According to Muffler (1967), the Hound Island Volcanics conformably overlie the Cornwallis Limestone at several localities in the Keku Strait area, including its type locality and also at exposures on the eastern shore of Kuiu Island. Further east at Hamilton Island, the Hound Island Volcanics apparently rests conformably on Hamilton Island Limestone (Muffler, 1967; Katvala, 2004). Text-fig. 2 illustrates the stratigraphic relationships of Upper Triassic rocks in the Keku Strait area.

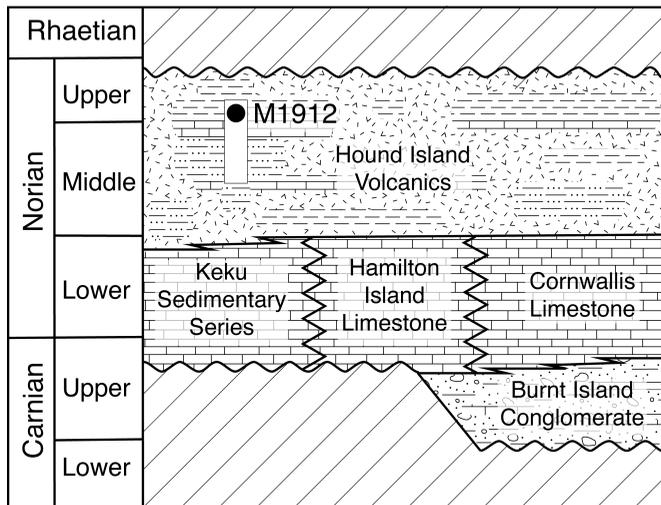
At the Gill Harbor locality, some seven km southeast of the type locality, the Hound Island Volcanics consist of nearly 40 meters of thin-bedded limestone and shale capped by several beds of coarser-grained limestone containing the silicified fossils at the top of the section (Text-fig. 3). These upper beds, about 3.5 m thick in total, consist of fossiliferous packstone, grainstone, rudstone, and carbonate floatstone and contain the silicified molluscan fauna described in this



Text-fig. 1. Locality map of the Keku Strait region of southeastern Alaska. Fossils described in this paper come from USGS loc. M1912 at Gill Harbor.

work. The contact between the underlying shale/thin-bedded carbonate succession and overlying silicified limestone beds is obscured and, based upon taphonomic and biochronologic evidence, may represent an erosional hiatus. The uppermost bed (1 m thick) of the silicified limestone is structurally deformed and its relationship with overlying strata is obscured. Although some confusion exists regarding precise stratigraphic horizons, USGS loc. M1912 most likely corresponds to the 3.5-m thick coarse-grained limestone beds at the top of the section. Collections made by Erik Katvala and George Stanley between 2001 and 2003 from this locality have been assigned the University of Montana locality number MI 0087, but the MI locality also includes fossiliferous horizons from the underlying 33-m thick succession of thin-bedded pelagic carbonates and shale that are variably exposed within the intertidal mudflat. Collections made by this author in 2003 are assigned field locality numbers CM03GHL and their stratigraphic positions are provided in Text-fig. 3.

The Triassic strata of the Keku Strait area of southeastern Alaska are part of a broader Paleozoic through Mesozoic succession of sedimentary and island arc-related volcanic rocks belonging to the Alexander terrane—one of the several allochthonous tectonostratigraphic terranes that comprise much of the Cordillera of western North America (Text-fig. 4; Jones *et al.*, 1972, 1977; Coney *et al.*, 1980; Gehrels & Saleeby, 1987). The Alexander terrane occurs as a northwest-southeast trending belt stretching from the Alaskan Panhandle, coastal British Columbia, and southwestern Yukon into the Wrangell Mountains and Gravina Island of eastern Alaska. The terrane is known to contain late Proterozoic and early Paleozoic conti-

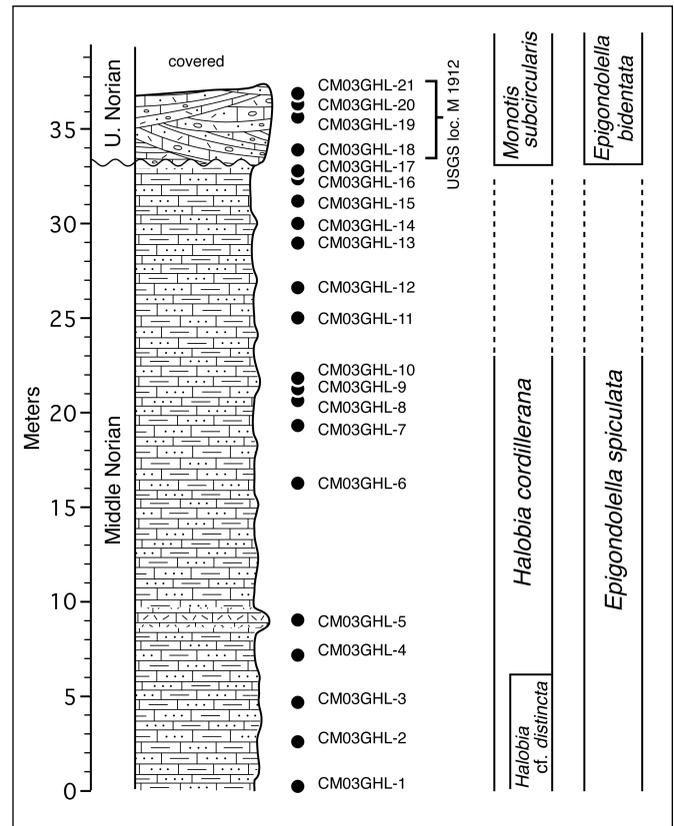


Text-fig. 2. Generalized stratigraphic relationships of Upper Triassic strata in the Keku Strait area. After Muffler (1967) and Katvala (2004).

nental crustal rocks overlain by a thick succession of Paleozoic and early Mesozoic sedimentary and volcanic rocks.

Although it is generally accepted that the early Paleozoic paleoposition of the Alexander terrane is associated with northeastern Baltica and northern Laurussia (e.g., Bazard *et al.*, 1995; Butler, *et al.*, 1997; Beranek *et al.*, 2013), its position during Late Triassic time and its accretionary history and linkages to other insular terranes (e.g., Wrangellia) are somewhat controversial. Geochronologic and geochemical studies of plutons suggest that the Alexander terrane and Wrangellia have shared a tectonic and geologic history since the Carboniferous (Gardner *et al.*, 1988) or perhaps as early as the Late Devonian (Israel *et al.*, 2014). An early magmatic linkage contrasts with stratigraphic and faunal differences, suggesting that the Alexander terrane and Wrangellia had distinctly different geologic histories throughout the Paleozoic and the early Mesozoic (Jones *et al.*, 1977; Blodgett & Frýda, 2001; Caruthers & Stanley, 2008a, 2008b; although see Belasky *et al.*, 2002 for an alternative view).

Available paleomagnetic evidence from basalts in the Hound Island Volcanics of the Keku Strait area is also contradictory and suggests a range of paleolatitudes for the Alexander terrane of about 10–23° to 44° N or S of the Late Triassic paleoequator (Hillhouse & Grommé, 1980; Panuska & Stone, 1985; Haeussler *et al.*, 1992). A tropical position for the terrane during the Late Triassic is corroborated with paleontological evidence of hypercalcifying corals and sponges (e.g., Caruthers & Stanley, 2008a, 2008b; Senobari-Daryan *et al.*, 2008). Since the Late Triassic, the Alexander terrane (perhaps already sutured with Wrangellia to form the southern Alaska superterrane) accreted to inboard intermontane terranes (e.g., Taku, Stikine, Yukon, etc.) in the Jurassic



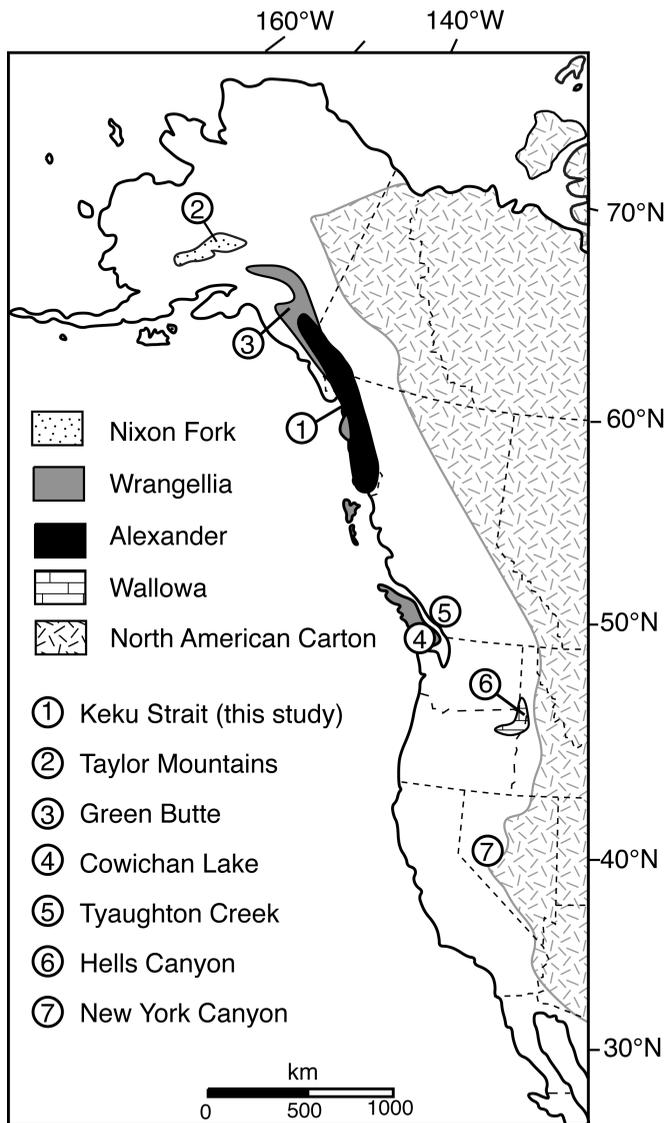
Text-fig. 3. Simplified stratigraphy of the Gill Harbor section. Sample numbers refer to field locality collection numbers. The primary silicified assemblage comes from USGS loc. M1912 in the upper 3.5 m of the section. Stratigraphic range of conodont species and Halobia species is provided.

and Cretaceous with significant northward transport and final accretion completed by the early Paleogene (Jones *et al.*, 1977; Gehrels & Saleeby, 1987; Haeussler *et al.*, 1992; Gehrels & Berg, 1994).

PREVIOUS REPORTS ON FOSSILS FROM USGS LOCALITY M1912

Late Triassic fossils from the Keku Strait region were first discovered by E.M. Kindle, as noted by Wright & Wright (1908). This, and subsequent reports by Attwood (1912), Martin (1916, 1926), Smith (1927), and Buddington & Chapin (1929) noted the presence of *Halobia* and *Monotis* species thus demonstrating a Carnian and Norian age for carbonate and clastic strata in the Keku Strait area.

The first comprehensive study of the geology of the Keku Strait area by Muffler (1967) included a regional synthesis on the late Paleozoic and early Mesozoic stratigraphic and igneous relationships of the Keku Strait area. Norman J. Silberling (cited in Muffler, 1967: C30) provided identifications of several biostratigraphically important bivalve and ammonoid taxa from numerous Upper Triassic localities from the Hound



Text-fig. 4. Generalized map of western North America showing the distribution of several tectonostratigraphic terranes and locations of significant Upper Triassic molluscan faunas. Numbered localities are discussed in text. Terrane boundaries adapted from Jones *et al.* (1987) and Silberling *et al.* (1994).

Island Volcanics, Cornwallis Limestone, and other units in the region. In Muffler's (1967: C30) work, Silberling remarked that USGS loc. M1912 includes *Monotis subcircularis* and the hydrozoan *Heterastridium* from the upper Norian and noted a "large diversified marine invertebrate fauna" from the same locality. Although collections were made by Muffler (most are conserved in the USGS facility in Denver), the diverse shallow water fauna from USGS loc. M1912 was not studied in detail.

Based on material from the U.S. Geological Survey collections, Newton (1983) listed nine bivalve taxa from USGS loc. M1912 including ?*Antiquilima*, *Cassianella bey-*

richi, *Gryphaea*, *Minetrigonia*, *Propeamusium*, *Schafhaeutlia*, *Septocardia* cf. *S. pascoensis*, and two indeterminate pectinoid-ecean species. Newton (1983) made particular note of the affinities of Keku *Septocardia* with the silicified molluscan fauna described from Peru by Cox (1949). Katvala (2004) noted that the M1912 locality contains *Monotis subcircularis* and the hydrozoan *Heterastridium conglobatum* confirming the earlier report of Silberling (cited in Muffler, 1967). The bivalve taxa listed by both Newton (1983) and Katvala (2004) were never described or illustrated, but are largely corroborated by materials described in this present study.

Several recent papers have highlighted the presence of shallow-water and hypercalcifying Scleractinia and Demospongia from the Upper Triassic of the Keku Strait area. Most of these are known from the somewhat older lower Norian Cornwallis Formation (*e.g.*, Caruthers & Stanley, 2008a; Senobari-Daryan *et al.*, 2008). Katvala & Stanley (2008) reported on, but did not illustrate, a taxonomically rich shallow-water fauna including sponges, corals, crinoids, echinoids, and gastropods from USGS loc. M1912.

MATERIALS AND METHODS

Fieldwork during the summer of 2003 entailed measuring and logging the 40-m-thick section at Gill Harbor. From the lower bedded shale interval, macrofossils, mostly halobiid bivalves, were collected in the field and integrated with bulk microfossil and geochemical samples. The upper carbonate bed with the silicified shell accumulations was sampled and approximately 60 kilograms were removed from the lower and upper parts of the carbonate bed for further processing in the laboratory. Individual limestone blocks, ranging from 5 to 10 kg each, were dissolved in 10% HCL at SUNY Cortland's Paleontology Laboratory. Insoluble residue larger than 0.2 mm mesh screen was hand picked and fragile silicified specimens were hardened using Alvar. Silicified specimens from acid processing were supplemented by additional material loaned from the University of Montana (collections of Erik Katvala and George Stanley), Robert Blodgett, and from the undescribed Mesozoic collections within the USGS repository in Denver.

Digital images of NH_4Cl coated specimens were captured on a Canon 7D fitted with a Canon EF-S 60 mm macro lens and post-processed using Adobe Photoshop (v. CS6) and ACD Canvas (v. 10) software for Macintosh. Scanning electron microscopy was performed using SUNY Cortland's JEOL JSM-6010LA scanning electron microscope (SEM) at 20 kV and a working distance between 10–20 mm. Secondary SEM imaging of silicification textures was performed on residual macrofossil specimens mounted on standard aluminum stubs with carbon tape and gold coating. Backscatter SEM imaging and elemental analyses using energy dispersive spectroscopy

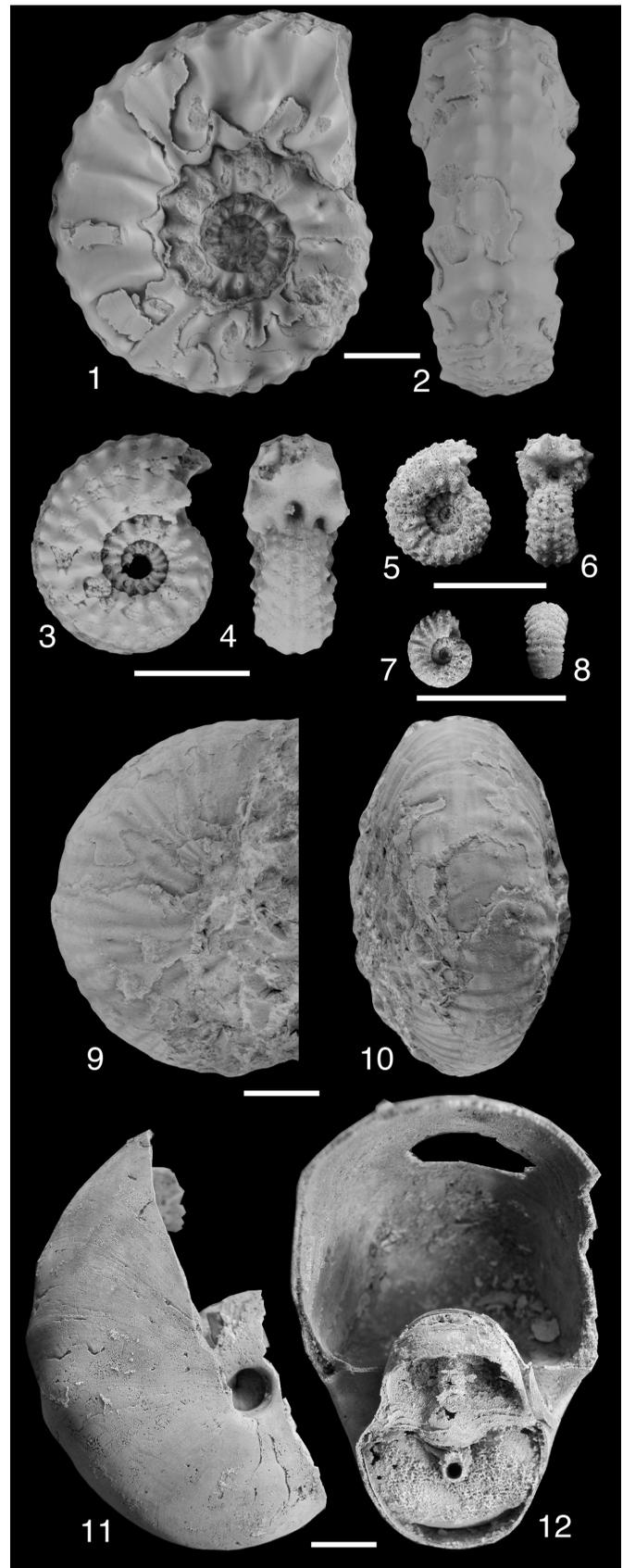
(EDS) were performed on carbon-coated polished thin sections. Sectioned hand samples were prepared as standard petrographic slides, epoxied, ground and polished to a thickness of approximately 30 μm and analyzed and imaged using a Leica DM750P petrographic microscope with an integrated digital camera and Leica Acquire software.

RESULTS

BIOSTRATIGRAPHIC AND AGE CONSTRAINTS

Cephalopods, particularly ammonoids, are fairly common from USGS loc. M1912, yet provide surprisingly little additional information regarding the age-significance of the silicified beds. A number of smaller silicified ammonoids were recovered from the acid-processed residue. Unfortunately, most of these well-preserved ammonoid specimens represent juvenile whorls and given that ammonoid shell shape and sculpture can change significantly during growth from the juvenile to adult stage, species identification is generally not practicable. Among the larger and more complete specimens recovered from USGS loc. M1912 are one nautiloid, *Cosmonautilus* sp. indet., and at least three species-level ammonoid taxa including *Eoethetidites* sp., *Parajuvavites* cf. *P. canadensis* and *Lissonites* sp. (Text-fig. 5). *Cosmonautilus* is not particularly age diagnostic and is largely known from the upper Carnian, with fewer occurrences from the Norian, including possibly from the Alexander terrane at Gravina Island Alaska (Buddington & Chapin, 1929; Kummel, 1953). The ammonoid specimen herein attributed to *Parajuvavites* cf. *P. canadensis* Tozer, 1994 (Text-figs 5.9, 5.10) was previously assigned by Katvala (2004) and Katvala & Stanley (2008) to either *Hellerites* sp. or *Parajuvavites* sp. Although species identification of the Gill Harbor ammonoids is not possible due to incomplete preservation of sutures, both *Eoethetidites* and *Parajuvavites* are known from middle Norian strata associated with *Mesohimavites columbianus* in northeastern British Columbia and Vancouver Island (Tozer, 1994). *Lissonites* on the other hand is known from only the upper Norian of northeastern British Columbia (Tozer, 1994). Thus, the ammonoids from USGS loc. M1912 provide two potential ages: upper middle Norian *Mesohimavites columbianus* II or III and upper Norian *Gnomohalorites cordilleranus* zones.

Katvala & Stanley (2008) provided a robust conodont biostratigraphy for the Gill Harbor locality, documenting both middle and upper Norian conodonts. From the lower 15 m of shale/carbonate sequence below the silicified beds, Katvala & Stanley (2008) and Orchard (pers. comm., 2014)



Text-fig. 5 (at right). Cephalopods from USGS loc. M1912. 1–6, *Eoethetidites* sp. indet.; 1, 2, UMIP 15651; 3, 4, UMIP 15652; 5, 6, PRI 69593. 7, 8, *Lissonites* sp. indet., PRI 69594. 9, 10, *Parajuvavites* cf. *P. canadensis* Tozer, 1994, UMIP 15653. 11, 12, *Cosmonautilus* sp. indet., PRI 69595. Scale bars = 10 mm.

reported several upper middle Norian conodont taxa, including *Epigondolella spiculata* and *E. triangularis*, which are characteristic of the *Epigondolella spiculata* zone (\approx *Mesohimavites columbianus* I ammonoid zone of Tozer 1994). The overlying silicified beds (USGS loc. M1912) have yielded platform elements of *Epigondolella bidentata*, *Epigondolella tozeri*, and *Epigondolella* sp. aff. *E. mosheri* and a few rarer forms similar to *Cypridodella* cf. *C. postera* (Katvala & Stanley, 2008; Orchard, pers. comm., 2014). While the majority of conodont taxa from USGS loc. M1912 constrain the locality to the *Epigondolella bidentata* conodont zone (ca. *Gnomohalorites cordilleranus* ammonoid zone), the few *Cypridodella* cf. *C. postera* elements recovered from this interval suggest a somewhat older *Cypridodella postera* conodont zone (ca. *Mesohimavites columbianus* II ammonoid zone), indicating possible reworking. It is significant to note that neither true *Epigondolella mosheri* nor other diagnostic species for the Rhaetian (e.g., *Misikella posthernsteini*) have been recovered from the Gill Harbor locality.

Not surprisingly, much of the shallow-water bivalve fauna described herein from USGS loc. M1912 represent previously unknown species, and therefore have little demonstrated biostratigraphic utility. Below USGS loc. M1912, however, the lower 15 m of the shale/bedded limestone sequence contains *Halobia cordillerana* and the lowermost 5 m contains *Halobia* cf. *H. distincta*. Taken together, these halobiids are in agreement with the conodont data and suggest an early middle Norian age equivalent to the *Mesohimavites columbianus* I ammonoid zone (see McRoberts, 2010, 2011). The upper limestone beds themselves (USGS loc. M1912) contain *Monotis subcircularis*, which is diagnostic of the late Norian *Gnomohalorites cordilleranus* ammonoid zone (McRoberts, 2010, 2011). *Monotis subcircularis* and other large monotid bivalves underwent complete extinction at the top of the Norian; their presence therefore indicates a late Norian age. Only two dwarf species occur in the lowest Rhaetian of the western Tethys, one crossing the Norian-Rhaetian boundary and the other first appearing in the basal Rhaetian (McRoberts *et al.*, 2008; McRoberts, 2010). The extinction of large *Monotis* at the top of the Norian is correlative with the top of the *Sagenites quinquepunctatus* ammonoid zone in the Tethys and the top of the *Gnomohalorites cordilleranus* ammonoid zone in the Americas (McRoberts *et al.*, 2008) and can be correlated throughout the circum-Pacific, Arctic, and Tethyan realms. The presence of *Monotis subcircularis* from USGS loc. M1912 provides a particularly strong biocorrelation point with the section at Levanto, Peru where *M. subcircularis* occurs 1.4 m below volcanic ash beds that have provided U-Pb zircon dates between 205.70 ± 0.15 Ma and 205.30 ± 0.14 Ma (Woltzlaw *et al.*, 2014).

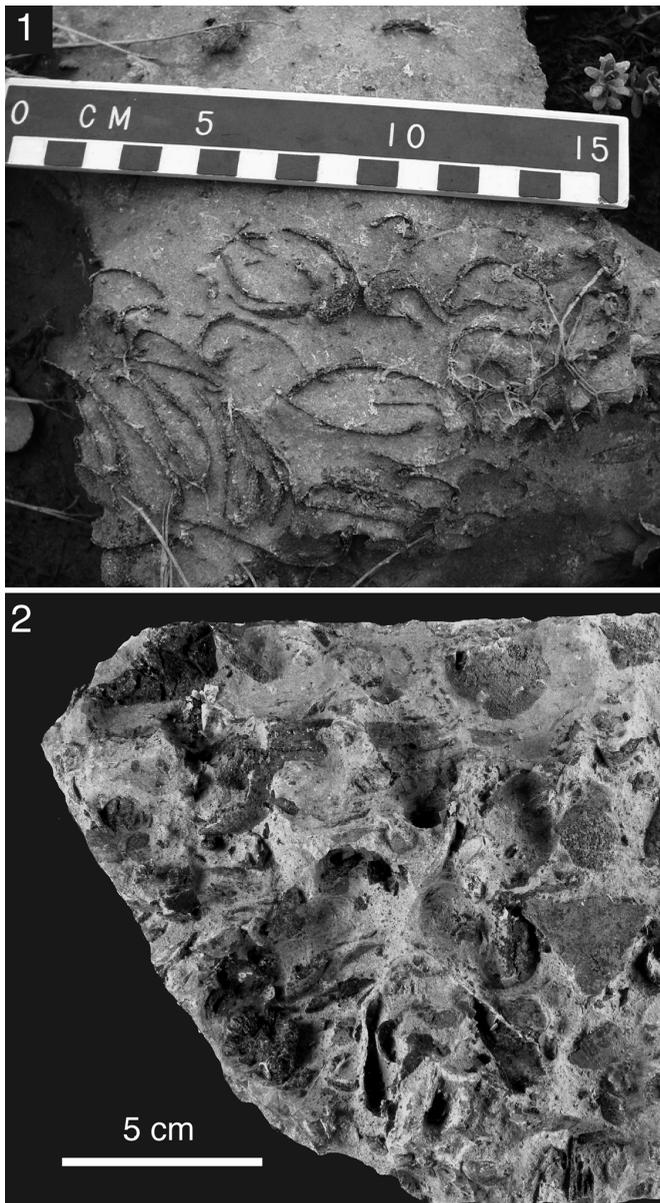
Taken together, bivalves, conodonts, and the ammonoid *Lissonites* sp. largely confirm an upper Norian age

(*Gnomohalorites cordilleranus* ammonoid zone of Silberling & Tozer, 1968, Tozer, 1994) for the primary silicified bed (USGS loc. M1912). This age is further supported by the presence of moderately large specimens of the pelagic hydrozoan *Heterastridium conglobatus*, an upper Norian index fossil associated with large *Monotis* (Silberling & Tozer, 1968; Campbell, 1974; Stanley *et al.*, 1994), which was reported by Katvala & Stanley (2008) from USGS loc. M1912 and corroborated with this present study. However, certain constituent taxa (mainly the ammonoids *Eotheidites* sp., *Parajuvatites* cf. *P. canadensis* and the conodont *Cypridodella* cf. *C. postera*), may represent slightly older ages, leading to the realistic possibility of time averaging in the lower part of USGS loc. M1912 incorporating elements from the underlying middle Norian. A late Norian biochronologic age from the silicified fossil assemblage places USGS loc. M1912 in close association with the Norian-Rhaetian boundary, which, at present, has not been defined with a global boundary stratotype section and point (GSSP) by the Subcommittee on Triassic Stratigraphy.

TAPHONOMY AND PRESERVATION

Biostratinomy and shell bed genesis.—A variety of taphonomic indices suggest that the silicified shell beds that comprise loc. M1912 have a complex taphonomic history. Apart from obstruction deposits which could potentially preserve a life (or census) community, shell beds commonly represent time-averaged assemblages that can be generated from a variety of processes including *in situ* accumulation from normal attritional mortality, concentration of skeletal debris by the biologic processes of burrowing and or scavenging, or through transportation and/or winnowing from storm events or currents (see Kidwell *et al.*, 1986 and Kidwell & Bosence, 1991 for thorough reviews). The completeness and condition of individual shells, their orientation, size, and sorting—together with other taphonomic indices, including the presence of epibionts and borings on skeletal bioclasts—provide valuable information on the biostratinomy and genesis of the shell beds. This information also serves to establish the conditions under which the silicified fossils accumulated and were ultimately buried, providing the basis for interpreting the paleoecology of the silicified assemblage.

The primary shell bed producing the silicified fauna is approximately 1 m thick and occurs as a lensoid bed within the 3.5 m-thick carbonate unit at the top of the measured section. Exposure of the carbonate unit is not complete, thus the lower boundary of the primary shell bed (and any potential scour features) was not observed in the field. However, the upper boundary (Text-fig. 6.1) shows a gradational transition with carbonate packstone and grainstone of the upper part of the exposed carbonate outcrop. Ripple cross beds or other current-generated structures were not observed within the shell bed or in the overlying carbonates. The densely packed



Text-fig. 6. Photographs of limestone blocks from locality USGS loc. M19121. 1, Field photograph (courtesy of G. Stanley) of in situ block showing a number of articulated bivalves (mostly *Pinna keexkwaanensis* n. sp. and *Plagiostoma scallanae* n. sp.). 2, Excavated block showing portion of shell bed with higher degree of fragmentation.

bioclast supported shell bed is comprised of a wide range of skeletal bioclasts that comprise approximately 20–30% of the rock by volume. Carbonate matrix surrounding larger silicified skeletal bioclasts ranges from micrite to silt- to sand-sized carbonate peloids and skeletal bioclasts and has a much lower hydraulic equivalence than the larger silicified elements. This matrix is similar in composition and texture to the carbonate above the main shell bed (Text-fig. 6.1). Within the primary shell bed, orientations of preserved skeletal bioclasts observed

from weathered surfaces (Text-figs 6.1, 6.2) show a largely unorganized fabric with many shells exhibiting perpendicular, oblique, and concordant concave up and concave down orientations and a limited number of nested valves. Portions of the shell bed appear more fragmented with chaotic orientations.

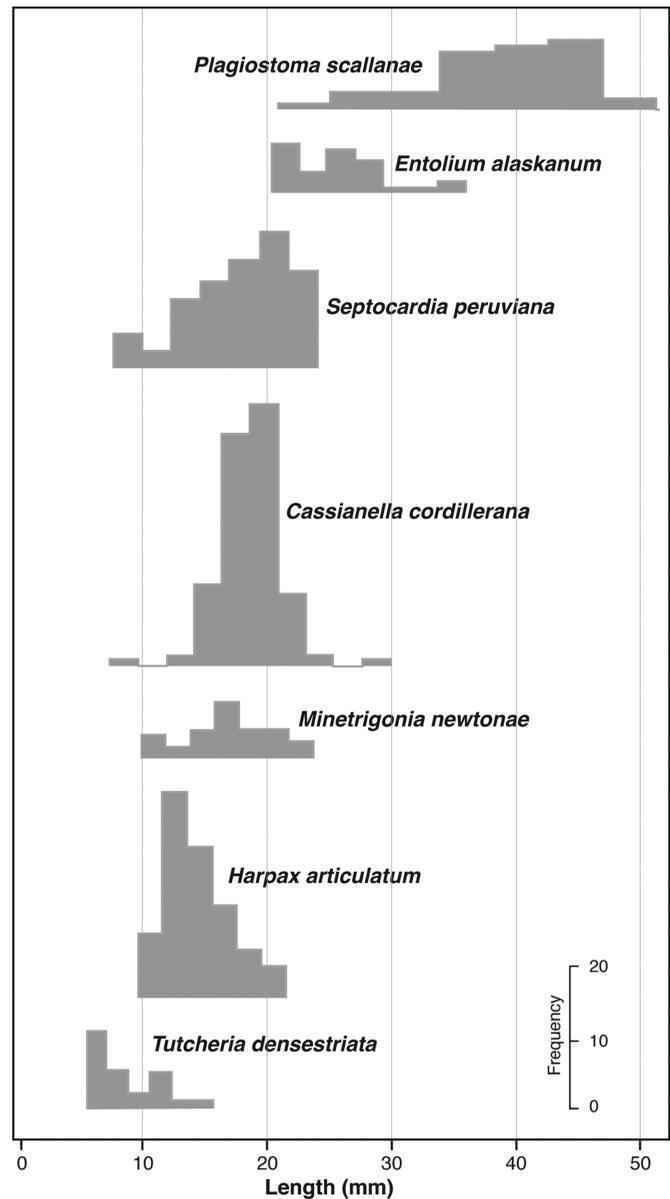
Physical characteristics (disarticulation, fracturing and abrasion) of the preserved bioclasts of the primary shell bed suggest limited, and likely short-lived, post-mortem transport. A majority of recovered bivalves from the primary shell bed are disarticulated, and instances of conjoined valves are largely constrained to small to moderate-sized infaunal Paleotaxodonta (e.g., *Palaeonucula*) and some Heterodonta (e.g., *Septocardia*). Some disarticulation no doubt occurred during the bulk acid-bath processing as numerous examples of larger, apparently articulated, valve pairs of *Plagiostoma scallanae* and several other species were observed in outcrop exposures (e.g., Text-fig. 6.1). A few disarticulated specimens recovered in the acid residue can be paired with opposing valves and can be assigned with confidence to the same individual. Fragmentation is common, especially for the larger shells, but not ubiquitous as a large number of fully intact valves were recovered. Fractured edges of valves are rather sharp and show no significant sign of abrasion or rounding. Surficial textures on most valves of ribbed or otherwise ornamented species show little abrasion.

Differential preservation of left versus right valves can be ascribed to several phenomena including differences in the durability of opposing valves related to their size and thickness, morphology, and in some instances their original mineralogy and skeletal microstructure, which may have influenced degree of silicification. In species that are equivalved and have similar mineralogical and microstructural characteristics (e.g., *Septocardia peruviana*, *Plagiostoma scallanae*, *Tutcheria densistriata*), the number of recovered left versus right valves is usually within 5–10% of each other. However, many of the bivalve taxa exhibit strongly unequal valve sizes, shapes, and shell thickness that likely resulted in the observed selective preservation and recovery between left and right valves. This is perhaps most evident in *Cassianella cordillerana*, in which 97% (of the 362 identified valves) are the larger and thicker-shelled left valves. Valve sorting resulting from size and valve thickness is also evident in *Liostrea newelli* and *Harpax articulatum* n. sp., although there may also be selectivity with respect to skeletal mineralogy, skeletal microstructure, or preferential silicification. An additional example of probable mineralogical/microstructure bias is seen in certain pectinoideans such as *Entolium alaskanum*, where there is a strong preference for preservation of right valves that likely had a different original mineralogy than left valves. Although the extent to which preferential valve preservation is due to selective hydraulic sorting versus selective dissolution or replacement is

difficult to fully address, a significant proportion of recovered valves belong to small or quite thin and fragile taxa, suggesting hydraulic sorting was minimal between taxa.

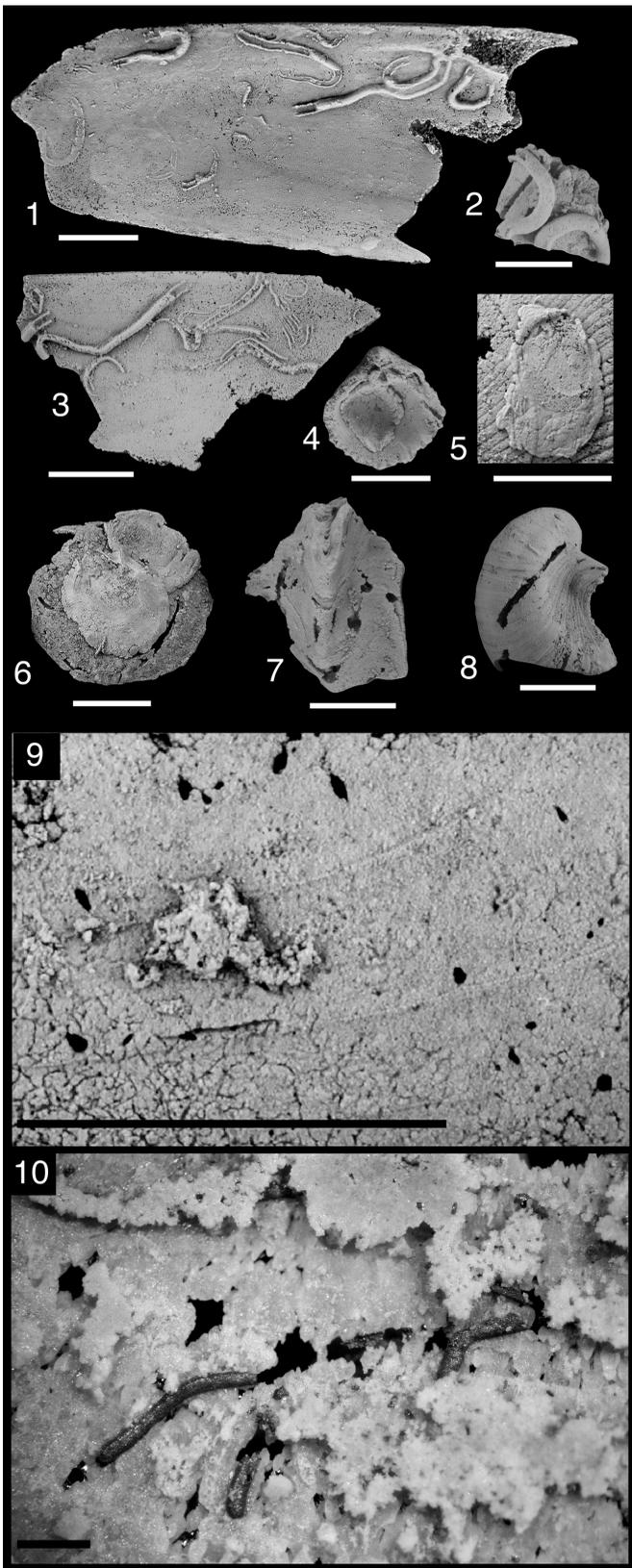
Size frequency histograms from bivalve species with sufficient sample size show a range of distributions that suggest a strong influence by taxonomic/ecologic factors. Of the seven distributions shown in Text-fig. 7, five show demonstrably non-normal distributions and include both left-skewed (*Septocardia peruviana* and *Plagiostoma scallanae* n. sp.), right-skewed (*Harpax articulatum* n. sp. and *Tutcheria densestriata*) and non-unimodal distributions (*Entolium alaskanum* n. sp.). It is interesting to note that the species data show an absence of very small (juvenile) valves less than 5 mm in length. Although this may be due to taphonomic processes related to hydraulic winnowing, the durability of juvenile specimens, or selective replacement, it is also in part a signal of underlying demographics of the parent populations represented in the death assemblage (e.g., low juvenile mortality rates for the species). Strongly reworked and size-sorted fossil assemblages typically show normal size-frequency distributions (e.g., Sheldon, 1965; Hallam, 1967; Kidwell & Bosence, 1991).

Many of the interior and exterior surfaces of isolated bivalve shells show evidence that vacant shells were exposed for some time on the sea bed or within the taphonomically active zone and further served as a firm substrate for epibiont attachment and endobiont boring (Text-fig. 8). Shells that exhibit encrustation are almost exclusively disarticulated and fragmented with epibionts frequently attached to both internal and external surfaces. Common hosts for epibiont encrusters and endobiont borings are *Palaeopharus orchardi* n. sp., *Plagiostoma scallanae* n. sp., *Septocardia peruviana* (Cox, 1949), and *Harpax articulatum* n. sp. The most common epibionts include the plicatulids, ostreoids, and prospondylids (*Harpax articulatum* n. sp., *Liostrea newelli*, *Noetingiconcha* sp. A). Additionally, serpulid worm tubes are found which prefer to encrust the valve interiors of cementing bivalves (although several examples show encrustation on the exterior of non-cemented bivalve species such as *Palaeopharus orchardi* n. sp.). Although the observed serpulid tubes with diameters of between 0.5–1 mm often have a coiled component, they are larger and more loosely coiled than spirorbiform taxa (often assigned to *Spirorbis*) now considered to be tentaculitid microconchids (Weedon, 1991, Taylor & Vinn, 2006). The Gill Harbor serpulids are similar to *Spiraserpula mikesia* Ziegler & Michalik, 1980 known from brachiopod and bivalve substrates from the Rhaetian of the Carpathians (Ziegler & Michalik, 1980). Although rare, several of the recovered specimens possess borings of variable sizes and morphologies. Observed borings are usually found on valve interiors and are seen to erode exterior valve surfaces and in a few cases penetrate through the entire valve. Two boring morphologies ap-



Text-fig. 7. Size frequency distributions of select taxa from USGS loc. M1912.

pear to be most common: Type I, a somewhat larger tunnel with diameters around 1 mm that penetrate normal to shell surface and occasionally erode middle and outer skeletal layers normal to shell substrate (e.g., Text-figs 8.7, 8.8); and Type II, a smaller (~0.2 mm in diameter), bifurcating tunnel system perpendicular to the shell surface within inner and middle shell layers (e.g., Text-figs 8.9, 8.10). Several of the smaller Type II tunnels are filled with pyritized casts (Text-fig. 8.10). It is somewhat surprising that none of the borings possess features typical of radular bioerosion that are known from only a few Triassic examples (e.g., Zardini, 1981, pl. 12, fig. 13a). Given the scarcity of systematic treatment of Triassic endobi-



ont borings, identification of these borings to ichnogenus has not been attempted. Several important studies have shown that the skeletons comprising time-averaged death assemblages may have had residence times of decades to thousands of years prior to final burial (e.g., Flessa & Kowalewski, 1994, Tomašových *et al.*, 2014), providing ample opportunity for the colonization of epibionts and boring endobionts.

These taphonomic indices taken together lead to the conclusion that the primary shell bed represents a parallochthonous storm-condensed assemblage in a shallow subtidal and relatively soft-bottom inner platform or ramp. Shell beds with similar ranges of textural fabrics, fragmentation and disarticulation, degree of encrustation, and bioerosion are common in nearshore storm event beds from a variety of ancient settings (e.g., Aigner, 1985; Kreisa & Bambach, 1982; Fürsich & Oschmann, 1988; Newton *et al.*, 1987). It is encouraging to note that the fidelity of similar within-habitat parallochthonous shell beds from Recent settings have been shown to be fairly representative in terms of ecologic structure from the live and death assemblages from which they are derived (e.g., Cummins *et al.*, 1986; Zuschin & Ebner, 2015), even after significant disturbance by large hurricane storms (e.g., Miller *et al.*, 1992). Furthermore, as shown by Cherns *et al.* (2008), storm driven reworking and winnowing of both live and dead shells from the taphonomically active zone could explain the admixture of epifaunal and infaunal (and mostly aragonitic) skeletal elements.

Diagenesis and silicification.—Petrographic analyses of polished thin sections from unprocessed bulk samples, and scanning electron microscopy on polished thin-sections and sectioned bivalve specimens isolated by acid digestion reveal a complex diagenetic history with variable modes of calcite and

Text-fig. 8 (at left). Endo- and Epibionts. 1–3, *Serpulid* *Spiraserpula mikesia* Ziegler, 1980; 1, encrusting left valve interior of *Palaeopharus orchardi* n. sp., PRI 69596; 2, encrusting (right?) valve exterior of *P. orchardi* n. sp., UMIP 15654; 3, encrusting left valve exterior of *P. orchardi* n. sp., PRI 69597. 4, *Harpax articulatum* n. sp. attached to right valve interior of *Septocardia peruviana* (Cox, 1949), PRI 69598. 5, *Harpax articulatum* n. sp. attached to left valve exterior of *Plagiostoma scallanae*, n. sp., PRI 69599. 6, two *Harpax articulatum* n. sp. individuals attached to left valve exterior of *Noetingiconcha* sp. A, PRI 69600. 7, multiple large endolithic (Type I) borings exposed along right valve exterior of indeterminate prospondylid, PRI 69601. 8, large endolithic (Type I) boring across posterior flank of a left valve of *Cassianella cordillerana* McRoberts 2002, PRI 69602. 9, small endolithic borings (Type II) perpendicular to the outer surface of a left valve of *Palaeopharus orchardi* n. sp., PRI 69603. 10, small endolithic boring (Type II) preserved with pyrite filled-tube within middle shell layer of *Plagiostoma scallanae* n. sp., PRI 69604. Scale bars for 1–9 = 10 mm, for 10 = 1 mm.

silica dissolution and precipitation. Diagenetic calcite terminology generally follows Folk (1965) and that of replacement quartz textures primarily follows Schmitt & Boyd (1981) and Carson (1991). Silicified bioclasts may be composed of megaquartz (with generally euhedral crystals greater than 20 mm), microquartz (crystals less than 20 mm often with pinpoint extinction), and one or more varieties of fibrous chalcedonic quartz. Following Schmitt & Boyd (1981), Maliva & Siever, (1988), and Mišík, 1995, three varieties of chalcedonic quartz are recognized in the Gill Harbor samples: spherulitic chalcedony, quartzine (c axis parallel to fibers) and lutecite (c axis $\sim 30^\circ$ to fibers). Megaquartz and microquartz fabrics were not observed. In the following discussion, texture refers to crystallinity shape and size, whereas fabric refers to morphology of crystal aggregates.

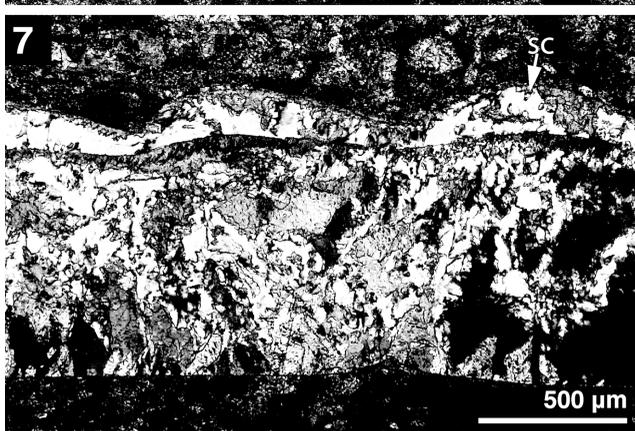
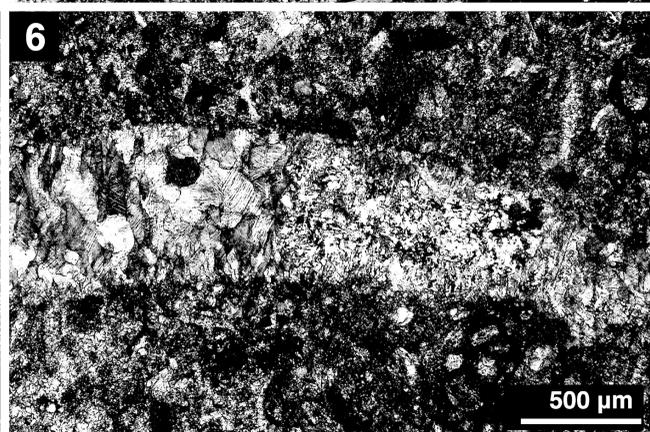
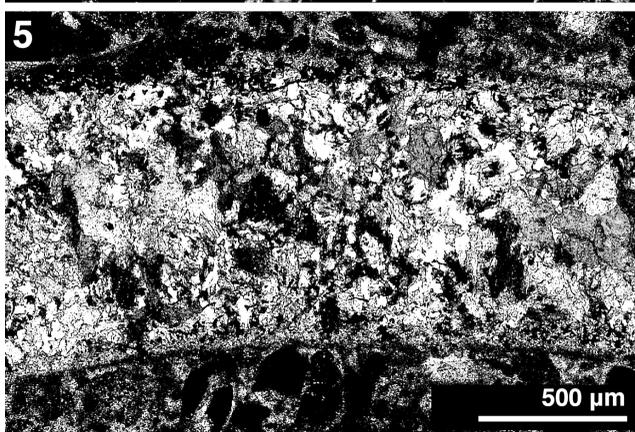
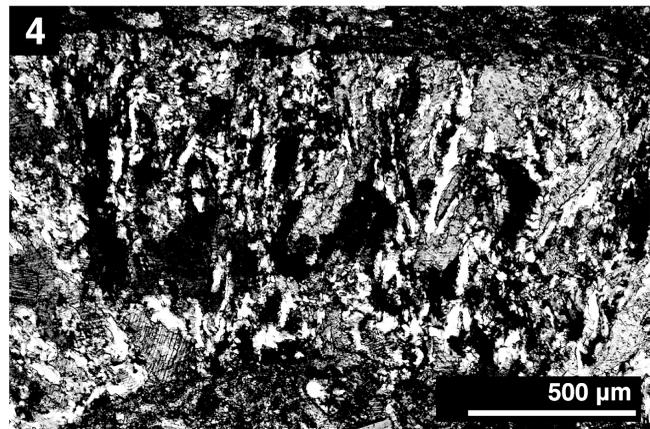
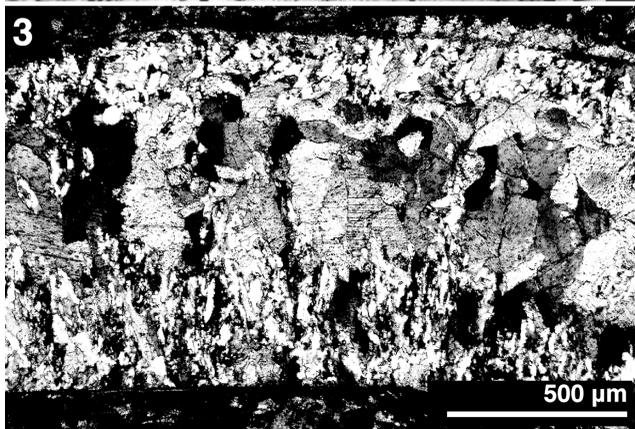
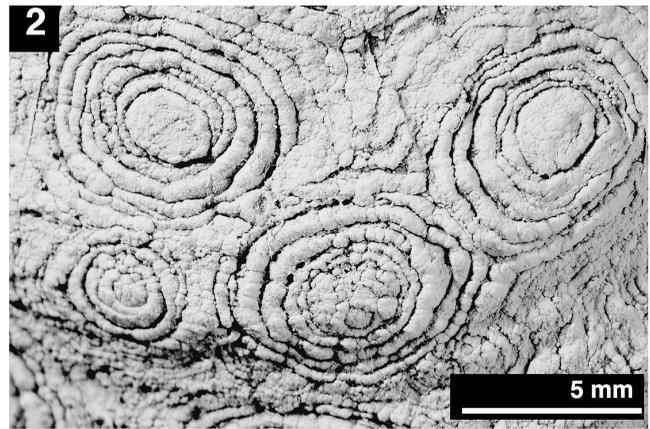
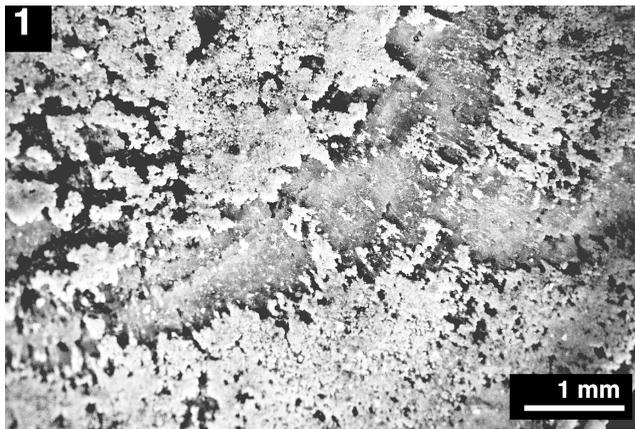
A majority of skeletal elements (bivalves and other taxa) were not silicified and therefore not recovered during the acid digestion process. These non-silicified bioclasts are mostly preserved as mosaics comprised of neomorphic calcite demarcated by micritic rims or opaque residular envelopes at the former skeletal boundary surfaces. Crystals within the mosaic are equant subhedral to anhedral drusy calcite which vary in size between relatively small ($\sim 100 \mu\text{m}$) near former skeletal boundary surfaces, to larger bladed crystals up to $200 \mu\text{m}$ long in the valve centers. These larger bladed calcite crystals tend to be oriented with their long axis perpendicular to the valve bounding surfaces suggesting void filling drusy cement. A few examples exhibit stratified layers of calcite with different textures and crystal sizes that may reflect relict skeletal structure. In one such informative example (Text-fig. 9.8), a thin ($\sim 100 \mu\text{m}$ thick) band, composed of smaller calcite crystals and bound by a thin residular film, is sandwiched between much larger equant and euhedral void-filling sparry calcite crystals. Although the taxonomic affinity of this bioclast is unknown, this finely-crystalline band may represent a middle skeletal layer relict and furthermore suggest selective dissolution and subsequent precipitation of the inner and outer skeletal layers followed by the neomorphic recrystallization of the middle skeletal layer. Taken together, these calcite textures suggest at least a two-fold process.

Complete silicification of skeletal bioclasts by replacement and/or reprecipitation is quite rare. Most bioclasts that do contain silica exhibit only partial silicification fabrics includ-

ing palisade networks of quartzine and lutecite chalcedonic quartz somewhat parallel to valve surfaces, zonal regions or masses of quartzine-lutecite aggregates, and outer layers or surficial crusts of spherulitic chalcedony. This partial silicification, especially in those specimens exhibiting zonal silicification or those transected by thick veins of diagenetic calcite, likely contributed to some of the observed skeletal fragmentation recovered during the acid immersion. In most cases, where complete or partial silicification has occurred, it is sufficiently fine-grained to preserve original surface features including ornamentation, growth lines, and muscle scars.

The primary mode of replacement silicification appears as a spongy and in some instances boxwork palisade fabric composed of a mosaic of blade-shaped crystal aggregates. These crystal aggregates exhibit imperfectly fibrous extinction, consisting of elongate regions of undulose extinction radiating from individual centers. Petrographic examination suggests these crystal aggregates include both quartzine and lutecite varieties of chalcedonic quartz. The aggregate of quartzine-lutecite masses are commonly concentrated near inner and outer skeletal boundaries and have typical orientations of elongated crystal bundles normal to the skeletal boundary or smaller, more equant crystal bundles with apparent random orientations. Generally, crystal aggregates are small ($10\text{--}50 \mu\text{m}$) and more equant at inner and outer skeletal boundaries and become larger ($50\text{--}200 \mu\text{m}$) and more elongate and blade shaped towards the valve centers, especially as they occur within dissolution fissures within calcite mosaics, producing a palisade open boxwork fabric (e.g., Text-figs 9.3, 9.4). This palisade fabric is best observed within backscatter and secondary SEM imaging of sectioned specimens (Text-figs 10.1–10.6) and has not, to the author's knowledge, been reported in other studies of silicified fossils. A variation of this mode of silicification is presented in several examples in which the smaller quartzine-lutecite aggregates are concentrated in certain regions of the valve (e.g., umbo or outer disk flank) and seem to radiate outwards towards the skeletal boundary (Text-fig. 9.6). Concentration of quartzine-lutecite aggregates near skeletal boundary surfaces, and occasionally as thin-bands within the middle portions of former bioclasts, may appear as thin stratified layers (e.g., Text-fig. 10.7), but are not representative of relict skeletal microstructural layering of original bioclasts.

*Text-fig. 9 (at right). Silicification textures. 1, surface texture of left valve interior of *Plagiostoma scallanae* n. sp. showing fine-scale replacement by quartzine-lutecite aggregates, PRI 69604. 2, surface texture of left valve of *Harpax articulatum* n. sp. showing well developed beekite rings of spherulitic chalcedony, PRI 69649. 3, 4, bivalve bioclast exhibiting partial replacement of neomorphic calcite by quartzine-lutecite crystal aggregates; note that orientations of quartzine-lutecite crystal aggregates are parallel and their size and length increase towards valve center and penetrate calcite mosaic; crossed polarizers, 3, PRI 69605, 4, PRI 69606. 5, nearly complete replacement of mosaic calcite, PRI 69607. 6, concentrated zone of quartzine-lutecite crystal aggregates in valve center, crossed polarizers, PRI 69606. 7, bivalve bioclast (mostly likely *Harpax articulatum* n. sp.) which exhibits spherulitic chalcedony in outer skeletal layer with inner layer dominated by quartzine-lutecite open boxwork nextork, PRI 69608. 8, bivalve bioclast filled with blocky void-filling sparry calcite surrounding middle (?skeletal) layer of finer-grained calcite mosaic, crossed polarizers, PRI 69609.*



A second silica fabric is represented by spherulitic chalcedony and chalcedonic overlay quartz that exhibits a clear fibrous structure within radial masses. This mode most commonly forms a discontinuous outer layer on some skeletal bioclasts with average thicknesses between 50–200 μm (Text-figs 9.2, 9.7, 10.4), but is also present as smaller globular masses within the interior of bioclasts. In some instances, the smaller chalcedonic spherules grade into discoid beekite masses that are variably presented and best observed at orientations normal to the shell surface (Text-fig. 9.2). Although often occurring in the same bioclast, chalcedonic overlays appear mostly discontinuous with the quartzine-lutecite palisade networks or zonal aggregates of the primary silicified fabric. Skeletal bioclasts of this type preserve only coarse external skeletal structures.

In most instances, relict internal structures of original bivalve skeletons are absent. In a few specimens, however, differential replacement of skeletal microstructural layers can be observed in certain bivalve taxa which possess biomineralic multilayered skeletal structures. For example, many *Harpax articulatum* n. sp. exhibit development of spherulitic chalcedonic beekite disks of the outer shell layer (originally of presumably foliated calcite), whereas middle and inner layers of crossed lamellar calcite exhibit very fine quartzine-lutecite fabrics (e.g., see Text-figs 27.1, 27.2). Interestingly, the myoconstraca of *H. articulatum* n. sp., which presumably possessed prismatic aragonite, was not replaced. Bivalves that were originally aragonitic in their entirety (e.g., Paleotaxodonta and trigonoideans), however, appear to be completely replaced with finer-grained quartzine-lutecite fabrics.

Most studies suggest that replacement of fossil skeletal material by various grades of silicification largely proceeds as a dissolution-precipitation reaction (e.g., Carson, 1991). For the primary mode of silicification (quartzine-lutecite), the silica phase was most likely precipitated following the partial dissolution of secondary sparry calcite. These textural fabrics suggest immediate replacement (*sensu* Schmitt & Boyd, 1981) in which no intervening void phase was developed. Evidence for this largely rests on the primary palisade fabric of the quartzine-lutecite crystal masses that demonstrably penetrate the corroded calcite mosaic. The timing and mechanism of replacement of the spherulitic chalcedony (and beekite disk masses) is somewhat more difficult to determine, as such intercrystalline relationships are not observed. Although

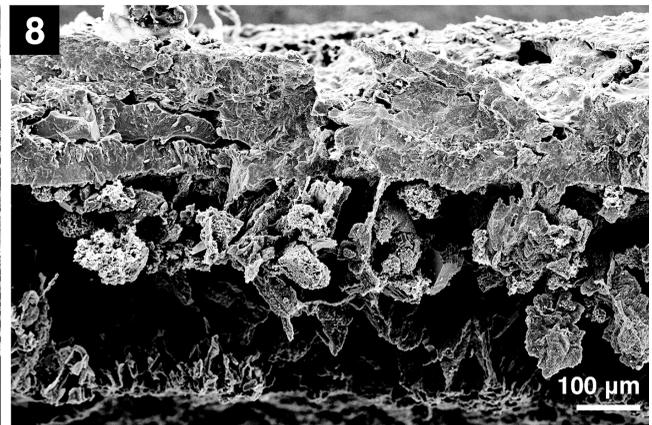
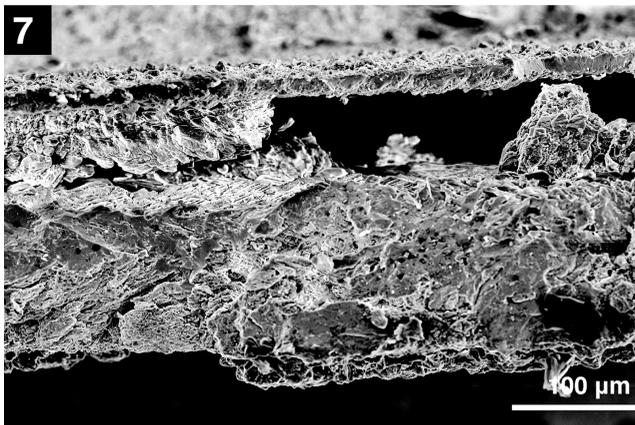
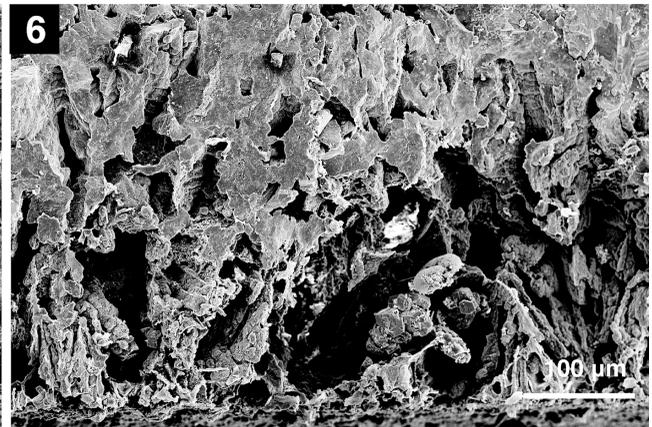
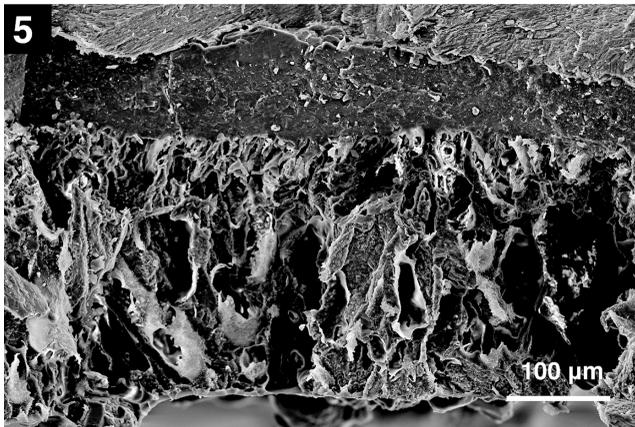
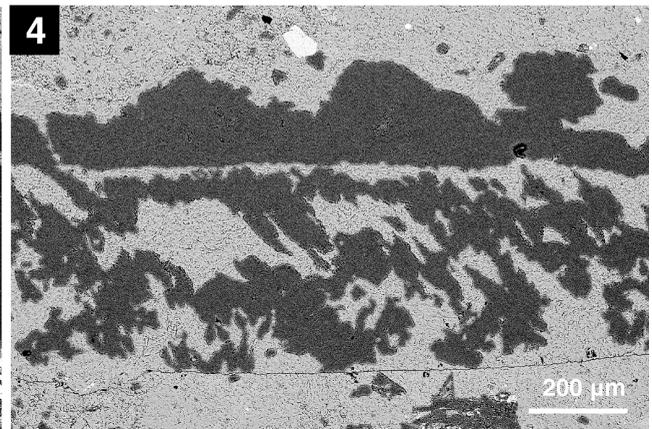
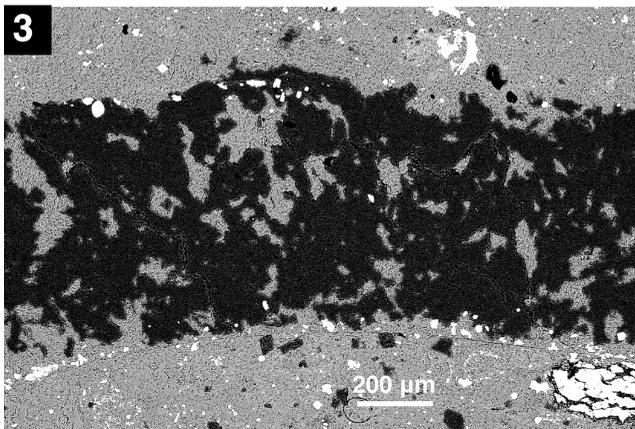
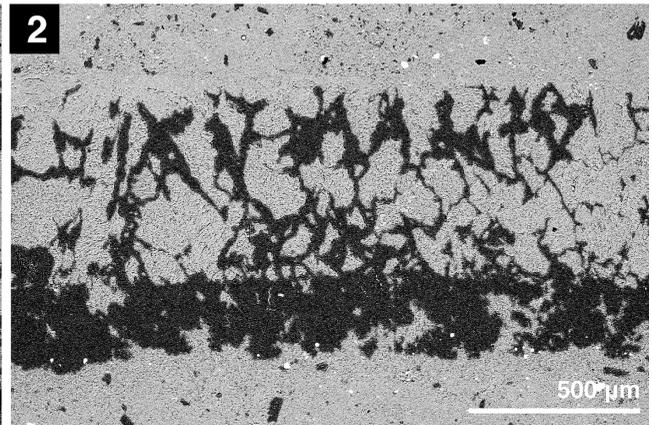
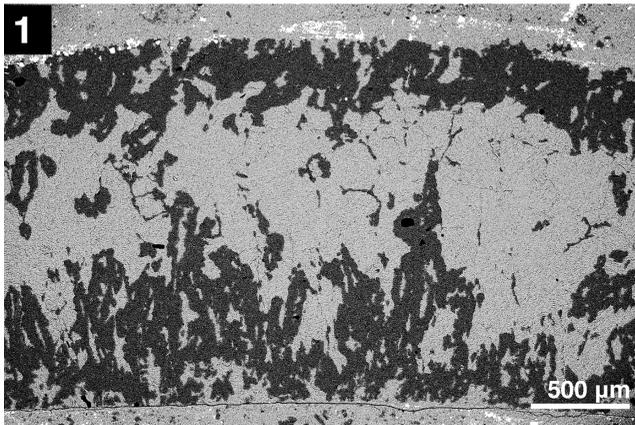
Schmitt & Boyd (1981) suggested that beekite chalcedonic phases observed in Permian bivalves from the Franson Member of the Park City Formation (their type IV) was of delayed replacement that involved a phase of moldic porosity, Newton *et al.* (1987) provided evidence that these too were a result of displacive silicification without an intervening void phase. Given the similarity of silicification textures from Gill Harbor with those observed by Newton *et al.* (1987) and Maliva & Siever (1988), it appears that the primary mode of silicification was by the simultaneous dissolution of calcite and precipitation of silica phases along a thin film solution boundary. Furthermore, as noted by several workers, silicification of fossils generally takes place during early diagenesis, often following aragonite dissolution/conversion and calcite neomorphism, but prior to burial diagenesis (e.g., Maliva & Siever, 1988; Carson, 1991).

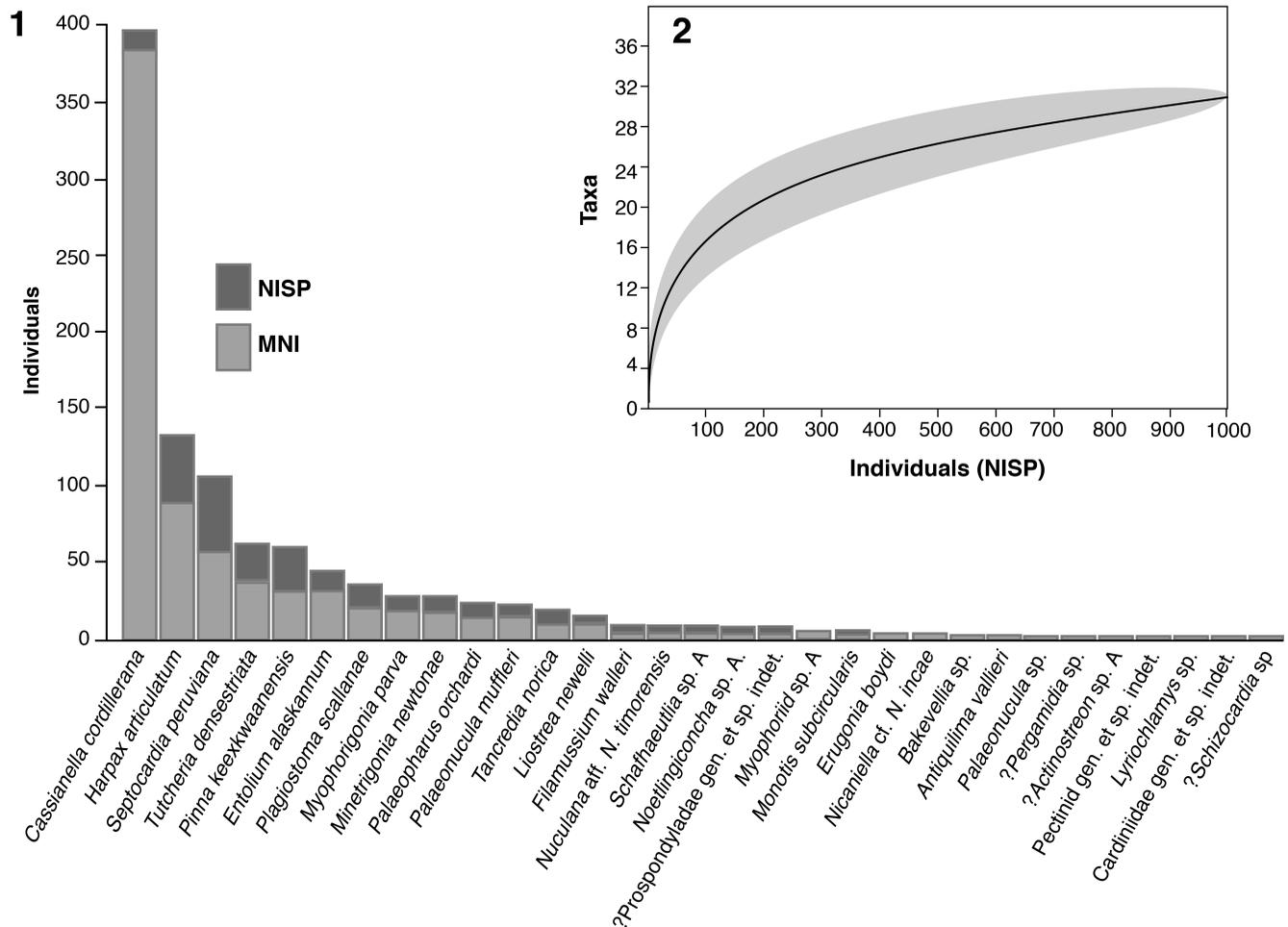
PALEOECOLOGIC AND PALEOGEOGRAPHIC SIGNIFICANCE

Richness and paleoecologic diversity metrics.—Previously discussed field and laboratory sampling and processing protocols (acid digestion of bulk samples) resulted in recovering a large number of silicified specimens across several phyla. Isolated individual bivalve specimens were by far the most abundant (in excess of 1000 identifiable individual specimens included in the following paleoecologic analyses). In addition to bivalves, numerous other specimens were recovered from the acid-bathed residue, including: cephalopods (51, mostly juvenile, ammonoids and large nautiloid), gastropods (14 specimens from at least three taxa), rare Scleractinia (3 fragmented phaceloid colony fragments greater than 0.5 cm), the planktonic hydrozoan *Heterastridium* (6 specimens), echinoid spines, crinoid ossicles, and a scaphopod.

Relative abundance of samples consisting of multielement skeletons, as in the bivalve animals, can be measured in several ways, with different estimates affected to various degrees by taphonomic factors and sampling biases. Estimates of the number of individuals made using the Minimum Number of Individuals (MNI) method is generally conservative and when the sample size is much smaller than the actual size of the population from which the sample is taken, then each valve of a bivalved organism most likely represents a unique individual (Gilinsky & Bennington, 1994). An estimate was also calculated using a modified Number of Identifiable Specimens (NISIP) method in which the number of individu-

*Text-fig. 10 (at right). Scanning electron micrographs of silicification textures on bivalve specimens. 1–3, backscatter SEM micrographs showing partial replacement by quartzine-lutecite crystal aggregates (darker shade) with boxwork palisades fabric; calcite is represented by intermediate gray, organic matter by white and pyrite by black shades, PRI 69605. 4, backscatter SEM micrograph of spherulitic chalcedony of outer skeletal layer and a lower layer with quartzine-lutecite boxwork palisades fabric, PRI 69608. 5, 6, secondary SEM micrographs showing quartzine-lutecite boxwork palisades fabric; 5, LV of *Harpax articulatum* n. sp., PRI 69610; 6, RV of *Plagiostoma scallanae* n. sp., PRI 69611. 7, secondary SEM micrograph showing multilayered-silicification with thin outer skeletal layer in RV of *Entolium alaskanum* n. sp., PRI 69612. 8, secondary SEM micrograph of spherulitic chalcedony of outer skeletal layer and a lower layer with quartzine-lutecite boxwork palisades fabric of LV of *Plagiostoma scallanae* n. sp., PRI 69613.*





Text-fig. 11. Sample metrics of recovered bivalves from USGS loc. M1912. 1, rank abundance and individual counts for species recovered. 2, rarefaction curve. MNI = minimum number of individual method; NISP = number of identifiable specimens method.

als was calculated by adding the left and right valves to the number of conjoined/articulated valves. However, partial and fragmented specimens were included in the individual counts only if the skeleton preserved sufficient morphological detail (e.g., the umbo/beak) to ensure that multiple fragments of the same individuals were not counted more than once. Of the 1121 total complete, partial, and fragmented specimens identified, individual bivalve animal estimates of 784 (MNI) and 1036 (NISP) were calculated. Although there is a 24.3% difference in the resultant MNI and NISP counts, the rank species/abundance patterns are essentially identical (Text-fig. 11) and therefore either measure can be used to adequately address the ecologic and trophic structure of the assemblage.

As discussed in the previous section, the fossil assemblage is interpreted to represent a within-habitat time averaged assemblage (from one or more death assemblages) with a demonstrable ecologic structure indicative of a single environment. As has been shown by Kidwell (2002), while death assemblages may have substantial taphonomic bias and time

averaging which affects the measure of richness of the once living community (life or census assemblage), the community structure is commonly preserved. Notwithstanding the spatial mixing, time-averaging, and taxon-specific sample bias (e.g., selective dissolution/replacement or breakage/abrasion of fragile skeletons or skeletal elements), which certainly played some role in the taxonomic composition of the recovered sample, the analyses below likely represent a snapshot of a single paleocommunity.

The Gill Harbor bivalve fauna is taxonomically rich and consists of 31 recognizable species (or equivalent taxa) distributed amongst 11 orders, 17 superfamilies, 24 families, and 30 genera. The taxonomic composition of the bivalve fauna is shown in Table 1 and the rank abundance plot (Text-fig. 11.1). The rarefaction curve of the sample (Text-fig. 11.2) shows a significant flattening at about 400–450 individuals suggesting that additional sampling would not increase the number of species substantially. The rank distribution of species abundance shows a rapid decline from a small number

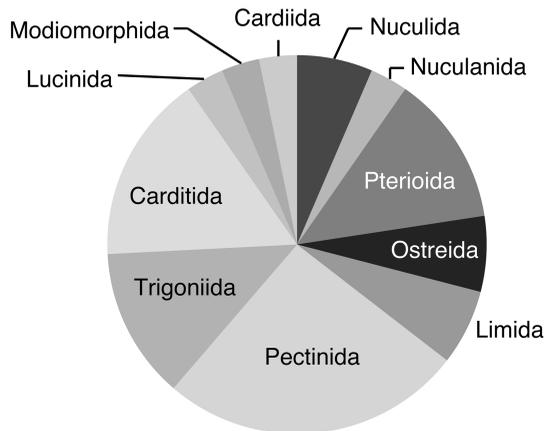
Table 1. Sample metrics and living habits of bivalve taxa from USGS loc. M1912. Abbreviations: LV=left valve, RV=right valve, CONJ=conjoined valve pair; life habit abbreviations: Is=shallow infaunal burrower, Id=deep infaunal burrower, By=byssate, Eb=endobysate, Mo=mobile, Se=sessile, Sw=swimming, Ce=cemented to substrate, Re=reclining, De=detritus feeder, Su=suspension feeder.

Order	Superfamily	Species	Sample Size	MNI	NISP	Life Habit
Nuculoida	Nuculoidea	<i>Palaeonucula muffleri</i> n. sp.	LV=8, RV=10, CONJ=4	14	22	Id, Mo, De
Nuculoida	Nuculoidea	<i>Palaeonucula</i> sp. indet.	LV=0, RV=0, CONJ=1	1	1	Id, Mo, De
Nuculanida	Nuculanoidea	<i>Nuculana</i> aff. <i>N. timorensis</i> (Krumbeck, 1924)	LV=3, RV=3, CONJ=0	3	6	Id, Mo, De
Pterioidea	Pinnoidea	<i>Pinna keexkwaanensis</i> n. sp.	LV=26, RV=26, CONJ=3	29	54	Se,By,Su
Pterioidea	Pterioidea	<i>Cassianella cordillerana</i> McRoberts, 2002	LV=386, RV=12, CONJ=0	386	398	Ep, Re/By, Su
Pterioidea	Pterioidea	<i>Bakevella</i> sp. A	LV=2, RV=0, CONJ=0	2	2	Ep/Se, By, Su
Pterioidea	Pterioidea	? <i>Pergamidia</i> sp. indet.	LV=0, RV=1, CONJ=0	1	1	Ep/Se, By, Su
Ostreida	Ostreioidea	<i>Liostraea newelli</i> Newton, 1987	LV=9, RV=2, CONJ=0	9	11	Ep, Ce/Re, Su
Ostreida	Ostreioidea	? <i>Actinostreon</i> sp. A	LV=1, RV=0, CONJ=0	1	1	Ep, Ce, Su
Limoida	Limoidea	<i>Antiquilima vallieri</i> Newton, 1987	LV=0, RV=2, CONJ=0	2	2	Ep, By, Su
Limoida	Limoidea	<i>Plagiostoma scallanae</i> n. sp.	LV=19, RV=21, CONJ=0	21	40	Ep, By, Su
Pectinida	Monotoidea	<i>Monotis (Pacimonotis) subcircularis</i> Gabb, 1864	LV=0, RV=3, CONJ=0	3	3	Ep, By/Re, Su
Pectinida	Pectinoidea	<i>Entolium alaskanum</i> n. sp.	LV=13, RV=38, CONJ=0	38	51	Ep, Re/Sw, Su
Pectinida	Pectinoidea	<i>Filamussium walleri</i> n. sp.	LV=4, RV=3, CONJ=0	4	7	Ep, By/Re/Sw, Su
Pectinida	Pectinoidea	<i>Lyriochlams</i> sp. indet.	LV=0, RV=1, CONJ=0	1	1	Ep, By, Su
Pectinida	Pectinoidea	Pectinid gen. et sp. indet.	LV=1, RV=0, CONJ=0	1	1	Ep, By, Su
Pectinida	Plicatuloidea	<i>Harpax articulatum</i> n. sp.	LV=43, RV=92, CONJ=0	92	137	Ep, Ce/Re, Su
Pectinida	Prospondylidea	? <i>Prospondyladae</i> gen. and sp. indet.	LV=1, RV=2, CONJ=0	2	3	Ep, Ce, Su
Pectinida	Prospondylidea	<i>Noetlingiconcha</i> sp. A	LV=1, RV=4, CONJ=0	4	5	Ep, Ce, Su
Trigonioida	Trigonoidea	Myophoriid sp. A	LV=3, RV=1, CONJ=0	3	4	Is, Mo, Su
Trigonioida	Trigonoidea	<i>Erugonia boydi</i> n. sp.	LV=1, RV=2, CONJ=1	3	2	Is, Mo, Su
Trigonioida	Trigonoidea	<i>Minetrigonia newtonae</i> n. sp.	LV=16, RV=18, CONJ=0	18	34	Is, Mo, Su
Trigonioida	Trigonoidea	<i>Myophorigonia parva</i> n. sp.	LV=15, RV=19, CONJ=0	19	34	Is, Mo, Su
Carditida	Crassatelloidea	<i>Nicaniella</i> cf. <i>N. incae</i> (Jaworski, 1922)	LV=0, RV=3, CONJ=0	3	3	Is, Mo, Su
Carditida	Crassatelloidea	Cardiniidae gen. et sp. indet.	LV=0, RV=1, CONJ=0	1	1	Is, Mo, Su
Carditida	Carditoidea	<i>Tutcheria densestriata</i> (Körner, 1937)	LV=22, RV=30, CONJ=3	33	55	Is, Mo, Su
Carditida	Carditoidea	<i>Septocardia peruviana</i> (Cox, 1949)	LV=62, RV=51, CONJ=1	63	113	Is, Mo, Su
Carditida	Carditoidea	? <i>Schizocardita</i> sp. indet.	LV=0, RV=1, CONJ=0	1	1	Is, Mo, Su
Lucinida	Lucinoidea	<i>Schafhaeutlia</i> sp. A	LV=3, RV=3, CONJ=0	3	6	Is, Mo, Su
Modiomorphida	Modiomorphoidea	<i>Palaeopharus orchardi</i> n. sp.	LV=11, RV=12, CONJ=2	14	25	Is, Mo, Su
Cardiida	Tellinoidea	<i>Tancredia norica</i> n. sp.	LV=7, RV=8, CONJ=1	9	16	Id, Mo, Su

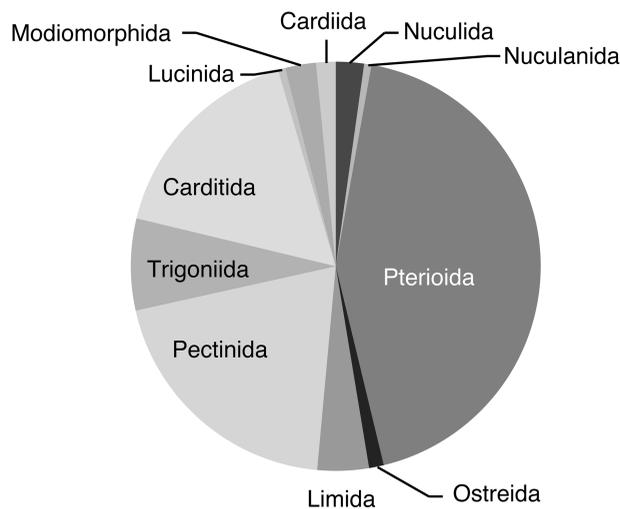
of abundant species to a progressively increasing number of rare species. More than half of the species are represented by fewer than 10 specimens and seven taxa (22% of the NISP) are represented by a single individual. Pterioidea, Pectinida, and Carditida collectively make up more than 80% of the individuals (Text-fig. 12.2). By a significant margin, the assemblage is dominated by *Cassianella cordillerana* McRoberts in McRoberts & Blodgett, 2002 with smaller contributions by *Harpax articulatum* n. sp., *Septocardia peruviana* (Cox, 1949), *Entolium alaskanum* n. sp., *Tutcheria densestriata*

(Körner, 1937), and *Pinna keexkwaanensis* n. sp. In spite of the high proportion of *C. cordillerana* individuals, metrics of assemblage dominance are quite low and evenness quite high. Simpson's Dominance Index (e.g., Hammer & Harper, 2006) equals 0.19, whereas, the Probability of Interspecific Encounter measure of evenness (Olszewski & Kidwell, 2007) for the assemblage equals 0.80. Both measures are likely quite sensitive to the very high number of rare species and minimize the few common ones.

1 Per-taxon Bivalve Orders



2 Proportional Bivalve Orders



Text-fig. 12. Distribution of taxonomic composition of bivalves from USGS loc. M1912. 1, per-taxon distribution of bivalve individuals by order. 2, proportional distribution of bivalve species by order.

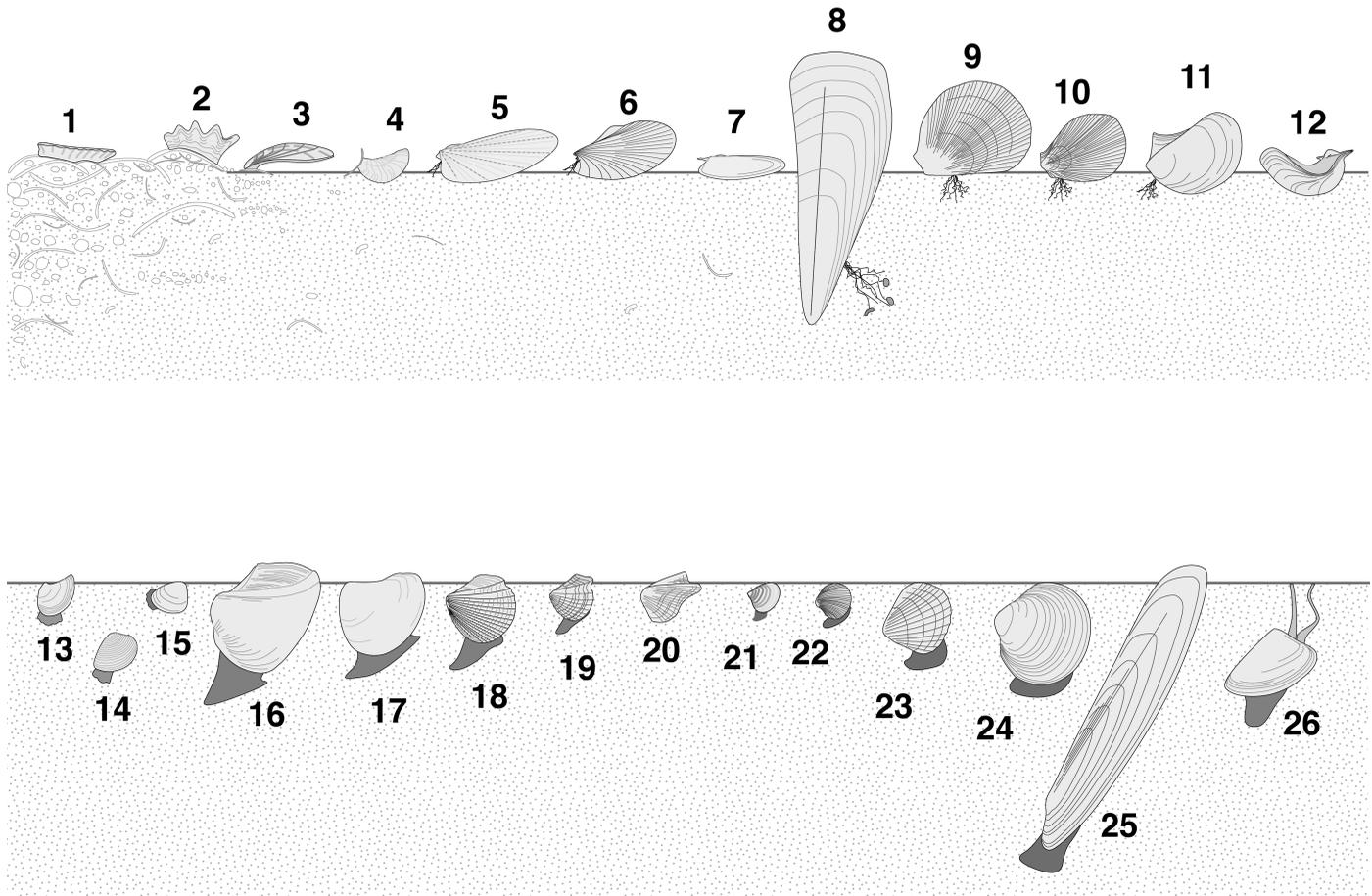
Trophic structure of the Gill Harbor assemblage.—A more complete discussion and rationale for the assigned living habits of individual taxa are provided in their respective systematic entries. However, it should be noted that assigning a single living habit to some taxa was hampered by apparent complexity in life histories of some species that exhibit a change in their ecology during ontogeny (e.g., *Cassianella cordillerana* McRoberts in McRoberts & Blodgett, 2002 is likely initially byssate in early ontogenetic stages but adults are free living recliners) or that may not be constrained to a single living habit

(e.g., some limids may detach their byssi, swim for a short distance, and reattach). For the analyses and discussion below, the primary life mode of adult individuals was considered.

The Gill Harbor bivalve assemblage contains species possessing a wide variety of living habits in terms of feeding strategy, mobility, and relation to substrate (Text-fig. 13). Greater than 97% of recognized individuals are suspension feeders, whereas less than 3% are deposit feeding nuculoids and nuculanoids. Among mobility and substrate preferences (Text-fig. 14, Table 1), approximately three-fourths of the assemblage is comprised of epifaunal, low-level suspension feeding individuals with a majority of these represented by reclining free-living species (43.9%) and, to a smaller extent, cementing (15.5%) and byssally attached (5.6%) species. Shallow, non-siphonate burrowers dominate the infauna making up 27.6% of the total assemblage. In terms of tiering, the assemblage is dominated by low epifaunal to shallow infaunal species. The high number of species with a wide spectrum of living habits and relatively low dominance metric for the assemblage suggests stability in communities that contributed to the fossil assemblage.

This trophic structure may provide information regarding the environments inhabited by the living assemblage(s) from which the sample was derived. As shown by Levinton (1972), suspension-feeding benthic marine communities were hypothesized to live in a trophically more varying environment and, additionally, a resource-independent environment. The dominant modes of life in the assemblage (reclining and shallow burrowing) suggest a relatively soft and probably medium to coarse-grained substrate. The small but significant representation of deposit-feeding mobile burrowers, however, also points to substrates with sufficient fine-grained, organic-rich detritus. The moderate proportion of cementing individuals may at first suggest a firm substrate, but all evidence of attachment substrates from the collection are other bivalve skeletal fragments and not a larger framework that might be expected in spongiomorph-coral thickets typical of wave-resistant settings. In addition, most of the cementing species (e.g., *Liostrea newelli* Newton in Newton *et al.*, 1987 and *Harpax articulatum* n. sp.) have relatively small attachment areas and have also spent their adult lives in a free-living or reclining mode. Based on the number of epibionts in the collection, there would no doubt be a variety of larger grain sizes in the sediment with a significant number of skeletal clasts composed of discarded and perhaps fragmented valves exposed on the seabed for an extended period to serve as suitable substrates for the cementing forms.

The paleosynecologic structure of the Gill Harbor bivalve fauna can be compared with several Late Triassic bivalve-dominated faunas from which comparable data are available. It is remarkable that many of the known Upper Triassic level-



Text-fig. 13. Schematic sketch of inferred living habits of bivalve taxa from USGS loc. M1912. 1, *Noetingiconcha* sp. A. 2, ?*Prospondylidae* gen. and sp. indet. 3, *Harpax articulatum* n. sp. 4, *Liostrea newelli* Newton in Newton et al., 1987. 5, *Filamussium walleri* n. sp. 6, *Monotis* (*Pacimonotis*) *subcircularis* Gabb, 1864. 7, *Entolium alaskanum* n. sp. 8, *Pinna keekwaanensis* n. sp. 9, *Plagiostoma scallanae* n. sp. 10, *Antiquilima vallieri* Newton in Newton et al., 1987. 11, *Bakevellia* sp. A. 12, *Cassianella cordillerana* McRoberts in McRoberts & Blodgett, 2002. 13, *Nuculana* aff. *N. timorensis* (Krumbeck, 1924). 14, *Palaeonucula muffleri* n. sp. 15, *Palaeonucula* sp. indet. 16, *Myophoriid* sp. A. 17, *Erugonia boydi* n. sp. 18, *Minetrigonia newtonae* n. sp. 19, *Myophorigonia parva* n. sp. 20, ?*Schizocardita* sp. indet. 21, *Nicaniella* cf. *N. incae* (Jaworski, 1922). 22, *Tutcheria densestriata* (Körner, 1937). 23, *Septocardia peruviana* (Cox, 1949). 24, *Schafhaeutlia* sp. A. 25, *Palaeopharus orchardi* n. sp. 26, *Tancredia norica* n. sp.

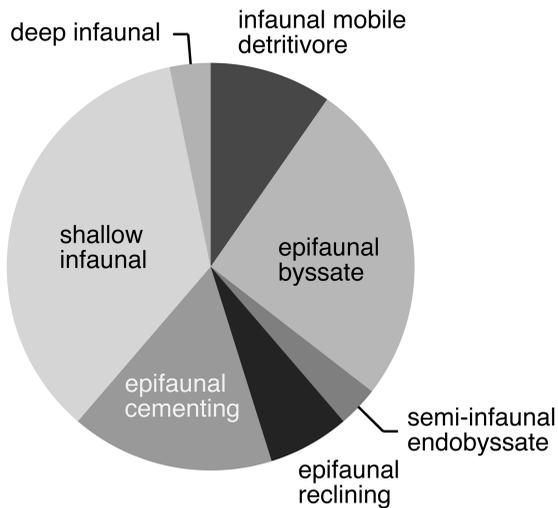
bottom faunas are not only dominated by low-level suspension feeding bivalves, but are ecologically and taxonomically characterized by species of *Cassianella*. Among these are the classic lower Carnian Cassian fauna from northern Italy (e.g., Fürsich & Wendt, 1977; Nützel & Kaim, 2014), the lower Norian fauna from Hells Canyon, Oregon (e.g., Newton et al., 1987), and the Rhaetian Tyaughton Creek fauna of western British Columbia (e.g., McLearn, 1942). It is unfortunate that quantitative abundance data from other potentially comparable faunas (e.g., Cerro de Pasco of Peru) do not exist.

In terms of trophic structure and supra-specific taxonomic composition, the Gill Harbor assemblage exhibits some striking similarities and some important differences with the Hells Canyon fauna. Although there are few species in common, agreement among genera and higher taxonomic ranks

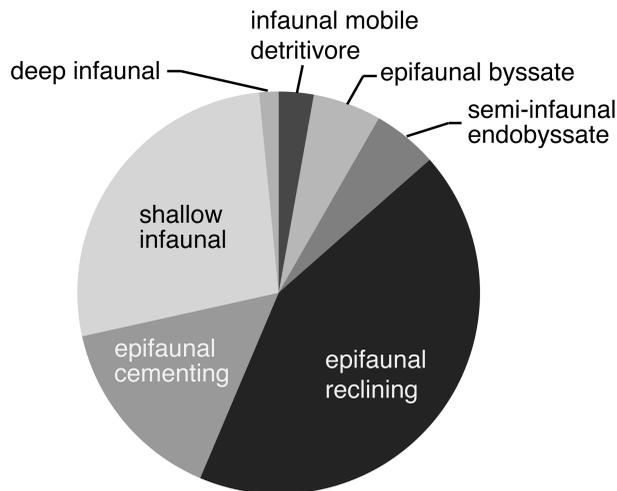
is relatively high. One important difference includes the very low percentage of infaunal deposit feeders from Hells Canyon as reported by Newton et al. (1987) (1 species and < 1% of individuals) that are much better represented at Gill Harbor (3 species and 3% of individuals). In addition, and perhaps equally important, is the relatively low proportion of nestling byssate bakevellid and arcoïd species from the Gill Harbor fauna, which are common constituents of the above-mentioned faunas.

The Gill Harbor fauna may also be compared to the lower Rhaetian (or upper Norian *sensu* Tackett et al., 2014) bivalve dominated fauna of the Gabbs Formation from west-central Nevada. Laws (1982) documented five successive bivalve-cephalopod dominated assemblages from the Gabbs Formation. The lower part of Laws' (1982) Middle Member (= Nun

1 Per-taxon living habits



2 Proportional living habits



Text-fig. 14. Trophic composition of recovered bivalves from USGS loc. M1912. 1, per-taxon distribution of bivalve species individuals by living habit. 2, proportional distribution of bivalve species by living habit.

Mine Member of Taylor et al., 1983) contains an interesting succession of two associations with many common taxa: the lower *Plicatula* Association and the overlying *Tutcheria* Association. It should be noted that based on a taxonomic review, the plicatulids from the Nun Mine Member are better placed into the genus *Harpax* (see systematic paleontology section). Taken together, these two faunas have a very similar taxonomic composition to the Gill Harbor assemblage described herein, but differ in the relative proportions of the shallow infaunal *Tutcheria* and epifaunal cemented *Harpax*

perimbricata and the significantly greater relative frequency of *Cassianella lingulata*. This difference is probably caused by a variety of ecologic factors, but may also be due to taphonomic bias or sampling failure of the rather delicate *Cassianella*, whose left valve is quite thin when compared to *Harpax* or a conjoined *Tutcheria*.

Paleobiogeographic implications.—Unraveling the Triassic paleobiogeographic patterns of eastern Panthalassa now preserved within the terrane belts of the western North and South America, is a daunting task and fraught with problems of tectonic transport of the terranes themselves, destruction by collisional tectonics, sampling bias, and issues related to taxonomy. This is further compounded by variability in the factors controlling the distribution of bivalves, including bathymetry, substrate, temperature, chemistry (e.g., dissolved oxygen), and oceanographic currents needed for dispersal and the dispersion potential of bivalve larvae. Given these factors, the distributional patterns of many Triassic macrofauna are quite complex and likely involve combinations of faunal dispersion, such as the Pantropical model of Newton (1988), tectonic displacement, or some combination thereof (e.g., Silberling, 1985; Stanley & González-León, 1995).

Dispersion of bivalve species across Panthalassa and the Tethys would most likely have been through passive transport of larvae via surface currents. Although some species of Triassic pelagic bivalves may have had planktotrophic larvae (McRoberts, 2000), almost nothing is known about the larval development of most species. Apart from Nuculidae, Nuculanidae, and several others families (Carditidae, Astartidae, and Fimbriidae) which are characterized by a non-planktotrophic larval development, most other modern bivalve groups (e.g., pteriods, pectinoids, ostreoids) have mostly planktotrophic larvae, although at least some oysters exhibit brooding larval development (Jablonski & Lutz, 1980, 1983). Thus, it is likely that many of the Gill Harbor species did have teleplanic larvae comparable to modern relatives. Regardless, even a short-lived planktonic larval stage could be transported great distances. For example, larvae having a pelagic stage of 2–6 weeks could be transported up to 500 km with only moderate currents; longer pelagic larval stages (e.g., three months or more) could effectively cross entire deep ocean basins (e.g., Sheltema 1977). Paleocurrents within Panthalassa and the Tethys have been hypothesized by several workers (e.g., Tollmann & Kristan-Tollmann 1985; Yan & Zhao 1991, Damborenea et al., 2013) and can be summarized as: low latitude north and south equatorial currents from the margin of Pangaea moving westwards across Panthalassa and into the Tethys with an equatorial counter current moving eastward, and two gyres, a clockwise gyre in northern Panthalassa and a counterclockwise gyre in southern Panthalassa both bring-

ing cooler water towards the equatorial margin of Pangaea. Those paleocurrents along tropical eastern Panthalassa would have direct bearing on the faunal distributional patterns observed among the bivalves species considered here in light of the low-latitude paleoposition inferred for the Gill Harbor locality and the Alexander terrane (e.g., Panuska & Stone, 1985; Caruthers & Stanley, 2008a, b; and see Geologic and Stratigraphic Setting section).

It is not unexpected that the bivalve fauna from Gill Harbor provides strong ties to other comparable faunas from likely coeval strata elsewhere in the Alexander terrane. For example, the Chapin Peak Formation exposed along the intertidal zone at Bostwick Inlet (USGS locs M5095, M5909), Gravina Island, Alaska, some 220 km to the SE of Gill Harbor, yields a taxonomically rich bivalve fauna identified by N. J. Silberling and D. L. Jones (as cited in Berg, 1973: 24) almost identical to that described herein from Gill Harbor. Although never illustrated or described in detail, Berg (1973) lists 10 taxa from Bostwick Inlet which are no doubt equivalents to those from the Keku Volcanics at Gill Harbor: *Cassianella* sp., *Gervilleia* sp., *Goniomya?* sp., *Minetrigonia* cf. *M. cairnesi* (McLearn, 1942), *Minetrigonia* cf. *M. suttonensis* (Clapp & Shimer, 1911), *Palaeopharus* cf. *P. buriji* Kiparisova 1954, *Pinna* sp., *Plicatula* cf. *P. perimbricata* Gabb, 1870, *Septocardia* sp., “*Variamusium*” sp., and indeterminate trigoniids, pectinoids, and nuculoids. According to Silberling (cited in Berg, 1973: 24), the fossils from Bostwick Inlet are “late, possibly latest, Norian and are younger than the Upper Triassic *Halobia*- and *Heterastridium*-bearing beds of the underlying Nehenta Formation.”

Comparison between the upper Norian Gill Harbor bivalve fauna and other described bivalve faunas of comparable ages (Norian–Rhaetian) throughout the American Cordillera has paleobiogeographic implications. Table 2 lists the reported bivalve taxa (uncorrected for taxonomic revisions) from these localities. Of the 17 positively identified bivalve species (of 31 species-level taxa) from Gill Harbor, only six have been reported from other regions outside of the Alexander terrane, with the remaining 11 (~ 65%) apparently endemic. The number of endemic species may be higher given the relatively high number of unresolved species. Given the high number of endemic species from Gill Harbor, it is reasonable to assume a broad geographic separation of Alexander terrane both from other terranes (e.g., Wrangellia and Wallowa) and from the western margin of Pangea. The distinctiveness of this fauna from those of Wrangellia (and also the Wallowa terrane) provides additional support for their separation as suggested by Jones *et al.* (1977), Blodgett & Frýda (2001), and Caruthers & Stanley (2008a, b). It is also important to note that there exists little to no taxonomic affinity between the Gill Harbor bivalves and well-known faunas of similar age from the Tethyan

paleogeographic region. This result may be contrasted with other Norian and Rhaetian faunas from Cordilleran accreted terranes (e.g., Wallowa) that show a small, but perhaps significant, number of species with a west-Tethys affinity (e.g., Newton, 1983, 1987, 1988). This in itself is not surprising given that during the Late Triassic, Panthalassa would have been 3000 km wider than the modern tropical Pacific (Smith & Westermann, 1990).

The most widely distributed species occurring at Gill Harbor (and elsewhere in the Alexander terrane) is *Monotis subcircularis* which is known from throughout eastern Panthalassa in fully open and deep marine settings both from other terranes (e.g., Wrangellia, Eastern Kalamath, Penninsular) and from autochthonous or parautochthonous craton-bound strata (e.g., northern Alaska, northeastern British Columbia, South America Cordillera) during the late Norian (e.g., Westermann, 1973; Tozer, 1980; Silberling 1985; McRoberts, 2010). While *M. subcircularis* may not provide useful high-resolution latitudinal or longitudinal biogeographic information within this broad range, it does suggest that the Gill Harbor locality was on the edge of or had significant connections to the open Panthalassa Ocean.

The strongest biogeographic connection of the Gill Harbor fauna can be found with the upper Norian of the South American Cordillera (Peru and Chile). Of the six species in common, several [e.g., *Septocardia peruviana* (Cox, 1949) and *Tutcheria densestriata* (Körner, 1937)] are also known from several North American terranes (e.g., Wrangellia, Nixon Fork, Wallowa) suggesting they likely had quite broad distributions across eastern Panthalassa. Examination of inferred close relatives of other Gill Harbor species, however, show a more compelling biogeographic connection to the bivalve dominated faunas of Chile and Peru. For example, *Schizocardita cristata* Körner, 1937 is the only known representative of the genus apart from the specimen described from Alaska. This faunal affinity (particularly with *Septocardia peruviana*) of the Gill Harbor fauna to South America was recognized by Newton (1983) and later noted by Panuska & Stone (1985) in support for a southern paleolatitude for the Alexander terrane during the Late Triassic.

The Gill Harbor fauna expands the geographic distributions of several genera and species, suggesting a reevaluation of previous interpretations of their paleogeographic ranges. For example, both *Liostrea newelli* and *Antiquilima vallieri*, thought to have been endemic to the Wallowa Terrane (Newton in Newton *et al.*, 1987), are now known from the Alexander terrane. Furthermore, the fauna from Gill Harbor expands the known range of several genera. For example, the distribution of *Palaeopharus* was previously known from largely boreal and western Panthalassa localities (e.g., Tokuyama, 1958, Kiparisova *et al.*, 1966). Additionally, Damborenea

Table 2. Bivalve faunal lists from comparable Norian–Rhaetian North and South American localities. Paleogeography and faunal list sources:

¹Autochthonous Panagean South American margin (Jaworski, 1922; Körner, 1937; Cox, 1949; Hayami et al., 1977); ²Parautochthonous Pangean North American margin (Laws, 1982); ³Wallowa terrane (Newton et al., 1987); ⁴Wrangell terrane (Clapp & Shimer, 1911; Tozer, 1963; Stanley, 1989); ⁵Wrangell terrane (Newton, 1983); ⁶Caldwaller terrane (McLearn, 1942; Tozer, 1963; Umhoefer & Tipper, 1998); ⁷Nixon Fork terrane (McRoberts & Blodgett, 2002).

Peru and Chile (Lower Norian) ¹	New York Canyon (Lower Rhaetian) ²	Hells Canyon (Lower Norian) ³	Vancouver Island (L. Rhaetian) ⁴	Green Butte (Lower Norian) ⁵	Tyughton Creek (Lower Rhaetian) ⁶	Taylor Mountains (Lower Norian) ⁷
<i>Palaeoneilo</i> sp.	<i>Arcavricula</i> sp.	<i>Nuculoida</i> indet.	<i>Nuculana silicea</i>	<i>Palaeoneilo</i> sp.	<i>Cassianella lingulata</i>	<i>Astarte</i> sp.
<i>Nucula subaequilatera</i>	<i>Cassianella lingulata</i>	<i>Parallelodon</i> cf. <i>monobensis</i>	<i>Parallelodon</i> sp.	<i>Septocardia</i> sp.	<i>Pecten</i> cf. <i>yukonense</i>	<i>Cassianella cordillerana</i>
<i>Nucula carantana</i>	<i>Chlamys</i> sp.	<i>Mysidiella cordillerana</i>	<i>Catella tyughtonae</i>	<i>Cassianella angusta</i>	<i>Pecten tyughtonae</i>	<i>Gryphaea arcuatiformis</i>
<i>Phaenodesmia</i> sp.	Heterodontid indet.	? <i>Arcavricula</i> sp.	<i>Cassianella</i> sp.	<i>Tutcheria</i> cf. <i>densestriata</i>	<i>Pecten pontianis</i>	<i>Maoritronia</i> sp.
<i>Nuculana silicea</i>	<i>Malletiidea</i> sp. 1	<i>Gervillia</i> (<i>Caltriopsis</i>) <i>angusta</i>	<i>Plicatula perimbricata</i>	<i>Palaeonucula</i> sp.	<i>Pecten caldwallerensis</i>	<i>Minertronia</i> cf. <i>suttonensis</i>
<i>Macrodon beyrichi</i>	<i>Malletiidea</i> sp. 2	? <i>Gervillia</i> sp.	" <i>Variamussium</i> " <i>yukonensis</i>	<i>Parallelodon</i> sp. 1	<i>Pecten</i> cf. <i>mihanius</i>	<i>Minertronia</i> sp.
<i>Macrodon formosissimus</i>	<i>Myophoria</i> sp.	<i>Cassianella angusta</i>	<i>Ergonia</i> sp.	? <i>Gryphaea</i>	<i>Pecten</i> cf. <i>saccoi</i>	<i>Septocardia</i> cf. <i>peruviana</i>
<i>Macrodon</i> sp. indet.	<i>Myophoricardium</i> sp.	<i>Krumbeckiella</i> cf. <i>tinorensis</i>	<i>Myophoria suttonensis</i>	<i>Nuculana</i> sp. 2	<i>Minertronia suttonensis</i>	<i>Tutcheria densestriata</i>
<i>Myophoria multicostata</i>	Pectinid sp. 1	<i>Antiquilima valleri</i>	<i>Myophoria</i> sp.	<i>Parallelodon</i> sp. 2	" <i>Myophoria</i> " <i>columbiana</i>	
<i>Myophoria paucicostata</i>	Pectinid sp. 2	<i>Antiquilima</i> sp.	<i>Myophorignia multicostata</i>	<i>Minertronia</i> sp. 2	" <i>Myophoria</i> " <i>adornata</i>	
<i>Myophoria?</i> (<i>Trigonia?</i>) <i>elegantoides</i>	Permphoridae sp.	<i>Mysidiopteria williamsi</i>	<i>Maoritronia columbiana</i>	<i>Plagiostoma</i> sp.	" <i>Myophoria</i> " <i>zaballos</i>	
<i>Cardita</i> n. sp. ex. aff. <i>gumbeli</i>	<i>Plicatula perimbricata</i>	<i>Mysidiopteria spinigera</i>	<i>Wallowaconcha raylenea</i>	<i>Nuculana</i> sp. 1	<i>Lima</i> (<i>Plagiostoma</i>) sp.	
<i>Cardita</i> aff. <i>benecke</i>	<i>Pseudolimea naumani</i>	? <i>Plagiostoma</i> sp.	<i>Tutcheria</i> cf. <i>densestriata</i>	<i>Parallelodon</i> sp. 3	<i>Lima</i> sp.	
<i>Schizocardia cristata</i>	<i>Schafaeulia</i> sp.	<i>Pseudolima naumanni</i>	<i>Astarte appressa</i>	Pretidae indet.	<i>Modiola</i> cf. <i>strigillata</i>	
<i>Tutcheria denesriata</i>	<i>Septocardia</i> sp.	<i>Liosrea newelli</i>	" <i>Astarte</i> cf. <i>incae</i> "	<i>Halobia austriaca</i>	<i>Macrodon</i> (<i>Catella</i>) <i>tyughtonae</i>	
<i>Cassianella peruana</i>	<i>Tutcheria</i> sp.	<i>Lopha</i> cf. <i>haidingeriana</i>	<i>Septocardia typica</i>	Permphoridae indet.	<i>Pteria</i> cf. <i>sturi</i>	
<i>Mysidia americana</i>	<i>Unionites carinata</i>	? <i>Ostreacea</i> Indet.	<i>Lucinidae</i> indet.	<i>Cassianella</i> sp.	<i>Oxytoma</i> cf. <i>intermedia</i>	
<i>Eonavicola inca</i>	<i>Unionites</i> sp.	<i>Plicatula heikensis</i>	Crassatellidae indet.	<i>Mysidiopteria spinigera</i>	<i>Plicatula perimbricata</i>	
<i>Monotis ochotica</i>		<i>Plicatula</i> sp.	Actinodontophoridae indet.	? <i>Plagiostoma</i> sp. 1	<i>Enamiosireon</i> sp.	
<i>Monotis subcircularis</i>		<i>Crenamussium concentricum</i>	<i>Tancredia</i> sp.	<i>Plicatula</i> sp.	<i>Pinna</i> sp.	

Table 2, continued.

Peru and Chile (Lower Norian) ¹	New York Canyon (Lower Rhaetian) ²	Hells Canyon (Lower Norian) ³	Vancouver Island (L. Rhaetian) ⁴	Green Butte (Lower Norian) ⁵	Tyaughton Creek (Lower Rhaetian) ⁶	Taylor Mountains (Lower Norian) ⁷
<i>Bakevellia donglasi</i>		" <i>Chlamys</i> " <i>mojsisovici</i>		<i>Minertrigonia</i> sp. 1	<i>Mytilus shulapsensis</i>	
<i>Leptochondria pascoensis</i>		? <i>Tosapecten subbiemalis</i>		<i>Schafaeutlia</i> sp.	<i>Pleuromya?</i> cf. <i>elongata</i>	
<i>Liotrea cimana</i>		? <i>Pleuronectites</i> sp.		? <i>Mysidiella</i> indet.	<i>Astarte</i> sp.	
<i>Myophoria jaworskii</i>		Pectinid indet.		<i>Cassianella</i> aff. <i>beyrichi</i>		
<i>Myophoria pascoensis</i>		? <i>Enantiostreon</i> sp.		Preridae sp. 1		
<i>Trigonodus cordilleranus</i>		<i>Cardinioides josephus</i>		Preridae sp. 2		
<i>Eotrapezium occidentale</i>		<i>Ergonia canyonensis</i>		<i>Plagiostoma</i> sp. 2		
<i>Astarte incae</i>		<i>Minertrigonia</i> sp.		Ostreacea indet.		
<i>Astarte andicola</i>		? <i>Frenguelliella</i> sp.		<i>Tutcheria</i> sp.		
<i>Schafaeutlia americana</i>		Permophoridae indet.		<i>Mysidiella</i> cf. <i>americana</i>		
<i>Palaeocardia peruviana</i>		<i>Tutcheria densestriata</i>		<i>Cardinioides</i> sp.		
<i>Septocardia peruviana</i>		? <i>Tutcheria</i> sp.		Pterioid indet.		
<i>Eopecten</i> sp.		<i>Palaeocardia silberlingi</i>		Bivalvia ?new fam.		
<i>Plicatula</i> sp.		<i>Astarte</i> sp.		Trigonacea indet.		
<i>Pseudolima chongi</i>		<i>Septocardia</i> sp.		Pectinacea indet.		
<i>Antiquilima atacamensis</i>				<i>Lopha</i> sp.		
<i>Gryphaea</i> sp.				? <i>Antiquilima</i> sp.		
<i>Unionites</i> sp.						
<i>Isopristes</i>						

et al. (2013) noted that several trigonoidean genera listed in this study are bipolar (or didemic), including *Minetrigonia*, yet these finds from the Alexander terrane, as well as from other terranes (Table 2, see also Tamura, 1995), demonstrate a much broader distribution for the genus that includes low-paleolatitudes of the circum-Pacific.

SYSTEMATIC PALEONTOLOGY

Except where otherwise indicated, supra-generic systematic assignments follow the *Treatise of Invertebrate Paleontology* (Cox *et al.*, 1969). Significant advancements in our understanding of many supra-generic and higher taxonomic groups and their phylogenetic positions have been made since the publication of the *Treatise* and have contributed significantly to the organization and preparation of this section. These include: Waller (1978, 1998), Carter (1990a), Carter *et al.* (2011) and Bieler *et al.* (2010). Arrangement of superfamilial taxa within this section largely follows Carter *et al.* (2011). Following the recommendation by Carter *et al.* (2011) the suffix ‘-oidea’ is used in superfamily names and ‘-ida’ for order names.

The excellent preservation and large number of individuals recovered from the Gill Harbor locality has resulted in recognition of morphological features that were poorly known in existing species and genus groups and therefore permit revised diagnoses and, in certain cases, revised and emended higher-level group assignments. The consequence of this is that the fauna includes a significant number of new lower-level taxa at the genus and especially species level. The approach used herein to recognize and define species is to emphasize the use of discrete character traits that are unique and, in species for which there are sufficient numbers of individuals, to establish the range of morphologic variation within the fossil population with a statistical presentation of morphologic data. In instances in which the sample sizes of individual taxa are small or the range of variation is indeterminate, open nomenclature is used to designate uncertainty (*e.g.*, sp. indet., species indeterminate), similarity (*cf.*) or likely affinity (*aff.*). Specimens that are clearly distinguishable from any known taxa and most likely represent new species, but are represented by too few individuals to adequately determine specific traits or their variability are designated with the informal species designators A, B, C, etc.

Institutional abbreviations include: BML, Natural History Museum, London; MCZ, Museum of Comparative Zoology at Harvard University, Cambridge; PRI, Paleontological Research Institution, Ithaca; STIPB, Steinmann Institut für Geologie, Mineralogie und Paläontologie, University of Bonn; UAM, University of Alaska Natural History Museum, Fairbanks; UMIP, University of Montana Invertebrate Paleontology, Missoula; USNM, U.S. National Museum of

Natural History at the Smithsonian Institution, Washington D.C.; USGS, Collections of the U.S. Geological Survey, Denver; GSC, Geological Survey of Canada, Ottawa.

Morphologic terms and measurement conventions often differ amongst different bivalve groups and to some extent previous workers. To provide some consistency and stability, terminology used throughout taxonomic descriptions generally follow Carter *et al.* (2012). Hinge dentition notation for Heterodonta taxa follows the Benard system (see Cox *et al.*, 1969) Abbreviations for commonly used morphological terms used in the taxonomic descriptions, tables, and figures include: H = height, L = length, LV = left valve, RV = right valve, W = width (inflation) of single valve.

Class **BIVALVIA** Linné, 1758

Subclass **PROTOBRANCHIA** Pelseneer, 1899

Order **NUCULOIDA** Dall, 1899

Superfamily **NUCULOIDEA** Gray, 1824

Family **NUCULIDAE** Gray, 1824

Genus **PALAEONUCULA** Quenstedt, 1930

Type species.—*Nucula hammeri* Defrance, 1825, by original designation, Middle Jurassic (Bajocian), Europe.

Remarks.—As summarized by Ros-Franch *et al.* (2014), *Palaeonucula* is fairly common from the early Middle Triassic through Early Cretaceous from the Tethys, Panthalassa, and Boreal seas. Late Triassic species are particularly common in the western, central and eastern Tethys (*e.g.*, Tamura *et al.*, 1975; Wen *et al.*, 1976; Fürsich & Wendt, 1977; Gou, 1993; Hautmann, 2001b).

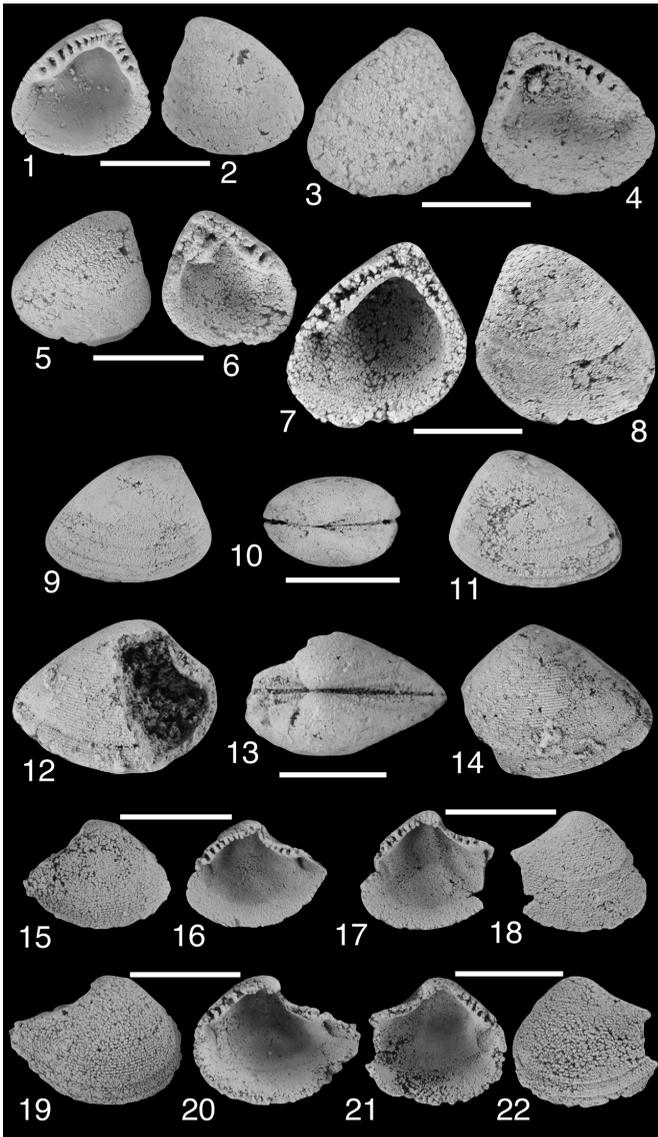
Palaeonucula muffleri n. sp.

Text-figs 15.1–15.11

Types and measurements.—Holotype, UMIP 15655 (Text-figs 15.1, 15.2), a RV. Paratypes: UMIP 15659 (conjoined valve pair), UMIP 15658 (RV), UMIP 15657 (LV), and UMIP 15656 (LV). Measurements provided in Table 3. All from USGS loc. M1912, Kuiu Island, Alaska, from upper Norian, Hound Island Volcanics.

Other material examined.—In addition to the types, the entire collection consists of eight left valves, six right valves, and four conjoined valves of variable completeness and degree of silicification.

Diagnosis.—Small and inflated *Palaeonucula*; umbo broad, situated slightly posterior of mid-point, with narrow incurved opisthogyrate beak; dorsal margins steep, anterodorsal margin convex, posterodorsal margin nearly straight, angle formed at



Text-fig. 15. *Protobranchia*. 1–11, *Palaeonucula mufferi* n. sp. 1, 2, holotype, UMIP 15655, a well preserved RV; 1, interior showing dentition and resilifer; 2, exterior view. 3, 4, paratype, UMIP 15656, a LV; 3, interior view; 4, exterior view. 5, 6, paratype, UMIP 15657, a LV; 5, exterior view; 6, interior view. 7, 8, paratype, UMIP 15658, a RV; 7, interior view; 8, exterior view. 9–11, paratype, UMIP 15659, a conjoined valve pair; 9, LV exterior view; 10, dorsal view with anterior margin right; 11, RV exterior. 12–14, *Palaeonucula* sp. indet., PRI 69614, a conjoined valve pair; 12, LV exterior; 13, dorsal margin with anterior towards right; 14, right valve exterior. 15–22, *Nuculana* aff. *N. timorensis* (Krumbek, 1924). 15, 16, UMIP 15660, a LV; 15, exterior view; 16, interior view. 17, 18, UMIP 15661, a LV; 17, interior view; 18, exterior view. 19, 20, UMIP 15662, a LV; 19, exterior view; 20, interior view. 21, 22, UMIP 15663, a RV; 21, interior view; 22, exterior view. Scale bars = 5 mm. All from USGS loc. M1912.

the umbo by anterior and posterior dorsal margin generally less than 90°; hinge with prominent, slightly curved to chevron teeth adjacent to both sides of small triangular opisthocline resilifer; dentition series gradidentate with anterior row of 8–12 teeth and posterior row of 4–6 teeth; surface ornamented with sets of fine commarginal lirae bundled together into larger bands delimited by commarginal lamellae.

Description.—Small *Palaeonucula* (maximum L = 8.6 mm, maximum H = 9.9 mm), generally higher than long (mean H:L = 1.2), inflated (maximum W of conjoined valves = 7.0 mm), shape trigonal with steeply sloping dorsal margins forming an angle of slightly less than 90° (mean umbonal angle = 83°) at umbonal summit, anterodorsal margin convex, posterodorsal margin nearly straight; opisthogyrate umbones, positioned slightly posterior of midpoint and continuous with remainder of shell; escutcheon shallow and poorly defined, delimited by weak border ridges only near umbo which fade towards posterodorsal margin of shell; lunule oval and shallowly depressed; exterior ornamented with numerous commarginal striae bundled within larger commarginal bands; inner ventral margin not crenulate or denticulate; dentition taxodont; number of teeth somewhat variable with anterior series more numerous (8–12 teeth) than posterior series (4–6 teeth), both anterior and posterior series gradidentate from resilifer; individual teeth slightly curved to nearly chevron-shaped, especially on posterior side of hinge, corresponding to deep sockets on opposing valve; resilifer opisthocline and triangular, without submarginal extension, terminating near incurved beak and not submarginal; anterior adductor scar faint, situated anteroventral to hinge, oval in shape; posterior adductor scar not observed.

Etymology.—Trivial name, *mufferi*, after L. J. Patrick Muffer, geologist, who provided the first detailed synthesis of the geologically complex Keku Islands region of southeastern Alaska.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Placement in *Palaeonucula* is based on the roundness of the posterior margin (*i.e.*, not pointed or rostrate), the absence of distinct ridges bordering a deeply impressed escutcheon, and lacking antimarginal/divicariate ornament as in certain *Trigonucula* (see Ichikawa, 1949; Hautmann, *et al.*, 2011). *Palaeonucula mufferi* n. sp. can be distinguished from other species of *Palaeonucula* primarily by its shape, details of the umbo, surficial ornament, and dentition. Particularly diagnostic of *P. mufferi* is the gently convex anterodorsal margin.

Table 3. Measurements of *Palaeonucula muffleri* n. sp.

Specimen	Valve	Length (mm)	Height (mm)	Width (mm)	UA	PD-t	AD-t	Remarks
UMIP 15659	Conjoined	7.5	8.6	3.5	91.1	--	--	Paratype
UMIP15656	LV	7.7	8.0	3.0	74.0	--	--	Paratype
UMIP 15655	RV	6.4	7.4	2.3	90.8	4	9	Holotype
UMIP 15657	LV	6.6	6.2	2.3	79.6	4	9	Paratype
UMIP 15658	RV	8.6	9.9	2.7	86.3	--	--	Paratype
--	LV	7.0	7.4*	3.6	88.1	--	--	--
--	LV	6.7	6.6	2.1	76.1	--	--	--
--	RV	8.8	9.4	3.4	81.0	--	--	--
--	Conjoined	7.9	7.3	2.7	85.5	--	--	--

*Restored measurement.

Among the better-known and preserved Upper Triassic *Palaeonucula* are those that occur in the Carnian Cassian Formation of northern Italy (see for example Laube, 1865; Bittner, 1895; Zardini, 1981). These have largely been assigned several species including *P. strigilata* (Goldfuss, 1838), *P. expansa* (Wissmann, 1841), and *P. subobliqua* (d'Orbigny, 1849). Unfortunately, with several notable exceptions discussed below, these species are largely known from conjoined specimens in which details of the valve interior are unknown, or steinkerns in which the external ornament, and to some degree shapes, are not preserved.

The Gill Harbor specimens are most similar to *Palaeonucula subobliqua* (d'Orbigny, 1849) and *P. expansa* (Wissmann, 1841). The obvious difference between these two Carnian taxa is their shell shape, with *P. subobliqua* having a somewhat more pronounced and less oblique umbo than *P. expansa*. Both of these species, however, differ from *P. muffleri*, whose relatively straight posterodorsal margin and slightly convex anterodorsal margin is unlike the Carnian species. These differences in shape can be observed in well-preserved *P. subobliqua* from the Carnian (Bittner, 1895, pl. 17, figs 35–39; see also Zardini, 1981, pl. 2, figs 1–3). The LV dentition of *P. expansa* was well illustrated by Bittner (1895, pl. 17, fig. 33) and shows 10 teeth in the anterior series and 6 in the posterior, and is within the range of variation for *P. muffleri*. It differs from the Gill Harbor specimens, however, in having a less opisthogyrate umbo and a concave anterodorsal margin (as opposed to the convex margin of *P. muffleri*), resulting from a slight anterior elongation.

The Gill Harbor specimens may also be compared to *Palaeonucula strigilata* (Goldfuss, 1838) from the Cassian Formation of northern Italy and also from other Carnian and Norian, and potentially even Rhaetian, localities throughout Alpine Europe, eastern and southeastern Asia, and the Pacific (e.g., Laube, 1865; Bittner, 1895, Krumbeck, 1924; Reed, 1927; Chen, 1976). *Palaeonucula strigilata* is more anteriorly elongate, with the umbo situated in a more poste-

rior position than *P. muffleri*. Additionally, although it can not be discerned in the left valve illustrated by Bittner (1895, pl. 17, fig. 16), the left valve of *P. strigilata* shown in Zardini (1981, pl. 1, figs 8b, 9b) clearly demonstrates the submarginal resilifer projecting into the main body cavity, which is not evident on *P. muffleri* in which the internal hinge margin is continuous without projection.

Palaeonucula muffleri can easily be distinguished from other Norian *Palaeonucula* by its shell outline and shape characteristics. It differs from the Norian-Rhaetian *P. sundaica* (Krumbeck, 1924)—known from Timor, Vietnam, China, and Iran (e.g., Krumbeck, 1924, pl. 19, figs 3, 6–7; Wen *et al.*, 1976, pl. 2, figs 9–11, 13; Hautmann 2001b, pl. 1, figs 1–5, 8)—in its less elongated anterior and less deeply impressed escutcheon and lunule. Although Krumbeck (1924: 376) noted that *P. sundaica* is characterized by a posterior anterior tooth ratio of 6:10, Hautmann (2001b: 25) remarked that *P. sundaica* possess up to 16 teeth on the anterior series and eight in the posterior series.

Paleoecology.—*Palaeonucula muffleri* is inferred to be a shallow mobile deposit feeder similar to other Nuculidae (Text-fig. 13.15). As described by Yonge (1939, see also Morton, 2012), modern species live just beneath the sediment water interface and slowly travel through sediment in search of food, which is collected by labial palps.

***Palaeonucula* sp. indet.**

Text-figs 15.12–15.14

Material examined.—A partial conjoined valve pair (PRI 69614) in which the posterior third of left valve is not preserved.

Description.—Shell moderately large, longer than high (L = 9.5 mm, H = 7.3 mm), moderately inflated (combined W of closed conjoined valve pair = 6.1 mm), subtrigonal, with

opisthogyrous umbo anterior of midpoint of valve; antero-dorsal margin nearly straight, posterior-dorsal margin slightly concave; escutcheon moderately impressed, oval, separated from anterior flank of valve with moderately strong ridge; lunule weakly developed; dentition, as viewed through small gape along dorsal margin, consisting of approximately 18 teeth in anterior series and approximately eight teeth in posterior series, morphology of teeth or resilifer features not observed. Exterior ornamented with numerous closely spaced commarginal striae.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Placement in *Palaeonucula* is based on the general shape of valves and, in particular, the weakly convex antero-dorsal margin and the nature of dentition. Although internal features are not observable, this specimen differs from *Palaeonucula muffleri* n. sp. in being significantly longer than high and having more numerous teeth. Based on shape, number of teeth, and external ornament, the specimen can be compared to numerous anteriorly elongated *Palaeonucula* from the marine Late Triassic (e.g., Carnian *P. strigilata* Goldfuss, 1838 to Rhaetian *P. sundaica* (Krumbeck, 1924), see remarks above). However, due to the small sample size, absence and lack of observable key features, and absence of information on variation in traits, species determination must be withheld until additional material becomes available.

Paleoecology.—Like the aforementioned *P. muffleri* and other Nuculidae, *Palaeonucula* sp. indet. is inferred to be a shallow mobile deposit feeder (Text-fig. 13.14).

Superorder **NUCULANIFORMII** Carter, Campbell & Campbell, 2000

Order **NUCULANIDA** Carter, Campbell & Campbell, 2000

Superfamily **NUCULANOIDEA** Adams & Adams, 1858

Family **NUCULANIDAE** Adams & Adams, 1858

Genus **NUCULANA** Link, 1807

Leda Schumacher, 1817: 173.

Type species.—*Arca rostrata* Chemnitz, 1774 (= *Arca penzula* Müller, 1771), by original designation, Recent, northern coast of Europe.

Remarks.—*Nuculana* Link, 1807 has a long and complex history, partly because many of its included species, especially early Mesozoic ones, are based on forms for which the valve

interiors (especially dentition or a possible internal ridge) and skeletal microstructure, are not fully known. As discussed in Carter (1990a: 151), Cenozoic *Nuculana* possesses a non-nacreous aragonitic skeleton and several early and middle Mesozoic genera (e.g., *Dacryomya* Agassiz, 1840 and *Ryderia* Wilton, 1830) possibly possessed a nacreous and prismatic microstructure and are better placed within the Polidevciidae Kumpera et al., 1960. Unfortunately, skeletal microstructure is not known from any named *Nuculana* from the Triassic and many of the forms demonstrably lack internal ridges (as in *Phestia* Chernyshev, 1951). The presence of a pallial sinus known in some *Nuculana* but apparently not in *Dacryomya* (e.g., Cox, 1940 and Hautmann et al., 2015) may provide additional criteria to separate these two genera. Following the more recent work (e.g., Hautmann, 2001b; Ros-Franch et al., 2014), until the microstructure, ligament, and muscle scars of Triassic species, including those discussed below, are better known, a conservative approach is taken retaining these species within Nuculanidae and *Nuculana*. Following Ros-Franch et al. (2014), *Leda* Schumacher, 1817 is considered a junior synonym of *Nuculana*, which has the same type species.

Nuculana aff. *N. timorensis* (Krumbeck, 1924)

Text-figs 15.15–15.22

aff. *Leda timorensis* Krumbeck, 1924: 235, pl. 19, fig. 11a–c.

Holotype and measurements.—The originals of Krumbeck (1924, pl. 19, fig. 11a–c) with measurements: L = 7.4mm, H = 4.1 mm, W of conjoined valve pair = 2.5 mm.

Material examined.—The collection consists of three left valves (UMIP 15660, UMIP 15661, UMIP 15662) and three right valves (UMIP 15663 and two uncataloged specimens) from presumably different individuals based on size differences, all with variable degrees of silicification.

Description.—Valves small for *Nuculana* (maximum L = 8.3 mm, maximum H = 6.1 mm, maximum W = 2.6 mm), inequilateral, with opisthogyrous umbo positioned anterior of midpoint of valve; posterior rostrum short, blunt; posterior-dorsal margin moderately concave and sloping; anterior-dorsal margin convex and steeply sloping, ventral margin rounded; with subdued ridges bordering escutcheon; one specimen (Text-fig. 15.15, 15.16, UMIP 15660, a RV) with well preserved dentition with eight teeth in the anterior series and seven the posterior series; teeth may have been chevron shaped; PRI 69614 with apparent small groove (ligament fossette?) extending from beak to posterior margin of dental series; submarginal resilifer not preserved; posterior adductor scar small, subovate with long axis parallel to hinge margin,

deeply impressed, positioned just posterior to and just below hinge plate near rostral extension; anterior adductor scar subovate with long axis nearly vertical; pallial line continuous without sinus; exterior ornamented with numerous closely-spaced commarginal striae.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Placement in *Nuculana* Link, 1807 rather than *Dacryomya* Agassiz, 1840, *Ryderia* Wilton, 1830, or *Xiaoschuiculana* Chen, 1983 is discussed above under genus remarks and is also determined based on valve inflation, the shape and length of posterior rostrum, and by possessing strictly commarginal external ornament rather than oblique or sinuous ribs (Chen *et al.*, 1983; Damborenea, 1987a; Hodges, 2000; Yin & McRoberts, 2006; see also Hautmann *et al.*, 2011).

The specimens at hand are most similar and likely closely related to, if not conspecific with, *Leda timorensis* Krumbeck, 1924, which is based on a single articulated valve pair (Krumbeck, 1924, pl. 19, figs 11a–c). Although it is unfortunate that Krumbeck's specimen does not reveal details of the valve interior, both its size and valve shape are indistinguishable from the range of forms represented by the Gill Harbor specimens. It is entirely possible that the two are conspecific, but until additional specimens from Timor are available confirming similarity in dentition, the Gill Harbor specimens are left in open nomenclature.

The Gill Harbor specimens may also be compared to *Leda skorochodi* Kiparisova, 1938 from the Anisian of northeast Russia. Although preserved as a steinkern, the single specimen of *Leda skorochodi* illustrated by Kiparisova (1938, pl. 1, fig. 1) exhibits a similar overall shape, size, and valve inflation and also a similar number of teeth. The Gill Harbor specimens can be distinguished from well known Norian and Rhaetian *Nuculana* from the western and eastern Tethys and western Panthalassa (*e.g.*, *Leda deffneri* Oppel, 1856, *Nuculana nainbandensis* Hautmann 2001b) largely based on details of valve shape and degree of rostrum extension. Additionally, *Nuculana timorensis* differs from *N. prelonga* Mansuy, 1914 (best illustrated by Wen *et al.*, 1976, pl. 3, figs 9–11; Vu Khuc, 1991, pl. 15 figs 19–27; Hautmann, 2001b, pl. 1 figs 20–23) in its less elongate rostrum. Nuculanids from the Cassian

Formation (*e.g.*, *Leda sulcellata* Wissmann, 1841) differ from the Gill Harbor specimens in that they exhibit sharper ridges bordering a much more deeply impressed escutcheon, as well illustrated by Bittner (1895, pl. 18, figs 8–10) and Zardini (1981, pl. 3, figs 6–13).

Paleoecology.—The life habit of *Nuculana* aff. *N. timorensis* is inferred to be shallow infaunal detritus feeder with limited mobility (Text-fig. 13.13). Unlike *Nucula* (and presumably *Palaeonucula*), *Nuculana* possess small siphons (passing through the rostrate posterior) that are largely used for water exchange and respiration, but also may be used for suspension feeding (Yonge, 1939).

Subclass **AUTOBRANCHIA** Grobden, 1984
 Infraclass **PTERIOMORPHIA** Beurlen, 1944
 Order **PTERIOIDA** Newell, 1965
 Superfamily **PINNOIDEA** Leach, 1819
 Family **PINNIDAE** Leach, 1819
 Genus **PINNA** Linné, 1758

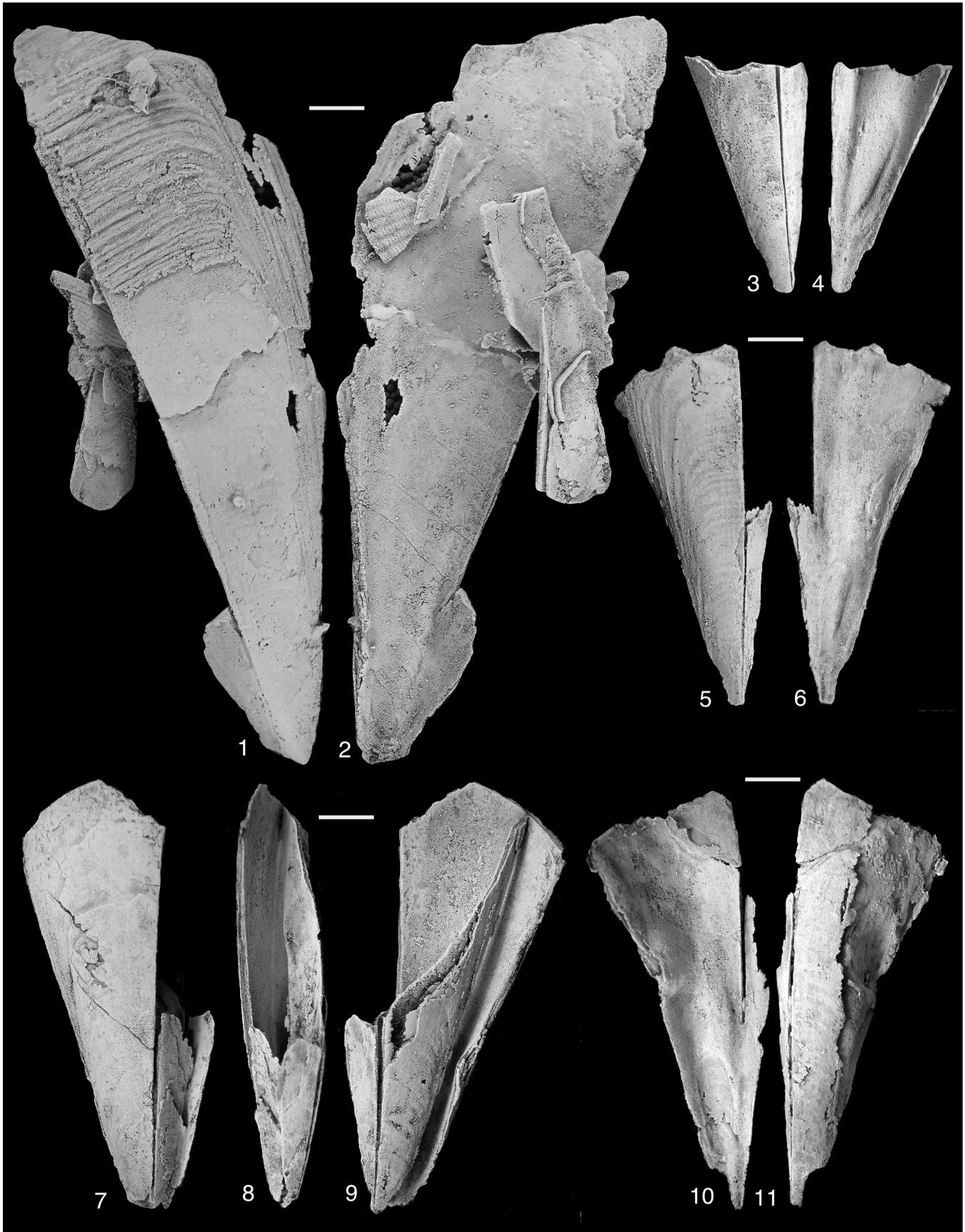
Type species.—*Pinna rudis* Linné, 1758, by subsequent designation (Children, 1823: 34), Recent, Caribbean.

Remarks.—Although *Pinna* Linné, 1758 is commonly reported from the Triassic, few demonstrably possess the medial carina that discriminates this genus from the closely related *Atrina* Gray, 1842 (Waller in Waller & Stanley, 2005). Triassic species that possess a medial carina and rightfully belong in *Pinna* are known almost exclusively from the Tethys and low to mid paleolatitudes from the margins of Panthalassa beginning perhaps as early as the Early Triassic and apparently flourished during the Late Triassic (Ros-Franch *et al.*, 2014).

Pinna keexkwaanensis n. sp.
 Text-figs 16.1–16.11

Types and measurements.—Holotype, PRI 69617 (Text-figs 16.7–16.9), an incomplete conjoined valve pair, measured L = 79.4 mm, H = 31.1 mm. Paratypes: UMIP 15664 (Text-figs 16.1, 16.2), a LV; PRI 69615 (Text-figs 16.3, 16.4), a RV; PRI 69618 (Text-figs 16.10, 16.11), a LV; and PRI 69616 (Text-figs 16.5, 16.6), a RV. All from USGS loc. M1912, Kuiu Island, Alaska, from upper Norian, Hound Island Volcanics.

Text-fig. 16 (at right). *Pinna keexkwaanensis* n. sp. 1, 2, paratype, UMIP 15664, a LV; 1, exterior view; 2, valve interior. 3, 4, paratype, PRI 69615, a RV; 3, exterior view; 4, valve interior. 5, 6, paratype, PRI 69616, a RV; 5, exterior view; 6, valve interior showing elongated muscle scar. 7–9, holotype, PRI 69617, conjoined valve pair; 7, right lateral view showing RV exterior; 8, dorsal view; 9 left lateral view showing LV exterior and right valve interior showing weak byssal sinus on ventral margin of right valve. 10, 11, paratype, PRI 69618, a LV; 10 interior view; 11, valve exterior. Scale bars = 10 mm. All from USGS loc. M1912.



Other material examined.—In addition to the types, more than 50 fragmentary specimens (including 2 conjoined valve fragments and the remainder approximately equally distributed between left and right valves) contributed to the description.

Diagnosis.—Medium-sized *Pinna* lacking radial ornament but with distinct commarginal undulations in outer calcitic shell layer; gently tapering at about 30° to a terminal beak; ventral margin relatively straight with very shallow sinus; posterodorsal margin truncated and posteroventral margin sharply rounded; with distinct medial carina in middle shell layer separating valves into two unequal sectors of which the ventral sector has the greater angular breadth.

Description.—Medium-sized shell (maximum L = 132.2 mm), equivalved, triangular in outline with terminal beak; dorsal and ventral margins relatively straight and form an anterior angle of about 30°; ventral margin with very shallow sinus; posteroventral margin sharply rounded and forming an acute angle of approximately 85°; articulated valves moderately inflated (maximum single valve W = 12.5 mm) and rhombic in cross section; edentulous with thin ligament groove along entire dorsal margin; valves dissected by prominent medial carina into two unequal sectors—a broader ventral sector with an anterior angle of about 20° and narrower posterior sector of about 10°; medial carina continuous to anterior end in middle shell layer but obsolete on inner shell layer for first 4 to 5 cm from anterior end; ventral sector with moderately large bean-shaped anterior adductor insertion scar extending nearly to beak; posterior adductor and retractor muscle scars not observed; exterior of shell lacking radial ornament; outermost prismatic layer exhibits closely spaced commarginal undulations; middle and inner shell layers generally smooth or have very subdued and widely spaced commarginal growth lines.

Etymology.—Trivial name, *keexkwaanensis*, after Keex' Kwáan, the Tlingit tribal name for native peoples of the coastal region around Kake and Keku Strait, Alaska.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Although commonly known, few Triassic pinniids have been illustrated with preserved outermost prismatic calcite layer preserving the external ornament or with a demonstrable medial carina. Most of those with the outer shell layer or preserved as external molds (including species assigned to both *Pinna* Linné, 1758 and *Atrina* Gray, 1842) exhibit a very distinct radial ornamentation and cannot be confused with the Gill Harbor specimens. A survey of Triassic pinniids

reveals that radial ornamentation is not restricted to the outermost layer and is occasionally expressed on the middle shell layer as well, especially during early ontogeny; see for example, *Pinna* cf. *P. tomassi* Wörhmann illustrated by Hautmann (2001b, pl. 9, fig. 6).

In addition to surficial ornament, *Pinna keexkwaanensis* differs from other *Pinna* in its size and details of shell shape, particularly the acuteness of its posteroventral margin and gentle angular expansion of its valves. *Pinna meriani* Winkler, 1859, a fairly common Upper Triassic *Pinna* in the western and central Tethys (e.g., Winkler, 1859; Zapfe, 1967; Hautmann, 2001b), differs from *P. keexkwaanensis* in its smaller adult size and its distinct radial ribs. *Pinna lima* Böhm (1903, pl. 5, figs 12–14) and *P. heeri* Böhm (1903, pl. 5, figs 12–14), from the same Carnian (?) locality in Svalbard and also the likely Norian of China (e.g., Chen, 1976), apparently lack radial ornament but exhibit a greater angular breadth than the Gill Harbor specimens. *Pinna keexkwaanensis* differs from *P. yunnanensis* Chen (1976: 261, pl. 42, fig. 21), known from Ladinian and Carnian of China, which has very strong commarginal folds accentuated along the posteroventral margin, but fade dorsally. The Gill Harbor species differs from *Mesopinna choboensis* Vu Khuc & Huyen, 1984, from the Norian of Vietnam in having a less acute posteroventral margin.

Paleoecology.—The life habit of Recent *Pinna* are well known (e.g., Yonge, 1953; Stanley, 1970) and show a nearly ubiquitous semi-infaunal habit in soft substrate and stabilization by means of attachment to coarse debris by a strong byssus (Text-fig. 13.8). Numerous fossil examples preserved in apparent living position confirm this habit (e.g., Damborenea, 1987a).

Superfamily **PTERIOIDEA** Gray, 1847

Family **CASSIANELLIDAE** Ichikawa, 1958

Genus **CASSIANELLA** Beyrich, 1862

Type species.—*Avicula gryphaeata* von Münster, 1836, by original designation, Upper Triassic (Carnian), southern Alps, Italy.

Remarks.—Known definitively from the Middle Triassic (Anisian), and quite possibly as old as Permian, *Cassianella* Beyrich, 1862 is among the most common bivalve genera of the Upper Triassic (Ros-Franch *et al.*, 2014). From the Carnian through the Rhaetian, the genus is particularly well-represented (with over 30 named species) throughout the Tethys, as well as low to mid paleolatitudes of the Panthalassa margins and the Boreal province of northeastern Russia (e.g., Bittner, 1895; Körner, 1937; Kiparisova *et al.*, 1966; Fürsich & Wendt, 1977; Newton *et al.*, 1987).

As considered by most previous workers, *Cassianella* includes a wide array of species that show great variability in

their external ornament, ligament, dentition, and perhaps even their skeletal mineralogy and microstructure. While most *Cassianella* are apparently edentulous, several species clearly exhibit taxodont dentition (see Zardini, 1981, pl. 14, fig. 1b; Carter, 1990a, fig. 30c). Similarly, in addition to differences in ligaments, Carter (1990a) noted that some *Cassianella* possess a simple prismatic calcite outer layer and nacreous inner and middle layers, whereas other species have an aragonitic fibrous prismatic structure. The significance of this variability in traits is of taxonomic and phylogenetic significance and may support subdividing this broadly construed genus.

Cassianella cordillerana McRoberts in McRoberts & Blodgett, 2002
Text-figs 17.1–17.16

Cassianella cordillerana McRoberts in McRoberts & Blodgett, 2002: 58, pl. 1, figs 1–11.

Holotype and measurements.—Holotype, UAM 2591 (McRoberts in McRoberts & Blodgett, 2002: 58, pl. 1, figs 1, 2), L = 17.9 mm, W = 9.9 mm; lower Norian, Taylor Mountains, southwest Alaska.

Material examined.—The collection consists of over 350 left valves and 12 right valves of variable preservation. Of these, four left valves (PRI 69619–69621, PRI 69625) and three right (PRI 69622, PRI 69623, and PRI 69624) valves significantly contributed to the species description. Measurements of the Gill Harbor specimens of *C. cordillerana* are graphically provided in Text-fig. 18.

Description.—Left valve of moderate size (maximum L = 22.7 mm, maximum H = 36.2 mm), and inflation (maximum W = 14.2 mm); LV exterior smooth, highly convex and torted with nearly centrally positioned incurved beak extending up to 7 mm above hinge margin; central portion of flank rounded and steeply sloping to posterior and anterior valve margins; anterior auricle relatively short (8–10 mm) with upper surface slightly sloping (6°–12°) with respect to hinge line, and lower margin joining valve flank at between 120°–140°; anterior auricle separating from flank by a single furrow; posterior auricle is slightly more extended than anterior auricle and joins posterior flank at a more acute angle (~ 115°) and lacking notch; hinge plate broad and slightly concave with between 5–7 grooves running parallel to hinge margin; single triangular ligament pit prominent below beak is well developed and acline to weakly opisthoclinal and slightly extends ventrally into body cavity; LV interior with anterior septum sloping obliquely from hinge plate to the anterior-ventral position where the auricle joins the valve flank; RV thin-shelled, small (maximum H = 22.1 mm, maximum L = 16.9 mm) slightly

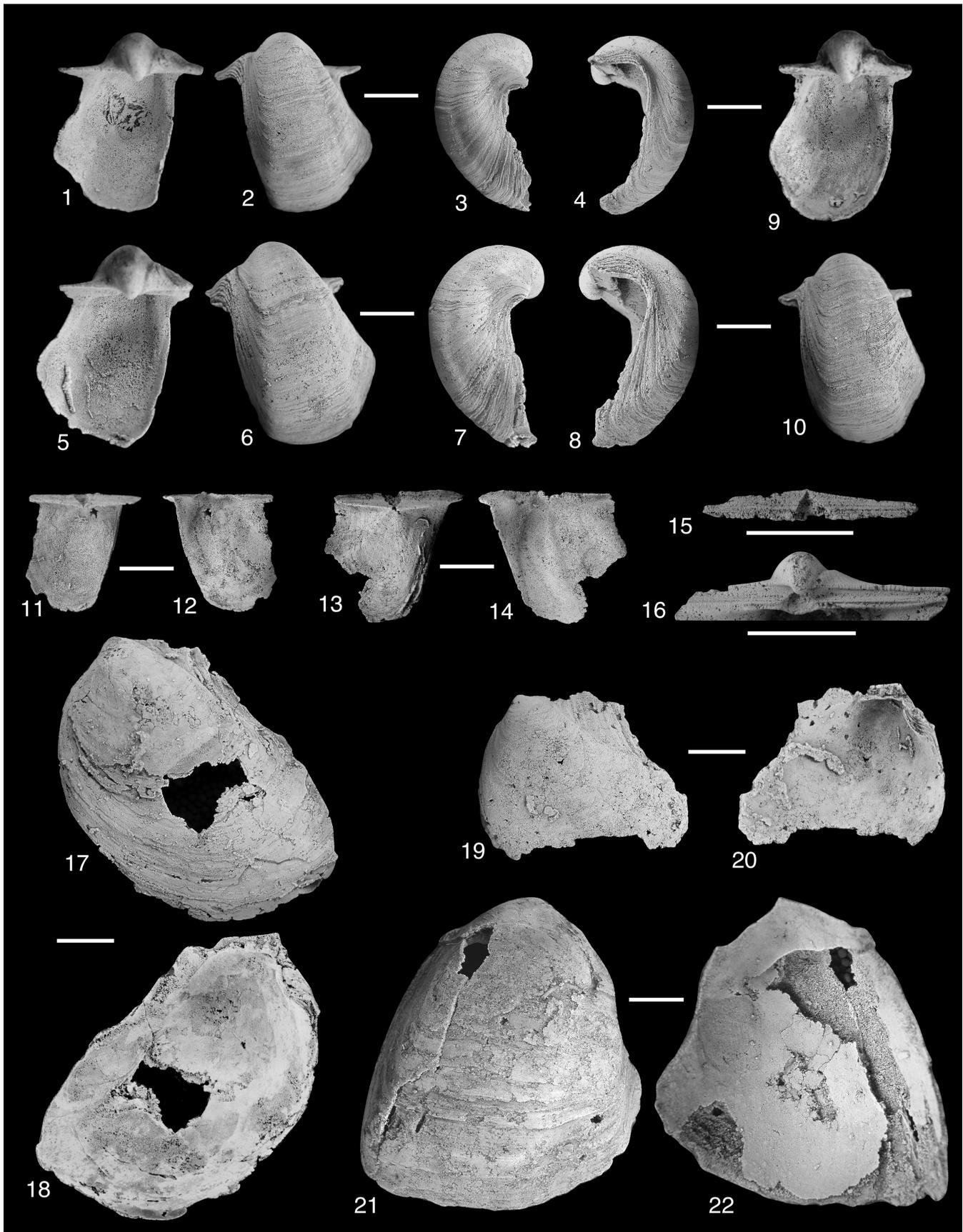
concave flank that strongly recurved inwards towards hinge, major axis of flank height slightly inclined in a posterior direction with respect to hinge margin subtending an angle of 105°–115° from horizontal; exterior of RV ornamented with faint commarginal narrowly-spaced growth lines; hinge long and straight, supporting 3–5 thin grooves that extend the entire length of the hinge; triangular resilifer prominent, positioned in middle of hinge, acline to slightly opisthoclinal.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912), and lower Norian from the Taylor Mountains, Alaska (Nixon Fork terrane).

Remarks.—The Gill Harbor specimens agree in almost every detail to *Cassianella cordillerana* McRoberts in McRoberts & Blodgett, 2002 from the lower Norian of the Taylor Mountains, Alaska (McRoberts in McRoberts & Blodgett, 2002). The present collection is substantially larger in number of specimens and contains several right valves that are unknown from the topotype collection, thus providing a more complete understanding of the form and variability within this species. This new occurrence extends the temporal range of this taxon throughout almost the entire Norian.

The reader is referred to McRoberts (in McRoberts & Blodgett, 2002) for a lengthy discussion on comparable *Cassianella* species, including *C. gravinaensis* Smith, 1927, *C. angusta* Bittner, 1891 (including *C. angusta* described by Newton in Newton *et al.*, 1987), and *C. lingulata* Gabb, 1870. However, the Gill Harbor collection permits a re-assessment of the potential affinities of *C. cordillerana* specimens referred to as *C. angusta* from the Wallowa terrane, Oregon (USGS loc. M2672) by Newton (in Newton *et al.*, 1987). The umbo in the Oregon specimens is clearly narrower and beyond the range of variation of those described herein from Alaska. Furthermore, the right valve exteriors of the Oregon specimens exhibit a more pronounced commarginal ornament and are more quadrate in their outline.

This species can be compared to several known from Upper Triassic North and South American localities. The specimens differ substantially from *Cassianella beyrichi* var. *crickmayi* McLearn, 1942 from the Rhaetian of the Tyaughton Group, B.C., Canada, in being quite a bit smaller, having relatively smaller auricles, and perhaps most significantly, in having a smooth right valve. *Cassianella peruana* Körner (1937, pl. 12, figs 10a, 10b) from Nevado de Acrotambo Peru are—like those illustrated as *Cassianella cf. peruana* Körner, 1937 by Damborenea & Manceñido (2012, pl. 1, figs 2, 6, ?)—relatively small specimens which lack a well-defined umbonal carina and radial posterior sulcus. Those illustrated as *Cassianella* sp. from the likely Rhaetian of Chile (Chong & Hillibrandt, 1985, pl. 3, figs 8, 9) are quite a bit larger,



more prosogyrate, and have a more narrow umbo than the Gill Harbor specimens and appear more similar to those from the Rhaetian of Tyaughton B.C. and New York Canyon, Nevada discussed above.

Paleoecology.—Like other *Cassianella* (e.g., Fürsich & Wendt, 1977), *C. cordillerana* was likely a reclining suspension feeder (Text-fig. 13.12). The presence of a small notch below the anterior auricle suggests that, as described by Newton (in Newton *et al.*, 1987), *C. cordillerana* may have possessed a weak byssus, thus permitting fixation to the substrate.

Family **BAKEVELLIIDAE** King, 1850

Genus **BAKEVELLIA** King, 1848

Type species.—*Avicula antiqua* Münster (1836), by subsequent designation (King, 1850: 168), Upper Permian, Germany.

Remarks.—The status of bakevelliid genera and subgenera is highly fluid and not adequately resolved (see for example Cox, 1969a; Kurushin, 1980; Damborenea, 1987b; Muster, 1995; Geyer *et al.*, 2005), allowing for a range of taxa into which these specimens could be placed. Assignment of this species to *Bakevella* rather than available subgenera *Bakevella* (*Bakevella*), *B. (Neobakevella)*, *B. (Maizuria)*, and *B. (Bakevellioides)* follows the rationale of Cox (1940: 108) who suggested that all *Pteria*-like ‘*Gervillias*’ can best be accommodated into a broader definition of *Bakevella* which tends to de-emphasize the highly variable dentition. This assignment is further substantiated by the recent synonymy of both *B. (Neobakevella)* and *B. (Costibakevella)* by Geyer *et al.* (2005).

Bakevella sp. A

Text-figs 17.17–17.20

Material examined.—Two partially preserved left valves (PRI 69626, PRI 69627).

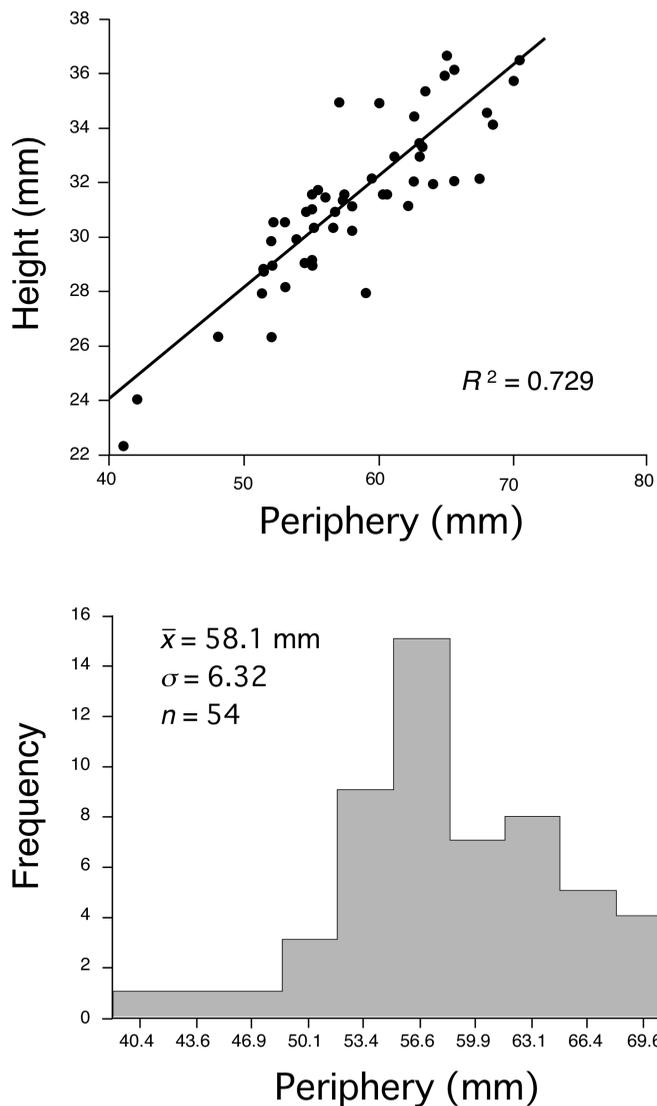
Description.—Left valves comparatively large (maximum L = 51.5 mm), pteriform, with main part of shell subovate, higher than long, oblique, and broadly inflated (maximum inflation = 9.8 mm); obliquity (measured as angle between dorsal mar-

gin and posteroventral maximum growth vector) approximately 20°; dorsal margin relatively straight; umbo broad with weakly prosogyrate beak slightly extending above dorsal margin and subterminal; anterior auricle/lobe not preserved but presumably present; anterior sinus below anterior lobe which would correspond to byssal gape (see Text-figs 17.18, 17.20); remainder of anterior and ventral margin broadly curved; posterior auricle apparently short and demarked from main shell with weak sulcus. Although the two specimens are fragmentary, posterior auricle intersects the dorsal margin at approximately 90°; exterior of valve covered with finely-spaced commarginal growth lamellae; interior hinge and ligament area poorly preserved, but apparently narrow and possessing multiple channel-like vertically oriented ligament pits; both lower and lateral hinge areas which may have supported dentition either not preserved or not present.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Assignment of the Gill Harbor specimens to *Bakevella* is based on its pterioid outline and the presence of multivincular ligament as opposed to alvincular ligament found in Pteriidae. Although the Gill Harbor specimens may represent a new species of *Bakevella*, the right valves are unknown and the only two left valves are incomplete and insufficiently known to fully assess the range of traits, particularly those of the hinge area and auricles. However, the material is of sufficient completeness to compare with other known Upper Triassic species. It is most similar to *Bakevella douglasi* Cox, 1949 (pl. 1, figs 6, 7) from the Norian of Peru, but the Gill Harbor specimens are larger, less oblique, and have a much less acute posterior auricle. The Gill Harbor specimens are also similar to the single left valve attributed by Krumbeck (1914, pl. 16, fig. 11) to *Gervilleia (Odontoperna) bouéi* (Hauer, 1857) from the Norian of Sumatra. However, Krumbeck’s specimen, in spite of being taphonomically crushed, exhibits a very narrow and acutely pointed posterior auricle quite different from that inferred for the Keku specimens. Similarly, the upright and less oblique outline, blunt auricle, and potentially narrow hinge plate lacking dentition also differentiates this species from other better known Norian and Rhaetian bakevelliids

Text-fig. 17 (at left). Pterioida. 1–16, *Cassianella cordillerana* McRoberts in McRoberts and Blodgett, 2002. 1–4, PRI 69619, a LV; 1, valve interior; 2, exterior view; 3, posterior-lateral view; 4, anterior-lateral view. 5–8, PRI 69620, a LV; 5, valve interior; 6, exterior view; 7, posterior-lateral view; 8, anterior-lateral view. 9, 10, PRI 69621, a LV; 9, valve interior; 10, exterior view. 11, 12, PRI 69622, a RV; 11, valve exterior; 12, interior view. 13, 14, PRI 69623, a RV; 13, valve exterior; 14, interior view. 15, PRI 69624, detail of hinge area and resilifer of a RV. 16, PRI 69625, detail of hinge area of a LV. 17–22, *Bakevella* sp. A. 17, 18, PRI 69626, a LV; 17, valve exterior; 18, interior view. 19, 20, PRI 69627, a LV; 19, valve exterior; 20, interior view. 21, 22, ?Pergamidia sp. indet., PRI 69628; 21, valve exterior; 22, interior view. Scale bars = 10 mm. All from USGS loc. M1912.



Text-fig. 18. Measurements and descriptive statistics of left valves of *Casianella cordillerana* McRoberts in McRoberts and Blodgett, 2002 from USGS loc. M1912. Upper plot, scatterplot and least squares regression of height and periphery; lower plot, histogram of periphery.

from the western Tethys, including *Bakevella bouei* (Hauer, 1857) and *Gervillia inflata* (Schafhäutl, 1851).

Paleoecology.—Following Stanley (1970), Seilacher (1984), and Muster (1995), similar pteriform *Bakevella* species are inferred to have been endobyssate with the commissure plane vertical or nearly so (Text-fig. 13.11).

Family **PERGAMIDIIDAE** Cox, 1969
Genus **PERGAMIDIA** Bittner, 1891

Type species.—*Pergamidia eumenea* Bittner, 1891, by subsequent designation (Diener, 1923: 135), Upper Triassic (Norian), Turkey.

?*Pergamidia* sp. indet.
Text-figs 17.21, 17.22

Material examined.—One incomplete RV, PRI 69628.

Description.—Right valve large (maximum H = 51.2 mm), higher than long, strongly convex and inflated (maximum inflation = 17.2 mm) with central portion of valve broadly convex and folding steeply towards both anterior and even more steeply towards posterior margins; anterior margin weakly concave passing sharply to a near horizontal ventral margin; posterior margin nearly straight passing sharply to ventral margin; exterior with irregular growth lamellae and weakly developed radial sculpture evident only on anterior third of valve; interior with relatively large oval anterior adductor scar (measuring 14.9 mm in longest axis approximately perpendicular to anterior margin). Details of hinge/ligament area, dentition, anterior auricle, and byssal sinus not preserved.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Questionable assignment to the Pergamidiidae is largely based on the single RV that is quite large, highly convex, and thin-shelled. Externally, *Pergamidia* Bittner, 1891 resembles *Krumbeckia* Ichikawa, 1958 (now included within *Schafhaeutlia* Cossmann, 1897 as per Hautmann, 2001b) and can be distinguished from the later by possessing a distinctively large byssal gape and an obliquely alvincular ligament system extending on both sides of the beak (Waller in Waller & Stanley, 2005). Other Pergamidiidae (e.g., *Manticula* Waterhouse, 1960) are less inflated and possess a more mytiliform shape than PRI 69628. Following the reassignment of lower Norian *Krumbeckia* cf. *K. timorensis* (Krumbeck, 1924) from Oregon of Newton (in Newton *et al.*, 1987) to the genus *Mysidiella* Cox, 1964 (Waller in Waller & Stanley, 2005), demonstrable Pergamidiidae are unknown from eastern Panthalassa. Known *Pergamidia* species have been described from Indonesia, China, and Turkey which would have occupied the margins of the central and eastern Tethys (e.g., Crame, 1995; Sha *et al.*, 2005).

Paleoecology.—Irrespective of its generic affiliation, the life habit of the Gill Harbor specimen is interpreted to be an epibyssate suspension feeder. It is interesting to note that several *Pergamidia* species are associated with sulfide deposits

and have been interpreted by Sha *et al.* (2005) and Lin *et al.* (2011) to be adapted to hydrothermal vent environments.

Order **OSTREIDA** Férussac, 1822
 Superfamily **OSTREOIDEA** Rafinesque, 1815
 Family **GRYPHAEIDAE** Vyalov, 1936
 Genus **LIOSTREA** Douvillé, 1904

Type species.—*Ostrea sublamellosa* Dunker, 1846 [= *Liostrea hisingeri* (Nilsson, 1832)], by original designation, Lower Jurassic (Hettangian), Halberstadt, Germany.

Remarks.—Given the wide range of morphologic, and likely ecophenotypic, variation in Triassic gryphaeate oysters, due in no small part to their living habit and choice and size of substrate to which left valves attach, it can be difficult to assign species into either *Liostrea* Douvillé 1904 or *Gryphaea* Lamarck 1801. The Jurassic gryphaeiid genus *Catinula* Rollier, 1911 can easily be separated from *Liostrea* and *Gryphaea* in that they are quite small, have a pronounced radial ornamentation, and a large resilifer. The diagnoses for *Liostrea* and *Gryphaea* in the *Treatise* (Stenzel, 1971) provide some guidance (*e.g.*, the left valves of *Gryphaea* are more strongly inflated and incurved than in *Liostrea*) but still somewhat unsatisfactory as intermediate species are known (*e.g.*, lower Norian *Gryphaea nevadensis* McRoberts, 1992). The left valves of both genera have a retrorescentic and incurved growth program, the degree of which is largely dictated by the size of attachment area and age of the individual. The systematic approach employed herein to discriminate the two genera is based on the range of sizes of attachment surface and xenomorphic area and the depth of the radial posterior sulcus differentiating the posterior lobes that are well developed in *Gryphaea* and more subdued in *Liostrea*. Adult *Liostrea* are also generally smaller in overall size than *Gryphaea*. An excellent review of Triassic gryphaeiids and their possible origin in the Ladinian can be found in Waller (in Waller & Stanley, 2005). Following Ros-Franch *et al.* (2014), the oldest demonstrable *Liostrea* are from the Carnian of Japan (Tokuyama, 1960c). The specimens questionably referred to *Liostrea* from the Ladinian of Nevada (Waller in Waller & Stanley, 2005) may be among the gryphaeiid oysters in that they clearly attach by their left valves and possesses a calcitic shell with a fine, and likely foliated, microstructure, but assignment to *Liostrea* in the strict sense is still somewhat in doubt. Given that most Triassic *Liostrea* were originally named under *Ostrea* Linné, 1758 and some under *Plicatula* Lamarck, 1801, the genus is likely more common than named occurrences might suggest. For example, “*Ostrea Pictetiana* (Mort.)” of Wöhrmann (1889, pl. 6, fig. 6, 6a) from the Carnian Raibl Formation of the Northern Alps appears to attach by its left valve and lacks radial sculpture. Additionally, *Plicatula? papiracea* illus-

trated by Stoppani (1860–1865, pl. 17, figs 1–4) has small left valves that apparently lack some form of radial sculpture (as in *Plicatula*, *Lopha*, and *Enantiostreon*, etc.), but clearly possess a posterior lobe.

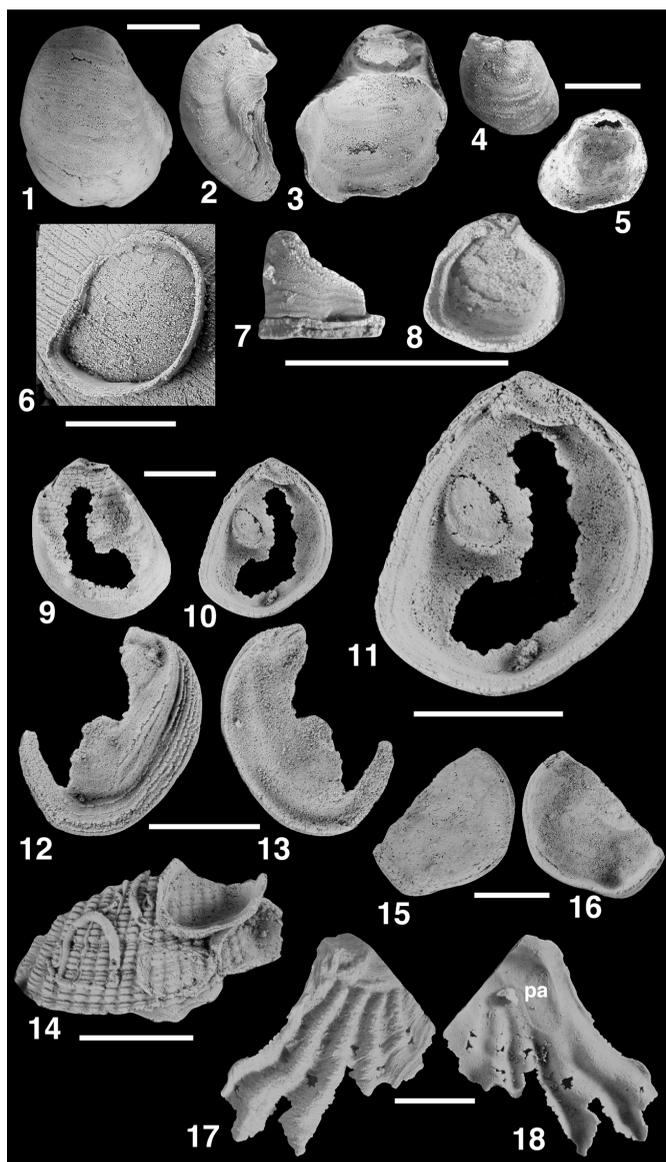
Liostrea newelli Newton in Newton *et al.*, 1987
 Text-figs 19.1–19.16, 20

Liostrea newelli Newton in Newton *et al.*, 1987: 36, figs 29, 30.

Holotype and measurements.—USNM 417293, a LV (Newton in Newton *et al.*, 1987: 36, fig. 30.4); H = 10.2 mm, L = 6.3 mm; from USGS loc. M2672, Spring Creek, Oregon, lower Norian.

Material examined.—The collection consists of six LV (PRI 69629–69632, PRI 69634, UMIP 15665) and two RV (PRI 69635, PRI 69633).

Description.—Left valves of moderate size (maximum L = 16.9 mm, maximum H = 22.2 mm), with large but highly variable attachment area (60–100% of valve height); obliquely ovate in outline and slightly elongated in posterior-ventral direction; posterior margin relatively straight, becoming slightly concave corresponding to posterior sulcus (see below), then sharply convex along margin where posterior lobe intersects posteroventral margin; anterior and ventral margins broadly rounded; left valves are deeply cupped with unattached margins rising steeply and growing at a greater rate along the ventral margin, producing shells with significant dorsal-ventral curvature; posterior lobe well developed on larger specimens with small attachment areas, separated from main part of shell by weak sulcus and commencing approximately 5 mm from beak. Specimens with well developed lobe and sulcus gryphaeate in appearance; surface generally smooth except for finely-spaced commarginal growth lines; one of the specimens (PRI 69630, Text-figs 19.4, 19.5) exhibits fine antimarginal lines that appear to be an artifact of the silicification process; left valve interior with broad ligamental area with anterior-sloping platform whose ventral edge extends over umbonal cavity, resilifer shallow and opisthocline, bordered by weakly developed anterior and posterior bourrelets; posterior adductor scar orbicular and prominent and raised above rest of valve interior, situated adjacent to posterior margin nearly one-third the distance from the beak to the posteroventral margin; commissural shelf well developed; right valves operculiform, exterior relatively flat to weakly convex, valve margin may be steeply projected inward; one of the left valves (PRI 69632, Text-figs 19.10, 19.11) shows a well preserved partial posterior adductor scar which is elevated above rest of valve interior surface.



Text-fig. 19. Osteroids. 1–16, *Liostrea newelli* Newton in Newton *et al.*, 1987. 1–3, PRI 69629, a LV; 1, valve exterior; 2, posterior view; 3, interior view showing large attachment area. 4, 5, PRI 69630, a LV; 4, valve exterior; 5, interior view. 6, PRI 69631, a partial LV attached to a LV of *Plagiostoma scallanae* n. sp. 7, 8, UMIP 15665, a LV cemented to small skeletal fragment; 7, posterior; 8, interior view. 9–11, PRI 69632, a LV; 9, valve exterior showing large attachment area; 10, interior view; 11, enlarged view of interior showing resilifer and PA scar. 12, 13, PRI 69633, a RV; 12, valve exterior; 13, interior view. 14, PRI 69634, a partial left valve attached to *Septocardia peruviana* (Cox, 1942) fragment and serpulid encrusters. 15, 16, PRI 69635, a RV; 15, valve exterior; 16, posterior view. 17, 18, ?*Actinostreon* sp. A, UMIP 15666, a RV; 17, valve exterior; 18, valve interior showing posterior adductor muscle scar (pa). Scale bars = 10 mm. All from USGS loc. M1912.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Clear indication of cementation by left valve, gryphaeate shape lacking radial ornamentation and large attachment surfaces place this species within *Liostrea* and the Gryphaeidae. The range of variation of LV shape and convexity is remarkable, which seems to be influenced by the size of the attachment area. Those specimens exhibiting small attachment areas assume a more typical gryphaeate shape with demarked posterior lobe (e.g., PRI 69629, PRI 69630, UMIP 155665) and those with relatively larger attachment areas (e.g., PRI 69631, PRI 69634) have less deeply concave valves and apparently do not exhibit significant growth above the attachment surface. Given the relatively small sample size and apparently high degree of morphologic variability of this species at Gill Harbor, it may turn out that the collection represents more than one species. Given the apparent morphologic intermediates in the collection, all are here considered to represent a single species: *Liostrea newelli*.

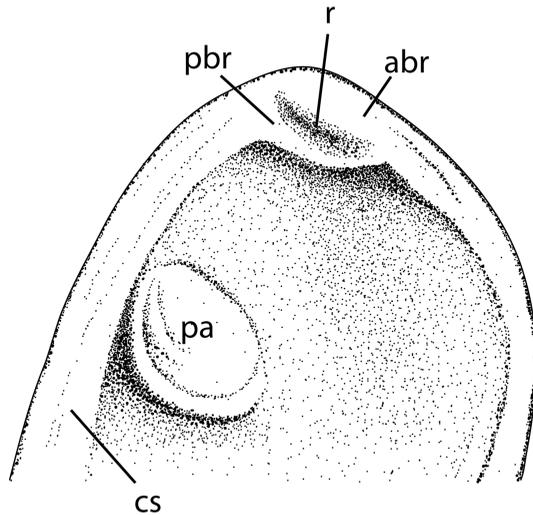
Although the Gill Harbor specimens obtain a larger maximum size than the type collection, the specimens agree in all other important characteristics with *Liostrea newelli*. Of particular note are both the lamellose structure and the variably developed posterior lobe and sulcus of the RV that were highlighted by Newton (in Newton *et al.*, 1987) as characteristic of the species. This is the first report of this species outside of the type locality at Hells Canyon, Oregon.

Liostrea newelli is most similar to *Liostrea (Catinula) shiraiwensis* Tokuyama, 1960c from the Carnian of Japan which also exhibits a wide range of morphologies, including some very *Gryphaea*-like unattached specimens. Based on the illustrated specimens of Tokuyama (1960c, pl. 12, figs 8–12), *Liostrea (Catinula) shiraiwensis* is generally larger in adult size and also possesses a deep pedal retractor scar below the resilifer, a feature not observed in *L. newelli* from Gill Harbor or the type collection from Oregon.

The Gill Harbor species also closely resembles *Liostrea tibetica* Yin & McRoberts, 2006 from the Rhaetian-Hettangian transitional beds of the Germig Formation of Langola, Tibet. Although approximately the same maximum size and convexity as *L. newelli*, *L. tibetica* does not possess the weak sulcus and also possesses a narrower cardinal area which lacks details of the resilifer.

Liostrea newelli differs significantly from *Liostrea* from the Rhaetian and Early Jurassic of Northwest Europe. *Liostrea bristovi* (Richardson, 1905) is significantly larger, reaching sizes of 60 mm long and 55 mm high and is less convex (see Ivimey-Cook *et al.*, 1999, pl. 13, figs 5, 6). Likewise, *L. hisingeri* (Nilsson, 1832) exhibits a much narrower and less incurved umbo (see Ivimey-Cook *et al.*, 1999, pl. 13, fig. 7).

Paleoecology.—All *Liostrea newelli* exhibit attachment by their left valves to variably sized skeletal substrates (Text-fig. 13.4). Some of the specimens, however, possess a smaller



Text-fig. 20. Illustration of internal features of LV of *Liostrea newelli* Newton in Newton *et al.*, 1987. Abbreviations: r = resilifer, pbr = posterior bourrelets, abr = anterior bourrelet, cs = commissural shelf, pa = posterior adductor scar.

attachment area and were, like typical *Gryphaea*, reclining throughout most of their ontogeny with the animal rotated so that the ventral margin was reoriented horizontal relative to the substrate. Similar life-habit interpretations were suggested for this species by Newton (in Newton *et al.*, 1987) and for similar gryphaeate *Liostrea* by Tokuyama (1960b). It is interesting to note that all specimens with preserved attachment substrate, regardless of size of attachment area, are or were affixed to valve interiors and exteriors of *Plagiostoma scallanae* n. sp. Although not observed in the Gill Harbor collection, lower Norian specimens from Oregon also can be found as small clusters on larger substrates (Newton in Newton *et al.*, 1987).

Family **OSTREIDAE** Rafinesque, 1815

Genus **ACTINOSTREON** Bayle, 1878

Type species.—*Ostrea solitaria* J. Sowerby, 1825, subsequent designation (Douvillé, 1879: 91), Upper Jurassic (Oxfordian), France.

Discussion.—Significant debate continues regarding the status of generic and familial nomenclature of *Lopha*-like oysters which occur in the Triassic. Like other cementing bivalves of the Triassic (irrespective of which valve cemented and affinity to or inclusion within the Ostreidae), many were originally placed under the genera *Ostracites* and *Ostrea* and have since been shown to be dextrally cemented and thus likely belong to the Prospodylidae (e.g., *Terquemia* Tate, 1868, *Newaagia* Hertlein, 1952, or *Noetingiconcha* Hautmann & Hagdorn, 2013). True oysters (Ostreidae) are sinistrally cemented, pos-

ses an alvincular-arcuate ligament, generally lack a pallial line, and, except for a few early Mesozoic forms whose inner shell layer was aragonitic nacreous, have calcitic shells (Hautmann, 2001a, 2006; Márquez-Aliaga *et al.*, 2005). Since publication of the oyster volume of the *Treatise on Invertebrate Paleontology* (Stenzel, 1971), Triassic Ostreidae have largely been assigned to one of several genera including *Actinostreon* Bayle, 1878, *Lopha* Röding, 1798, *Palaeolopha* Malchus, 1990, *Umbostrea* Hautmann, 2001a, and *Nacrolopha* Carter & Malchus, 2011. Malchus (1990: 102) erected *Palaeolopha* (type species *Ostrea haidingeriana* Emmerich, 1853) to accommodate *Lopha*-like oysters lacking (at least in Triassic species) chomata and possessing a simple foliated calcite shell microstructure and structural chambers filled with a chalky substance. Citing the discovery of chalky deposits in *Lopha sensu stricto* and Malchus' (1990) inclusion of the type species of *Actinostreon* into *Palaeolopha*, Hautmann (2001a: 367) considered *Palaeolopha* a junior synonym of *Actinostreon* which would have priority. In spite of Hautmann's recommendation, *Palaeolopha* continues to occasionally be used (e.g., Carter *et al.*, 2011, Damborenea *et al.*, 2013). More recently, Carter & Malchus (in Carter *et al.*, 2011) erected *Nacrolopha* (type species *N. carolae* Carter & Malchus in Carter *et al.*, 2011) for an interesting *Lopha*-like oyster from the Carnian Cassian Formation of Italy that has a nacropismatic LV, possesses both a small pedal retractor and AA scars, and lacks foliated skeletal structure and structural chambers.

Of the *Lopha*-like specimens recovered from the Gill Harbor locality, few preserve sufficient details of skeletal structure, ligament, or musculature to confidently assign to available genus-level taxa or even families. Of the three cementing *Lopha*-like forms described herein, one is determined to be sinistrally attached and tentatively placed in *Actinostreon*, and the remaining two are likely dextrally attached and included within the Prospodylidae.

?*Actinostreon* sp. A

Text-figs 19.17, 19.18

Material examined.—A single left valve fragment (UMIP 15666) in which the posterior and dorsal sectors are missing.

Description.—Right valve moderately large (maximum H = 31.0 mm) irregularly shaped and thin shelled. Xenomorphic area somewhat large (8.0 mm preserved diameter). With relatively strong antimarginal plicae abruptly beginning beyond xenomorphic area with irregular and slightly sinuous course, but extending obliquely from xenomorphic area at a slight angle towards ventral direction. The preserved ribs are narrow, moderately high frequency (rib wavelength at shell margin = 4.0–5.4 mm), with sub-round crests and not increasing in

number (*i.e.*, not bifurcating or intercalated). Exterior ribbed surface squamose and covered with fine commarginal lamellae; valve interior relatively smooth with more subtle undulations corresponding to plicae; posterior adductor scar elongated and concave, moderately large (10 mm) and situated some distance from posterior margin (but presumably still posterior of the medial line), slightly depressed and somewhat more deeply inset along anterodorsal margin of scar. Details of hinge area and ligament system not preserved.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Although the specimen is incompletely preserved (large portions of the posterior and dorsal regions are missing), the position of the adductor muscle scar and opisthogyrate deflection of plicae from the xenomorphic area strongly suggest that the specimen is a RV and that the individual was sinistrally cemented. The irregular shell shape and rib pattern are typical for the genus and other cementing Ostreidae and Prospodylidae. Tentative placement in *Actinostreon* rather than *Umboostrea* is based on the relatively thin shell and shape of the adductor muscle pad and it is distinguished from *Nacrolopha* Carter & Malchus in Carter *et al.*, 2011 by lacking small AA and pedal retractor scars. Complete preservation would presumably illustrate the rib bifurcation, which is commonly observed in other *Actinostreon*.

Given the quality of the single fragment, species identification is not attempted. The Gill Harbor specimen can be compared to Norian-Rhaetian *Actinostreon haidingeriana* (Emmrich, 1853), which is common throughout Alpine and northwestern Europe (*e.g.*, Winkler, 1861; Ivimey-Cook *et al.*, 1999; Hautmann, 2001a), Asia (*e.g.*, Healey, 1908), and North America (*e.g.*, Newton in Newton *et al.*, 1987). The Alaskan specimen is similar to *Actinostreon haidingeriana* in its large size and shallower valve convexity, but differs in the more abrupt commencement of antimarginal plicae. Newton (in Newton *et al.*, 1987, fig. 33) illustrated several well-preserved specimens as *Lopha* cf. *L. haidingeriana* (Emmrich, 1853) from the lower Norian of Oregon (USGS loc. M2672); these also have a similarly large attachment areas, but exhibit greater valve convexity.

The Gill Harbor specimen can also be compared to *Ostrea montiscaprellis* Klipstein, 1943 which was originally named from the Carnian Cassian Formation (northern Italy), but is now known from multiple Carnian and possibly Norian localities in Alpine Europe and possibly western North America (*e.g.*, Diener, 1923; Stanley, 1979; Szente *et al.*, 2010). The taxonomic position of *Ostrea montiscaprellis* has a complex history and has been placed into various ostreoid genera including

Lopha Roding, 1798, *Alectryonia* Fischer de Waldheim, 1807, *Palaeolopha*, Malchus, 1990, and more recently, as suggested by Szente *et al.* (2010), as possibly belonging to *Umboostrea* Hautmann, 2001a. *Ostrea montiscaprellis* differs from the Gill Harbor specimens in its narrower valve width with respect to its height and posteriorly curved axis of growth.

Paleoecology.—Although left valves of ?*Actinostreon* sp. remain unknown, some indication of attachment is provided by the xenomorphic area of the RV. Like other *Actinostreon* (Hautmann, 2001a; Hautmann & Hagdorn, 2013), it is assumed to have cemented by its left valve to variably-sized skeletal substrates.

Order **LIMOIDA** Waller, 1978
 Superfamily **LIMOIDEA** Rafinesque, 1815
 Family **LIMIDAE** Rafinesque, 1815
 Genus **ANTIQUILIMA** Cox, 1943

Type species.—*Lima antiquata* J. Sowerby, 1818 (= *Chamites succinctus* Schlotheim, 1813), by original designation; Lower Jurassic (Sinemurian), Gloucestershire, Great Britain.

Remarks.—Although listed in the *Treatise* (Cox *et al.*, 1969) as originating in the Lower Jurassic, *Antiquilima* is now known to be present in strata as old as Ladinian (Waller in Waller & Stanley, 2005). Upper Triassic representatives are few (only four species known), but are widely distributed across the Tethys, Panthalassa, and Boreal seas (*e.g.*, Kiparisova *et al.*, 1966; Hayami *et al.*, 1977; Newton in Newton *et al.*, 1987; Hautmann, 2001b; Yin & McRoberts, 2006).

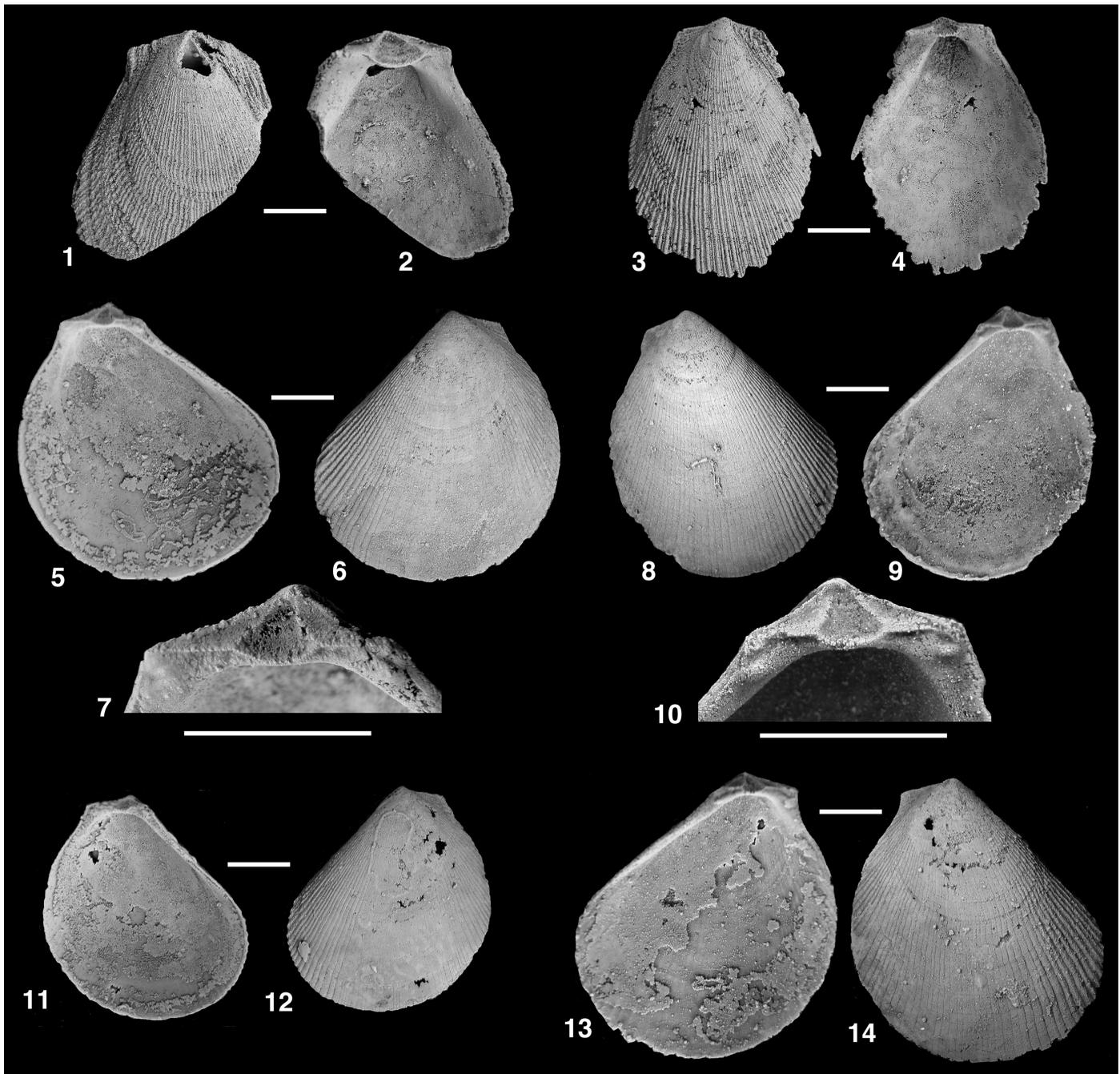
Antiquilima vallieri Newton in Newton *et al.*, 1987
 Text-figs 21.1–21.4

Antiquilima vallieri Newton in Newton *et al.*, 1987: 28, figs 22.1–22.4, 22.6, 22.7.

Holotype and measurements.—UMIP 7341, a LV (Newton in Newton *et al.*, 1987: 28, fig. 22.1, 22.2); H = 37.9 mm, L = 22.4 mm, W = 7.75 mm; from USGS loc. M2672, Spring Creek, Oregon, lower Norian.

Material examined.—The Gill Harbor collection consists of two incomplete right valves (PRI 69636, PRI 69637).

Description.—Right valves medium-sized (maximum H = 37.9 mm, maximum L = 27.4 mm), elongate oval in outline and slightly opisthocline, higher than long and with moderate convexity (maximum W = 9 mm); beak slightly posterior (about 45% of hinge length) and situated above dorsal mar-



Text-fig. 21. *Limoidea*, *Antiquilima valleri* Newton in Newton et al., 1987. 1, 2, PRI 69636, a RV; 1, exterior view; 2, interior view. 3, 4, PRI 69637, a RV; 3, exterior view; 4, interior view. 5–14, *Plagiostoma scallanae* n. sp. 5–7, paratype, PRI 69638, a LV; 5, interior view; 6, exterior view; 7, detail of hinge area. 8–10, holotype, PRI 69639, a RV; 8, exterior view; 9, interior view; 10, detail of hinge area. 11, 12, paratype, PRI 69640, a LV; 11 interior view; 12, exterior view. 13, 14, paratype, PRI 69641, a RV; 13, interior view; 14, exterior view. Scale bars = 10 mm. All from USGS loc. M1912.

gin, which slopes ventrally away from beak; posterior auricle of right valve poorly delimited from main part of disk, with commarginal sculpture, but weak or absent radial costae; posterior margin of posterior auricle relatively straight and obliquely joining dorsal margin at about 120° and ventrally joining disk with slight concavity; anterior auricle of RV well separated from disk and apparently much higher than

posterior auricle, extending ventrally approximately one-half of shell height; anterior margin of anterior auricle broadly concave, enclosing elongate byssal gape; surface ornamented by at least three orders of fine, round-topped radial costae that curve slightly anterior with narrow intercostal furrows; around 50 primary costae; second-order costae are inserted between some primary costae at about 10 mm from beak;

third- and fourth-order costae inserted at about 15–20 mm from beak; costae relatively straight during early ontogeny except where deflected by commarginal growth-stops and becoming sinuous and somewhat nodose later in ontogeny (at about 25 mm from beak); internal hinge plate broad and triangular in shape with large, centrally situated triangular resilifer with a curved ventral margin that slightly extends below the hinge margin; internal umbonal cavity somewhat deep; posterior adductor scar weakly impressed, circular, fairly large (12.3 mm in diameter) and medially positioned about 10 mm ventral to hinge line.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912) and lower Norian Martin Bridge Formation, northeast Oregon (Wallowa terrane) as originally described in Newton *et al.* (1987).

Remarks.—Although lacking left valves, the observations above are consistent with most of the characters of *Antiquilima valleri* Newton in Newton *et al.*, 1987. When compared to the Oregon specimens, however, those from Gill Harbor exhibit a slightly larger byssal gape along the anterior auricle (*e.g.*, compare Text-figs 21.1, 22.3 to those of Newton in Newton *et al.*, 2007, figs 22.1, 22.4). This slight difference should be considered minor and is presumed to be a result of intraspecific variation.

This species is remarkably different from several other Triassic forms. As noted by Newton (in Newton *et al.*, 1987: 29), *Antiquilima valleri* has a greater height/length ratio and more numerous and less sharp costae than *A. atacamensis* Hayami *et al.* 1977 from the Norian of northern Chile. *Antiquilima valleri* differs from *A. hians* Hautmann 2001b from the Norian and Rhaetian of Iran in having a significantly higher rib count (*A. hians* has approximately 20 primary ribs, whereas *A. valleri* has approximately 50). Likewise, other Carnian and Middle Triassic *Antiquilima*, such as *A. ladinica* Waller (in Waller & Stanley, 2005), are more coarsely ribbed.

Paleoecology.—Recent limoideans include some species that are swimmers, some that are byssally attached nestlers, and some with the ability to detach their byssus and relocate (Yonge, 1953; Stanley, 1970; Newton in Newton *et al.*, 1987). The obliquely subovate outline of *Antiquilima valleri*, as well as the resulting flat anterodorsal border, together with pronounced anterior auricle and byssal gape, suggest a vertically-oriented life position, resting on its anterodorsal margin, fastened by a byssus for most of its life (Text-fig. 13.10).

Genus **PLAGIOSTOMA** J. Sowerby, 1814

Type species.—*Plagiostoma giganteum* J. Sowerby, 1818, by subsequent designation (Stoliczka, 1871: xxii); Lower Jurassic, Great Britain.

Remarks.—As summarized by Ros-Franch *et al.* (2014), *Plagiostoma* is known from the Middle Triassic through Upper Cretaceous and has a cosmopolitan paleogeographic distribution. The earliest Triassic representatives are known from numerous Anisian and Ladinian localities in the Germanic Muschelkalk and elsewhere along the Panthalassa margin (*e.g.*, Seilacher, 1954; Waller in Waller & Stanley, 2005; Hautmann, 2006). By the Upper Triassic, *Plagiostoma* began to flourish with over 15 named species from throughout the Tethys, Panthalassa, and Boreal seas (*e.g.*, Hudson & Jefferies, 1961; Allasinaz, 1966; Kiparisova, 1972; Wen *et al.*, 1976; Ivimey-Cook *et al.*, 1999; Yin & McRoberts, 2006). Several of the uppermost Triassic species (*e.g.*, *P. punctatum* J. Sowerby, 1815 and *P. giganteum* J. Sowerby, 1814) have temporal ranges well into the lower Jurassic and span the end-Triassic extinction.

***Plagiostoma scallanae* n. sp.**

Text-figs 21.5–21.14

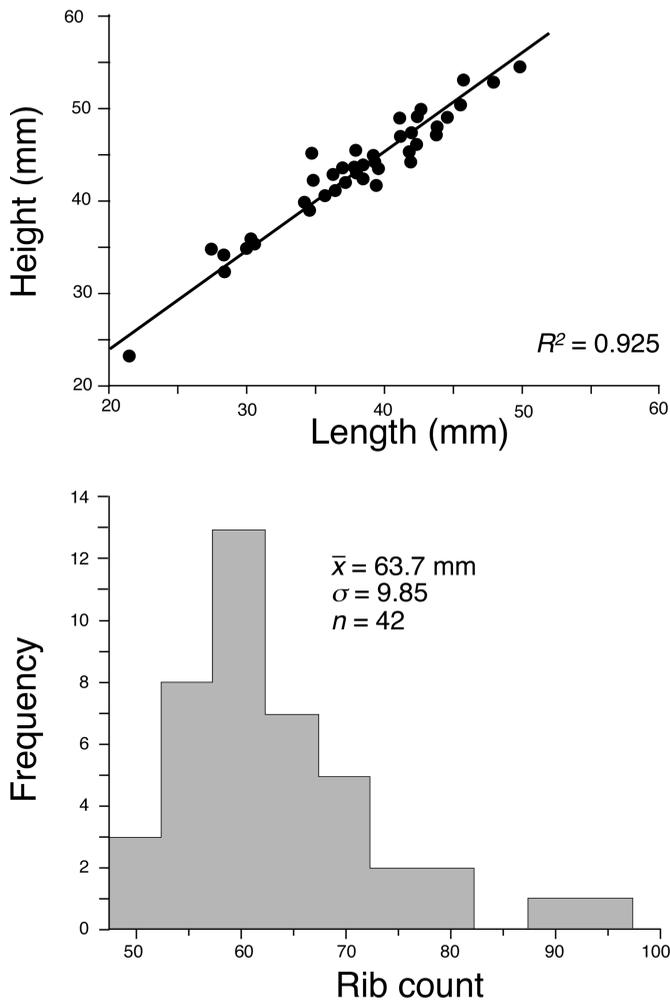
cf. ?*Plagiostoma* sp. Newton in Newton *et al.*, 1987: 33, figs 22.12–22.15.

Types and measurements.—Holotype, PRI 69639, a RV (Text-figs 21.8–10); H = 43.8 mm, L = 37.7 mm, W = 7.6 mm, umbonal angle = 116°. Paratypes: PRI 69638, a LV (Text-figs 21.5–21.7); PRI 69640, a LV (Text-figs 21.11, 21.12); and PRI 69641, a RV (Text-figs 21.13, 21.14). Additional measurements graphically represented in Text-fig. 22. All from USGS loc. M1912, Kuiu Island, Alaska, upper Norian, Hound Island Volcanics.

Other material examined.—In addition to the types, the collection consists of 17 left valves, 19 right valves, and numerous fragments from at least 45 individuals.

Diagnosis.—*Plagiostoma* of moderate size, moderately procre-scent, slightly higher than long, with sharp anterior umbonal ridge, bi-auriculate with anterior auricle smaller than posterior one, and with a relatively high number of costae (mean = 63.7) which run relatively straight, but may become disrupted and wavy in later growth stages.

Description.—Valves medium-sized (maximum H = 54.6 mm, maximum L = 51.0 mm), equivalved, slightly higher than long (H:L ~ 1.1), moderately inflated (maximum W = 10.9 mm), trigonal-oval in outline, procre-scent, with nearly straight anterodorsal margin sloping about 35° from hinge,



Text-fig. 22. Measurements and descriptive statistics of *Plagiostoma scallanae* n. sp. Upper plot, least-squares regression of length versus height; lower plot, frequency histogram of rib count.

posterior and ventral margins broadly rounded; umbonal area weakly inflated, umbonal angle of about 108° ; most of disk broadly arched except anterodorsal margin, which is steeply folded inward from anterior-most point of disk margin to juncture with hinge, forming a lunule; anterior umbonal ridge moderately sharp; valves bi-auriculate, posterior auricle relatively small with dorsal margin slightly sloping downward from beak and posterior margin subtending angle with hinge of 45° ; anterior auricle smaller than posterior one and relegated to lunule; surface ornamented with 47–95 (mean = 63.7) regularly-spaced undivided radial costae which are somewhat stronger on the anterior and posterior third of disk and equally strong on the anterior folded margin and posterior auricle and somewhat subdued on central third sector of disk; costae relatively broad with round to subangular crests and deep furrows on posterior and anterior flanks to flat-topped and separated by narrow and shallow furrows and in some cases even

absent in central part of disk; costae relatively straight across most of disk but occasionally becoming disrupted or wavy in later growth stages; exterior surface with several widely spaced commarginal and somewhat upturned growth lines beginning about 2–3 cm from beak and becoming more closely spaced towards ventral margin; very faint finely-spaced commarginal lirae crossing without interruption across radial costae and furrows and especially visible towards ventral margin, punctae not developed on inter-rib furrows; hinge area trigonal, fairly large, and sloping from beak downwards towards hinge; with prominent prosocline triangular resilifer; ventral hinge margin sharp, almost ridge-like and slightly extended downward below resilifer; with elongate posterior and anterior longitudinal teeth ventral to and subparallel with hinge. Smooth and continuous pallial line can be observed in a few of the better specimens (e.g., Text-figs 21.9, 21.11), occurring along at least 3 mm inward from, and commarginal to, the anterior and ventral shell margins. Other muscle scars not observed.

Etymology.—Trivial name, *scallanae*, after my wife, Jacqueline Scallan, who has lovingly supported my paleontological endeavors.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—This species is characterized by overall shape, rib count, and details of ligament and dentition. There are several Late Triassic and Early Jurassic *Plagiostoma* species that resemble *P. scallanae*. Most of these species, especially those that were originally described under the genus name *Lima*, are in need of thorough review. Additionally, several species of *Plagiostoma* have been named based upon the presence of punctae in the intercostal furrows. It is difficult to put much weight on intercostal punctae given that this feature most likely represents the eroded tops of radial costae and their intersection with commarginal striae, rather than true tubes or pores penetrating or passing through the skeleton (see Ivimey-Cook *et al.*, 1999).

Newton (in Newton *et al.* 1987: 33) described three partial specimens as ?*Plagiostoma* sp. that are similar in many regards, and perhaps conspecific to *Plagiostoma scallanae*. The Gill Harbor specimens, however, either did not possess the intercostal pores as in the Oregon specimens (and many other species of *Plagiostoma*) or they are not preserved. The incomplete preservation of the Oregon specimens does not permit full evaluation of similarities and therefore their assignment to *P. scallanae* is deemed tentative. Likewise, the one comparable *Plagiostoma* from the Larbarger area, Yukon (*Lima* (*Plagiostoma*) sp. near *rigidula* Phil of Lees, 1934, pl. 3, fig. 4) is too poorly preserved for meaningful comparison.

This species also closely resembles *Plagiostoma punctatum* J. Sowerby, 1815, *P. giganteum* J. Sowerby, 1814, and *P. praecursor* (Quenstedt, 1856) that are well known from Upper Triassic and Lower Jurassic throughout northwest Europe and the western Tethys. However, the new species is slightly higher than long, whereas the aforementioned European species are slightly longer than high. Furthermore, the new species lack the punctae-like structure of the intercostal furrows that are diagnostic of *P. punctatum* and many other *Plagiostoma* species (e.g., *P. acutum* Waller in Waller & Stanley, 2005).

The Gill Harbor species may be compared with Norian-Rhaetian *Plagiostoma subvaloniense* Krumbeck, 1923, known from Indonesia, Oman, and Iran and potentially into the western Tethys (Krumbeck, 1923; Hudson & Jefferies, 1961; Hautmann, 2001b). The type specimens of *P. subvaloniense* (Krumbeck, 1923, pl. 12, figs 17–19) exhibit greater inflation and valve curvature in the umbo and a smaller umbonal angle (approximately 90° as compared to over 100° for *P. scallanae*). Additionally, *P. subvaloniense* exhibits very regular costae across the entire disk (although, as per above, subdued radial ribs may be a taphonomic artifact) unlike *P. scallanae*. *Plagiostoma scallanae* is unlikely to be confused with other Late Triassic *Plagiostoma*, which have significantly different shapes or, as in the case of Carnian–Norian *P. nudum* (Parona, 1889) (see Hudson & Jefferies, 1961, text-fig. 7), possess smooth exteriors.

Paleoecology.—Like other *Plagiostoma*, *P. scallanae* n. sp. is interpreted to be a epibyssate suspension feeder (Seilacher, 1954). A straight anterior margin and equivalved condition suggests that *P. scallanae* was orientated with its anterior parallel to the substrate and with its commissure plane vertical or nearly so (Text-fig. 13.9). Several *P. scallanae* exhibit encrustation by *Liostrea newelli*, *Harpax articulatum* n. sp., and serpulid worm tubes on valve exteriors (see for example Text-figs 8.2, 8.5, 19.6).

Order **PECTINIDA** Adams and Adams, 1858
 Superfamily **MONOTOIDEA** Fischer, 1887
 Family **MONOTIDAE** Fischer, 1887
 Genus **MONOTIS** Bronn, 1830

Type species.—*Pectinites salinarius* Schlotheim, 1820, by subsequent designation (Herrmannsen, 1852: 86), Upper Triassic (Norian), Austria.

Remarks.—A significant literature exists on the taxonomy, paleoecology, and biochronology of the mostly Norian genus *Monotis* (e.g., Westermann, 1962; Grant-Mackie, 1978, 1980; Tozer, 1980; Ando 1987; Grant-Mackie & Silberling, 1990; Silberling et al., 1997; McRoberts, 2010, 2011). McRoberts

(2010) suggested that several of the subgenera (including *Monotis* Bronn, 1830, *Entomonotis* Marwick, 1935, *Pacimonotis* Grant-Mackie & Silberling, 1990, and *Maorimonotis* Grant-Mackie, 1978) represent a coherent clade arising from a likely *Meleagrinnella* Whitfield, 1855 ancestor during the Early or Middle Norian. Two dwarf *Monotis* species are known from the earliest Rhaetian of Austria (McRoberts et al., 2008).

Subgenus **PACIMONOTIS** Grant-Mackie & Silberling, 1990

Type species.—*Monotis (Pacimonotis) subcircularis* Gabb, 1864, by original designation; Upper Triassic (Norian), California.

Monotis (Pacimonotis) subcircularis Gabb, 1864 [emend. Grant Mackie, 1978c]
 Text-figs 23.1, 23.2

Monotis subcircularis Gabb, 1864: 31, pl. 6, figs 29, 29a; Westermann, 1962: 81, pl. 115, figs 6–9, pl. 116, figs 1–8, pl. 117, figs 1–5; Tozer, 1963, pl. 7, fig. 22.

Pseudomonotis subcircularis (Gabb). Smith, 1927: 120, pl. 95, figs 8, 9; pl. 101, fig. 8; pl. 104, figs 6, 7; pl. 106, figs 6, 7.

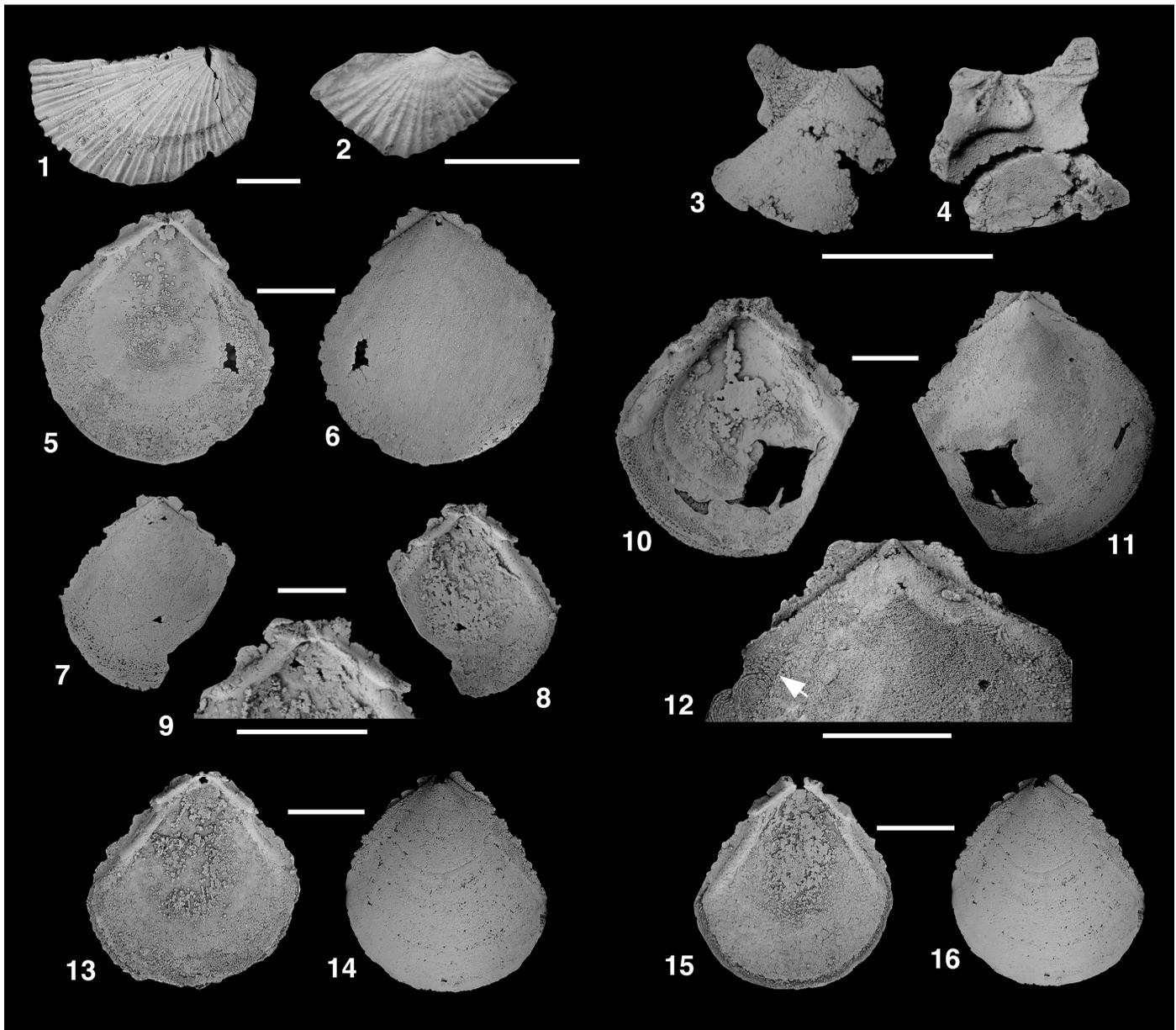
Monotis (Pacimonotis) subcircularis Gabb. Silberling et al., 1997: 5, pl. 1, figs 4–10, 13, 14, 17–21, pl. 2, figs 8–13, pl. 3, figs 1–3, ?18–19, pl. 4, figs 1–5; McRoberts, 2011: 645, figs 32.1–32.7.

Neotype and measurements.—USNM 139099, a LV (Westermann, 1962, pl. 115, fig. 6; H = 56 mm, L = 66 mm), selected by Westermann (1962: 782) based on topotype material, upper Norian, Taylorsville, California, USA.

Material examined.—Three incomplete right valves of which two are illustrated (UMIP 15667, UMIP 15668).

Description.—Right valves moderately large (maximum L = 34 mm, maximum H = 24 mm), obliquely oval with low valve convexity; beak extending above straight hinge margin and situated anterior (at about one fourth the shell length); ornamented with 14–20 strong primary ribs running relatively straight on posterior half of disk and on anterior sector curving anteriorly; separated by relatively broad and flat intercostal furrows; secondary ribs inserted between primaries at about 6–8 mm from beak and tertiaries beginning at approximately 12 mm; costae traversed by fine closely spaced commarginal striae. Anterior auricle small, somewhat flared dorsally, and weakly sloping in towards beak; the posterior auricle in UMIP 15668 (Text-fig. 23.2) is not completely preserved but likely extends some distance along hinge margin.

Occurrence.—Here reported from the upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound



Text-fig. 23. *Monotidae* and *Entoliidae*. 1, 2, *Monotis (Pacimonotis) subcircularis* Gabb, 1864; 1, UMIP 15667, exterior view of RV; 2, UMIP 15668, exterior view of RV fragment. 3–16, *Entolium alaskanum* n. sp. 3, 4, UMIP 15669, paratype, a RV; 3, exterior view; 4, interior view showing dentition. 5, 6, PRI 69642, paratype, a RV; 5, interior view; 6, exterior view. 7–9, PRI 69643, paratype, a RV; 7, interior view; 8, exterior view; 9, detail of cardinal area. 10–12, PRI 69644, holotype, a RV; 10 interior view; 11, exterior view; 12, expanded view of exterior showing differential silicification of outer and middle shell layers along posterior margin. 13, 14, PRI 69645, paratype, a LV; 13, interior view, 14, exterior view. 15, 16, PRI 69646, paratype, a LV; 15, interior view; 16, exterior view. Scale bars = 10 mm. All from USGS loc. M1912.

Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912). As noted by Silberling *et al.* (1997), this species is the most widespread *Monotis* in North America, with other significant occurrences from South America, northern Russia, Japan, Timor, and New Zealand (Tozer, 1980; McRoberts, 2011; Wotzlaw *et al.*, 2014). In all of these areas, it is restricted to the upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone).

Remarks.—Although the recovered specimens from Gill Harbor are all right valves and somewhat small for the species, they fall within the limits of variation in shape and ornament of the vast number of specimens assigned to this species (Westermann, 1962; Grant-Mackie & Silberling, 1990; McRoberts, 2011). It is distinguished from other species of *Monotis (Pacimonotis)* by its lower primary rib count and regular but delicate concentric ornament. This species often

co-occurs with or immediately below *Monotis* (*Entomonotis*) *ochotica* (Keyserling, 1848), but can be distinguished by its more numerous and straighter costae, possessing a greater height to length ratio, and a less inflated left valve.

Paleoecology.—As noted by previous authors (e.g., Grant-Mackie, 1980; Ando, 1987; McRoberts *et al.*, 2008) *Monotis* (*Pacimonotis*) possesses an anterior auricle with a narrow but deep byssal notch which suggests that it attached by a weak byssus to a semi-lithified (early cemented) sediment or shelly substrate or perhaps even other *Monotis* shells (Text-fig. 13.6). Given that large *Monotis* such as *M. subcircularis* are also inequivalved, with the left valve more inflated than the right (this is even more pronounced in other *Monotis* species), it is also likely that the animals were non-vertically oriented in life, with their left valve down and the commissure plane at some acute angle with respect to the substrate. The Gill Harbor occurrence of *M. (P.) subcircularis* in shallow water carbonate sediments is atypical for the species, which is more commonly known from deeper-water oxygen poor settings (see McRoberts, 2011).

Superfamily PECTINOIDEA Rafinesque, 1815

Family ENTOLIIDAE Teppner, 1922 [emend. Waller, 2006]

Remarks.—As noted by several authors (e.g., Allasinaz, 1972; Johnson, 1984; Damborenea, 2002; Waller, 2006), the Entoliidae suffers from the fact that it is largely represented by specimens which do not have adequately preserved characters with demonstrated value in species and supraspecific taxonomy, including shapes of the disks, exterior ornament, development of auricular scrolls, ligament and articulating structures, and skeletal microstructure. Through their treatment in the *Treatise* (Newell & Hertlein, 1969), the Entoliidae has been applied to generally smooth-shelled and weakly convex pectinoideans with relatively small, nearly equal triangular auricles projecting above the hinge line. With the exception of *Scythentolium* Allasinaz, 1972, Entoliidae lack a byssal notch and ctenolium in adult stages. Although a revision of this morphologically diverse and speciose family is beyond the scope of this present work, below is a brief discussion regarding suprageneric classification within the Entoliidae.

Recent years have seen the removal of several entoliid-form genera from the Entoliidae. The broad concept of the Entoliidae in the *Treatise* (Newell & Hertlein, 1969; see Newell & Boyd, 1995) included Paleozoic–Early Triassic *Pernopecten* Winchell, 1865 (type species *Aviculopecten limiformis* White & Whitfield, 1862). *Pernopecten* exhibits hinge crenulation and filusus structure of the inner surface of the outer calcite layer of the LV and is best considered distinct from other

Entoliidae (Allasinaz, 1972; Romanov, 1985; Waller, 2006). In his review of Triassic pectinoideans, Allasinaz (1972) erected several new ‘entoliids’ based on *Entolioides* for thin-shelled *Entolium*-like pectinoids which are inequivalved and possess outer ligament grooves and ridges (cardinal crura), resilifer teeth and sockets (pseudodenticles), basal auricular buttresses (auricular crura), lateral disk buttresses (marginal folds), commarginal ornament on both left and right valves, and radial ornament only on the left valve. Unlike *Entolioides*, *Filopecten* Allasinaz, 1972 was originally described as similar to *Entolium* in lacking outer ligament grooves and ridges, but possess a strong radial sculpture with filusus structure.

Waller (2006) recognized that several genera previously assigned to the Entoliidae have a distinct microstructure consisting of a thin columnar prismatic calcitic outer layer of the RV throughout ontogeny and thin non-prismatic calcite layer in the LV that exhibits filusus structure on its inner surface. Thus, Waller (2006) erected Entolioididae to include *Entolioides* Allasinaz, 1972, *Filopecten*, Allasinaz, 1972, *Scythentolium*, Allasinaz, 1972, *Calvaentolium* Romanov, 1985, and possibly *Kolymonectes* Milova & Polubotko in Bychkov *et al.*, 1972. Following Waller’s revision, the Entoliidae consists of three genus or subfamily groups: *Entolium* Meek, 1864 (type species *Pecten demissus* Quenstedt, 1858), *Palaeoentolium* Romanov, 1985 (type species *Pleuronectites discites* Schlotheim, 1820), and *Synclonema* Meek, 1864 (type species *Pecten rigida* Hall & Meek, 1854). *Palaeoentolium* is characterized by a byssal notch in early ontogeny, and an exterior surface that is generally smooth except for faint commarginal lirae/lamel-lae, but lacking radial ornamentation. *Entolium* differs from *Synclonema*, which lacks lateral disk buttresses, has asymmetrical auricles (with posterior one shorter) and a byssal notch (through adulthood in some, juveniles in all), and lacks ctenolium. *Synclonema* generally possess a smooth exterior with antimarginal microstructure and faint commarginal lines and/or commarginal undulations/plicae.

Genus ENTOLIUM Meek, 1865

Bupecten Guo, 1988: 118.

Type species.—*Entolium demissum* Meek, 1865 [= *Pecten demissus* Quenstedt, 1858; = *Pecten disciformis* Schübler in Zieten, 1833], by original designation, Middle Jurassic (Aalenian), Germany.

Remarks.—As discussed under the family remarks above, *Entolium* is here restricted to generally smooth shelled entoliids lacking a byssal notch throughout ontogeny and with well developed auricular and lateral buttresses. Following Fang *et al.* (2009), *Bupecten* Guo, 1988 is considered a junior syn-

onym of *Entolium*. *Bupecten* was originally discriminated from *Entolium* by the presence of scrolled auricles that were interpreted to be of generic significance; however, such auricles are typical of *Entolium* (including *E. alaskanum* n. sp.), albeit rarely preserved. Following the revisions by Waller (2006) and summarized by Ros-Franch *et al.* (2014), *Entolium* is cosmopolitan with a temporal range of Early Triassic through the Upper Cretaceous.

Entolium alaskanum n. sp.

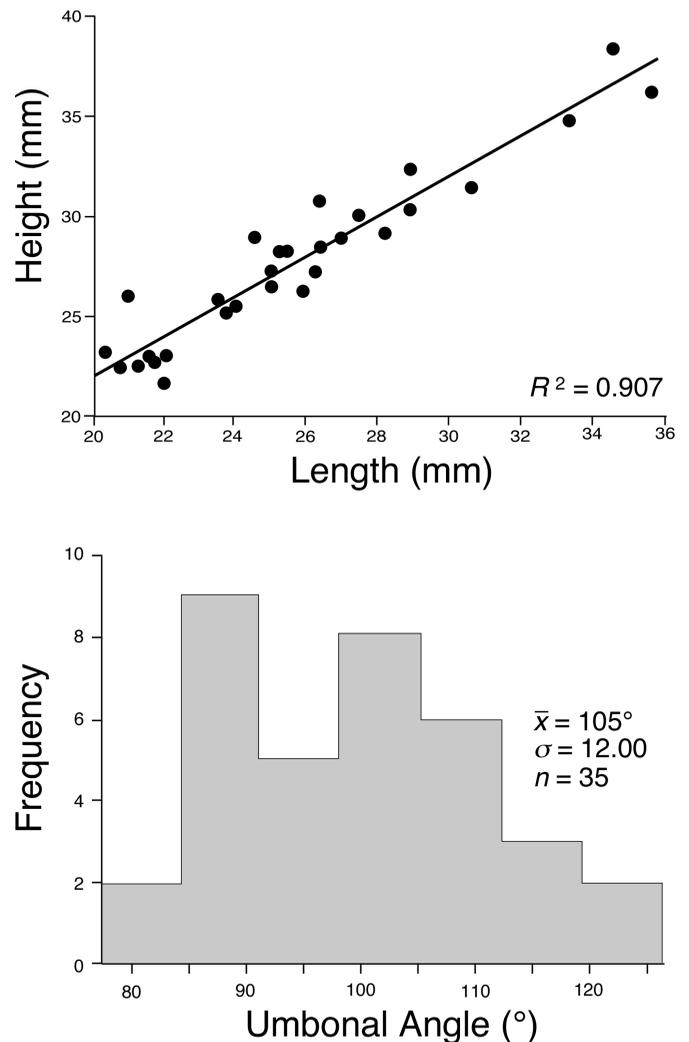
Text-figs 23.3–23.16, 25

Types and measurements.—Holotype, PRI 69644 (Text-figs 23.10–23.12), a RV; H = 38.4 mm, L = 34.4 mm, umbonal angle = 121°. Paratypes include three right valves (PRI 69642, Text-figs 23.5, 23.6; PRI 69643, Text-figs 23.7–23.9; UMIP 15669, Text-figs 23.3, 23.4) and two left valves (PRI 69645, Text-figs 23.13–23.14; PRI 69646, Text-figs 23.15–23.16). Measurements graphically summarized in Text-fig. 24. All from USGS loc. M1912, upper Norian, Hound Island Volcanics Kuiu Island, Alaska.

Other material examined.—In addition to the types, the collection consists of 79 largely fragmented valves, of which approximately 34 can be determined as right valves and 11 as left valves.

Diagnosis.—*Entolium* of moderate size, slightly higher than long, and relatively narrow umbonal angle of around 100°, and with posterior margin slightly straighter than anterior margin; with posterior (and possibly anterior) auricle of RV scrolled; resilifer prominent, triangular, with moderately strong resilifer teeth and longitudinal outer ligament groove in RV; prominent auricular buttresses distally thickening; lateral disk buttresses prominent but subequal in length; aragonite line well inside of valve margin.

Description.—Valves, moderate size (maximum L = 34.4 mm, maximum H = 38.4 mm), orbicular; height about equal length or slightly greater (H:L = 0.9–1.2, mean = 1.1), and very low and nearly equal convexity in both valves (maximum disk inflation of the best RV = 2.9 mm); umbonal angle variable but generally broad (80°–121°, mean = 100.4°) and slightly increasing in ontogeny; auricles moderate size, raised above beak with moderately elevated scroll on the posterior auricle of RV and possibly also on the anterior auricle of RV; without apparent byssal notch throughout ontogeny; both posterior and anterior auricles joining disk flanks at an obtuse angle; disk margins extending from base of auricles to point of maximum disk length, slightly curved on anterior side and nearly straight on posterior side; ventral margin uniformly rounded;



Text-fig. 24. Measurements and descriptive statistics of *Entolium alaskanum* n. sp. Upper plot, least-squares regression of length versus height; lower plot, frequency histogram of umbonal angle.

valve exterior smooth with very fine commarginal ornament; hinge area with prominent triangular resilifer, with moderately strong resilifer teeth and longitudinal outer ligament groove in RV, corresponding resilifer teeth sockets and outer ligament ridge presumably on LV, but not preserved; valve interior with well developed basal auricular buttresses (= auricular crura in older terminology) sloping ventrally at an angle similar to umbonal angle, distally thickened in ventral direction and in some specimens terminating in a rounded knob-like protrusion; lateral disk buttresses prominent, commencing inside of basal auricular buttresses at their mid length and extending ventrally at a relatively steep angle to valve margin with the posterior one slightly longer than anterior one and with both terminating at height equal to maximum disk length; pallial line and posterior adductor scar not preserved; inner “aragonite” line relatively deeply situated from valve margin.

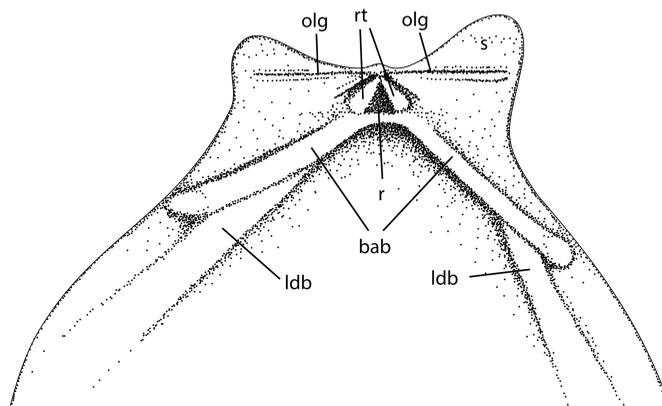
Etymology.—Trivial name, *alaskanum*, for the state of Alaska.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—The style of preservation, although typical for Triassic and Jurassic entoliids and entolioids, is such that most of the auricles, resiliifer, and lateral margins are incompletely silicified thus making determination of left from right valves difficult and characterization of the skeletal mineralogy and microstructure of left and right valves not possible. In spite of the scarcity of information from well-preserved auricles and musculature, differentiation between left and right valves is possible by subequal lengths of the lateral disk buttress (posterior being slightly longer than anterior) and curvature of lateral margins (anterior margins are more convex than posterior margins). Subequal lateral disk buttress lengths are present across multiple “entoliid” genus-group taxa as in *Entolium inornatum* (Stoppani) of Allasinaz (1972, pl. 36, fig. 5b), *Pleuronectites balatonicus* (Bittner) of Zardini (1981, pl. 18, fig. 16), and *Crenamussium concentricum* Newton in Newton *et al.* (1987, fig. 40.10), so it is difficult to attribute these features as determinant of species-level taxa.

Placement of these specimens in *Entolium* is based on the lack of radial ornament of the LV that would be present in *Entolioides*. Additional support for placement in *Entolium* can be found in the relative strength of auricular and lateral disk buttresses which are weak or absent in the Entoliidae subfamily Synclonematinae Waller, 1978 and the absence of byssal notch throughout ontogeny as in the Palaeoentoliinae Romanov, 1985 (see Waller, 2006). In spite of the lack of information of the LV auricles that are not preserved, the auricular scrolling evident in the one well preserved right valve (UMIP 15669, Text-figs 23.3, 23.4), and schematically represented in Text-fig. 25, details of the dentition including outer ligament articulation, basal auricular buttresses, and lateral disk buttresses are here considered sufficient to characterize the specimens as representing a new species.

Several specimens of North American entoliids can be compared to *Entolium alaskanum*. Smith (1927: 122) described *Pecten (Entolium) yukonensis* from the Carnian (or perhaps early Norian based on *Halobia* species from presumably the same locality studied by the author) from along the banks of the Yukon River near Nation, Alaska. Known from a single left valve (Smith, 1927, pl. 101, figs 9, 10), *P. (E.) yukonensis* exhibits a greater umbonal angle (~140° as compared to ~100° for *E. alaskanum*) and also is described by Smith as exhibiting a fine radial ornament which would suggest that it is a left valve and belongs to *Entolioides*. *Pecten (Entolium) ceruleus* Smith (1927: 121, pl. 95, fig. 13) from the upper



Text-fig. 25. Illustration of internal RV features of *Entolium alaskanum* n. sp. Abbreviations: r = resiliifer, rt=resiliifer teeth, bab = basal auricular buttresses, olg = outer ligament groove, s = auricle scroll, ldb = lateral disk buttresses.

Carnian of the Wallow terrane, northeast Oregon, although a poorly preserved internal mold lacking details of dentition and auricles, shows an extended pallial line and evidence of subequal lateral disk buttresses. Other North American entoliids such as *Pecten (Entolium) pittensis* Smith (1927: 121, pl. 7, fig. 5) possess commarginal rugae and are more similar to Jurassic and Cretaceous *E. orbiculare* (J. Sowerby, 1817) and *E. concentricum* (Koch & Dunker, 1837).

Entolium alaskanum may be compared to several entoliids from northeastern Russia. Kiparisova (1947: 112, pl. 22, figs 1–5) erected *Pecten (Entolium) kolymaense* [see also earlier illustrations of the same specimens as “*Entolium (Synclonema)* sp., nov. inden.” (Kiparisova, 1936: 105, pl. 5, figs 4–7) and “*Pecten (Entolium)* sp. nov. inden” (Kiparisova, 1938: 32, pl. 7, figs 9–12)] for what appears to represent at least two distinct taxa: those with a radial ornament and relatively narrow umbonal angle (e.g., Kiparisova *et al.*, 1966, pl. 15, figs 4–8) and those lacking discernable radial ornament and a broader umbonal angle (e.g., Kiparisova *et al.*, 1966, pl. 15, figs 9–15). While the former morphotype may belong to *Entolioides*, the latter are most similar to *Entolium alaskanum* but can be differentiated from the Gill Harbor species by having weaker auricular and lateral disk buttresses and relatively smaller auricles. Milova (1976) illustrated additional examples of *Entolium kolymaense kolymaense* from Priokhotye Russia that were later suggested by Waller (2006) as the oldest possible representatives of the Entoliinae. The specimens in Milova (1976, pl. 6, figs 2, 3) are better preserved than the original types and have similar subequal lateral disk buttresses as *E. alaskanum*, but have a broader umbonal angle and somewhat less elevated scrolled auricles of the RV than the Gill Harbor species. Additionally, Milova (1976: 56, pl. 6, figs 4, 5, pl. 7, figs 1, 2) described and illustrated a new subspecies, *Entolium kolymaense pachyfibrosum*, from the same locality with distinct antimarginal fibrous structure on the outer surface of

the middle (calcitic?) shell layer of left valves. Although other characters between the two subspecies are similar, it remains unclear if this fibrous structure is a result of enhanced preservation of *E. kolymaense pachyfibrosum* specimens or occurs in other *E. kolymaense kolymaense*.

Entolium alaskanum can also be compared to several west-Tethyan Carnian species. Among these, *E. alaskanum* is most similar to *Entolium hallense* (Wöhrmann, 1889), which was originally described from several Carnian localities in the Northern Calcareous Alps (Bavaria, Germany and northern Tirol, Austria) and is also relatively common from the Carnian Raibl and Cassian formations of northern Italy and Austria (e.g., Wöhrmann, 1889, pl. 6, figs 12, 13; Allasinaz, 1972, pl. 35, fig. 10, pl. 36, figs 1–4; Zardini, 1981, pl. 18, fig. 17). Although both species have fairly broad and somewhat similar range in umbonal angles (105°–115° for *E. hallense*) and disk outlines, *E. hallense* differs from *E. alaskanum* in having strong lateral disk buttresses, which ventrally terminate with a distinctive node. Similar nodes on the termini of lateral disk buttresses are also known from several other west-Tethyan species such as the Ladinian *Entolium inornatum* (Stoppani, 1858), but are not observed in *E. alaskanum*.

Another fairly common Upper Triassic “entoliid” is *Pecten* (*Syncyclonema*) *quotidianum* Healey, 1908, known from multiple localities from the central and eastern Tethys. It was first described from the Rhaetian of Napeng, Myanmar (Healey, 1908, pl. 7, figs 4–11) and subsequently as a species of *Entolium* from Sumatra (Krumbeck, 1914, pl. 15, figs 16, 17), Vietnam (Vu Khuc, 1991, pl. 23, figs 1–3), China (Ma *et al.*, 1976, pl. 29, figs 36–38), and possibly Iran (Hautmann 2001b, pl. 11, fig. 2). Given that specimens of *Pecten* (*Syncyclonema*) *quotidianum*, best illustrated by the type collection, do indeed possess strong lateral disk buttresses and have relatively equal auricles, they likely do not belong to *Syncyclonema*. Although *Pecten* (*Syncyclonema*) *quotidianum* superficially resembles *E. alaskanum* in general outline and umbonal angle, well-preserved examples of the east Tethyan species possess radial ornamentation and what appears to be filusus structure with the development of small tubercles (e.g., Healey, 1908, pl. 7, figs 11a, 11b), suggesting it does not belong in *Entolium*.

A final comparison can be made between *Entolium alaskanum* and one or more species groups of entoliids assigned to *E. demissum* (Phillips, 1829), *E. lunare* (Roemer, 1839), and *E. hehli* (d’Orbigny, 1850), which are known from numerous Hettangian localities in Alpine and northwest Europe and South America (see, for example, Staesche, 1926; Johnson, 1984; Damborenea, 2002). Although similar in disk shape and umbonal angles, these largely Jurassic forms lack (or have very poorly developed) auricular buttresses and, at least in juveniles of *E. lunare*, may possess a byssal notch (Johnson, 1984; Damborenea, 2002). The Triassic examples attribut-

ed to this group (e.g., *Pecten hehli* d’Orbigny of Stoppani, 1860–65, pl. 36, fig. 7 and *E. hehli* (d’Orbigny) of Allasinaz, 1972, pl. 27, fig. 1) exhibit a slightly narrower umbonal angle than found in *E. alaskanum*, but are often too poorly preserved or are only represented by valve exteriors, making meaningful comparisons difficult.

Paleoecology.—The moderate size, low convexity, and discoidal form, together with the absence of byssal notch throughout ontogeny, suggests a reclining free living habit (Text-fig. 13.7). Given the equivalved convexity and ornamentation, it is unknown if the animals had a preference for reclining with the RV or LV down. Although the size and position of PA remain unknown for this species, an umbonal angle of up to 120° that increased during ontogeny suggests that it may have been able to swim for short distances by clapping its valves.

Family **PROPEAMUSSIIDAE** Abbott, 1954
Genus **FILAMUSSIUM** Waller, 2006

Type species.—*Pecten schafhaeulti* Winkler, 1859 [= *Pecten velatus* Schafhäutl, 1852, non *Pecten velatus* Goldfuss, 1833], by original designation, Upper Triassic (Rhaetian), Bavaria, Germany.

Remarks.—Waller (2006) erected this genus—designating *Pecten schafhaeulti* Winkler, 1859 from the Kössen Formation, southern Germany as the type species—for propeamussiids exhibiting a filusus structure on the inner surface of the outer calcite layer of the left valve. Although the filusus structure of the LV is known among other genera (e.g., *Filopecten* Allasinaz, 1972, *Entolioides*, Allasinaz, 1972, and *Indopecten* Douglas, 1929), *Filamussium schafhaeulti* is characterized by a triangular resilifer which is bordered laterally by rather well-developed resilifer teeth and sockets (as in *Entolioides*) and internal radial ribs (buttresses) terminating well inside of the ventral margin. It is interesting to note that internal radial ribs characteristic of *Filamussium* are also known in *Indopecten*, suggesting a close phylogenetic relationship between the two genera. *Indopecten*, however, are largely inequivalved, with the right valve more convex than the left, and with a primary radial sculpture that approaches complete folding of the shell (plicae), with tubercles (e.g., Douglas, 1929, Hudson & Jefferies, 1961; Hautmann, 2001b) rather than costae as in *Filamussium*. In addition to the type species, Waller (2006) recognized two additional species as belonging to *Filamussium*: *Pecten* (*Variamussium*) *klushaensis* Lees, 1934, and *P. (V.) yukonensis* Lees, 1934, both from the upper Norian of Yukon, Canada which are more completely discussed in the species remarks below.

Filamussium walleri n. sp.

Text-figs 26.1–26.14

“*Variamussium*” *yukonensis* Lees. Tozer, 1963, pl. 12, figs 2, 3.
Non *Pecten* (*Variamussium*) *yukonensis* Lees, 1934: 38, pl. 3,
fig. 3

Types and measurements.—Holotype, UMIP 15670 (Text-figs 26.1–26.4), a nearly complete silicified RV; L = 49.9 mm, H = 51.1 mm, W = 5.5 mm, umbonal angle = 107°. Paratypes: UMIP 15673 (Text-figs 26.8, 26.9), incomplete RV; UMIP 15671 (Text-figs 26.5, 26.6), a LV; UMIP 15675 (Text-figs 26.12, 26.13), a LV; UMIP 15672 (Text-fig. 26.7), a LV; UMIP 15676 (Text-fig. 26.14), small fragment of LV; UMIP 15674 (Text-figs 26.10, 26.11), an incomplete RV. All from USGS loc. M1912, Kuiu Island, Alaska, from upper Norian, Hound Island Volcanics.

Other material examined.—In addition to the types, the collection consists of numerous smaller silicified fragments possessing the internal ribs. Examination of Tozer’s (1963) illustrated specimens of “*Variamussium*” *yukonensis* Lees (GSC14250 and GSC14251) also contributed to the description and diagnosis.

Diagnosis.—*Filamussium* of large size; with well developed resilifer teeth and sockets; lacking basal auricular buttresses, with subdued lateral disk buttresses, and prominent slat-like internal ribs (buttresses) extending nearly to valve margin and ventrally terminating in knob-like projections; external surface of outer shell layer of left valve with several orders of radial costae with small knob-like projections serially arranged on primary costae.

Description.—Valve moderately large for genus (maximum L = 49.9 mm, maximum H = 51.1 mm), circular in outline, slightly higher than long, equilateral; low valve convexity (maximum W = 5.5 mm); umbonal angle about 100°–120°, slightly increasing during ontogeny creating a slight outward concavity of disk flanks; auricles partially preserved, small, triangular, well separated from disk; dorsal margin of RV auricles fractured along outer ligament groove but likely extending above beak, posterior auricle meets disk at an obtuse angle (140°), anterior auricle of RV meeting disk at 90° forming a byssal notch; LV auricles subequal, flattened, sharply offset from disk, and separated from anterior and posterior portions of disk by steeply folded flanks forming nearly a right angle with the flattened auricles, which are approximately parallel to the commissural plane; LV anterior auricle joining disk at ~ 90° with shallow byssal sinus, posterior auricle obtusely joining disk margin at ~ 140°; apparently lacking ctenolium; inner surface of LV auricles with three radial ridges positioned

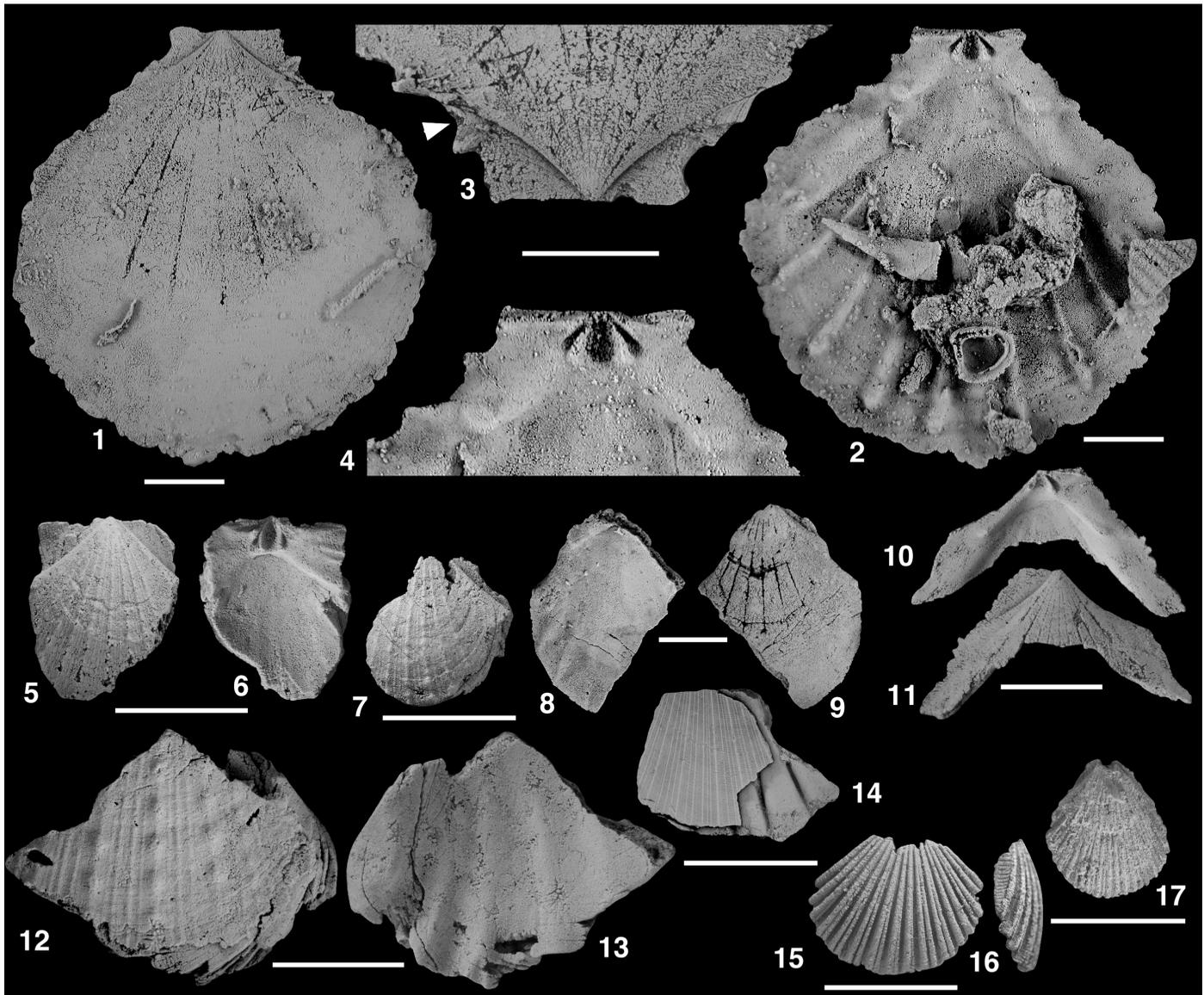
below hinge and lateral to resilifer dentition and extending to anterior auricular margins; external ornament of outer shell layer of LV with nine primary rounded radial ribs (costae) separated by broad intercostal spaces in which three or more narrow flat-topped secondary ribs of low relief are inserted; primary costae in central posterior parts of disk with small regularly-spaced tubercles down their length; outer surface of inner shell layer with narrow radial grooves extending from beak to about one half to one third the distance to the ventral margin and corresponding to internal radial ribs and lateral disk buttresses; hinge of RV relatively short (maximum hinge L = 17 mm), about one-third the maximum disk length, possessing medial triangular resilifer that is prominent and deep, inserted between two ridge-shaped resilifer teeth and possessing flanking sockets; hinge of LV with triangular resilifer bordered on each side with narrow ridges and flanking sockets to receive resilial teeth of RV; valve interior with seven radial round-topped ribs beginning about 10–15 mm from hinge, becoming more robust ventrally and terminating about 4–5 mm from ventral margin in knob-like processes; musculature unknown.

Etymology.—Trivial name, *walleri*, in honor of Thomas Waller who has made significant contributions to our understanding of the Bivalvia and particularly the Pectinoidea.

Occurrence.—Here reported from the upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912). As discussed below, also known from Rhaetian Sutton Member of the Parsons Bay Formation of Vancouver Island.

Remarks.—Although coarse silicification and dissolution may have obliterated any filus structure of the left valve, the extended internal radial ribs, nearly equilateral shell shape, radial and commarginal ornamentation of the LV exterior, and hinge structures suggest these specimens belong in *Filamussium*. These traits, along with the presence of tubercles on the primary costae of the LV are the basis for erecting a new species. Although the nodose primary costae with finer and secondary ribs are similar to certain specimens attributed, perhaps erroneously, to *Leptochondria* Bittner, 1891 by various authors (see for example Middle Triassic *Leptochondria minima* (Kiparisova, 1938) of Chen, 1976, pl. 29, figs 1–3; *Leptochondria monifera* (Bittner, 1895) of Zardini 1981, pl. 18, fig. 21; pl. 19, fig. 1-2), the presence of internal ribs, offset auricles, and entolioid-like hinges in the Keku specimens are different than in *Leptochondria*.

Filamussium walleri is most similar to *Pecten* (*Variamussium*) *yukonensis* Lees, 1934, originally described from the from the upper Norian of the Stikine terrane, Yukon, Canada (Lees,



Text-fig. 26. *Propeamussiidae* and *Pectinidae*. 1–14, *Filamussium walleri* n. sp. 1–4, UMIP 15670, holotype, a RV; 1, exterior view; 2, interior view; 3, detail of exterior cardinal region and auricles and byssal notch identified with arrow; 4, detail of cardinal area. 5, 6, UMIP 15671, a LV; 5, exterior view; 6, interior view showing details of hinge. 7, UMIP 15672, exterior view of LV. 8, 9, UMIP 15673, a ?LV fragment; 8, interior view; 9, exterior view. 10, 11, UMIP 15674, a LV fragment showing cardinal area and dentition; 10, interior view; 11, exterior view. 12, 13, UMIP 15675, a LV fragment; 12, exterior view showing surficial ornament; 13, interior view showing internal radial ribs. 14, UMIP 15676, a LV fragment showing exterior ornament of outer shell layer and radial internal ribs as internal mold. 15, 16, *Lyrioclamys* sp. indet., PRI 69647, a RV; 15, exterior view; 16, anterior view showing antimarginal sculpture. 17, pectinid gen. et sp. indet., PRI 69648, a ?LV exterior. Scale bars = 10 mm. All from USGS loc. M1912.

1934). Aside from being larger, *F. walleri* has a lower H:L ratio, a more reduced cardinal area, and has seven internal ribs rather than the nine reported from the Canadian species. Examination of the holotype, a LV (Lees, 1934, pl. 3, fig. 3, GSC 9625), clearly shows two orders of radial costae and, although not apparent in the published figure, also shows filusus structure. Although no right valves were illustrated, nor were any located in the GSC type collection, Lees (1934: 38) noted that the RV is smooth. Tozer (1963, pl. 12, figs 2, 3) subsequently illustrated a right and left valve attributed

to “*Variamussium*” *yukonensis* Lees from the Rhaetian Sutton Member of the Parsons Bay Formation of Vancouver Island, Canada. These specimens (GSC 14250, a RV and GSC 14251, a LV), in addition to exhibiting the filusus structure in the LV, also possess small regularly spaced tubercles along the crests of primary costae in the central part of the LV disk, which are not observed in Lees’ type specimens but are present in *F. walleri*. Hence, the Vancouver Island specimens are considered conspecific with *F. walleri* but not with Lees’ type specimens of *Pecten* (*Variamussium*) *yukonensis*.

Filamussium walleri can be compared to *Pecten* (*Variamussium*) *klushaensis* Lees, 1934. Although the type specimens of *Pecten* (*Variamussium*) *klushaensis* (Lees, 1934, pl. 3 figs 1, 2; GSC 9624, GSC 9624a) are poorly preserved and apparently lack the outer shell layer, they exhibit a narrow and more convex umbonal region than *Filamussium walleri*. Additionally, the Canadian species exhibits a longer hinge, with more strongly asymmetric auricles than *F. walleri*. Given the nature of preservation and small sample size of the Canadian species, the relationship between *P. (V.) yukonensis* and *P. (V.) klushaensis* is difficult to determine.

The present species can also be compared with the type, *Pecten schafhaeutli* Winkler, 1859, initially described from the Rhaetian Kössen Formation of the Bavarian Alps of Germany and subsequently reported from similar aged strata, under the generic names *Pecten*, *Variamussium*, and *Parvamussium* from elsewhere in the Northern Calcareous Alps of Austria, the Carpathians, Lombardian Alps of northern Italy, and more recently Iran (see Hautmann 2001b for a synonymy). Examination of the holotype of *Pecten schafhaeutli* Winkler (1859, pl. 1, fig. 4) located in the Bayerische Staatssammlung für Paläontologie und Historische Geologie Museum (Munich) reveals the specimen to be a poorly preserved exterior fragment of a presumably LV lacking details of the dorsal region, including auricles and dentition. Other illustrated specimens of *F. schafhaeutli* (e.g., Hautmann, 2001b, pl. 11, figs 4–6; Waller, 2006, figs 7a–c) differ from *F. walleri* in possessing fewer internal ribs and apparently lacking a byssal notch or sinus. Similarly, the internal rib count of *F. walleri* is less than specimens assigned to *Propeamussium* cf. *P. schafhaeutli* from the upper Norian of Sonora Mexico illustrated by McRoberts (1997, figs 3.4–3.6). None of the aforementioned examples of *F. schafhaeutli* possess the external ornament of tubercles along radial elements of the left valve.

Other Upper Triassic species assigned to *Propeamussium* or *Variamussium* such as *Pecten* (*Variamussium*) *margariticostatus* Diener (1908, pl. 18, figs 1–4) are likely not propeamussiids but are better placed in *Indopecten*. As mentioned under the genus remarks, *Indopecten* also possess filus structure on the LV and internal radial ribs and may be closely related to *Filamussium*.

Paleoecology.—The moderate size, low convexity, and discoidal form support a primarily reclining habit for adult *Filamussium walleri* (Text-fig. 13.5). The moderately small byssal notch also suggests that a byssus may have been functional during early growth stages but may have been obsolete later in ontogeny. An observed umbonal angle of 120° for *F. walleri* is well within the accepted range of known Recent pectinoideans that occasionally swim by clapping their valves (Stanley, 1970) and such a life habit seems likely. Although many extant propeamussiid species are restricted to deep-water (baythal and

abyssal depths), others, especially those thicker-shelled species which exhibit strongly ornamented right valves, can be found in a variety of shallow-water habitats (Damborenea, 1998). Jurassic propeamussiid species also exhibit ecological variety and are found in a variety of habitats ranging from coarse-grained high-energy biofacies to organic-rich oxygen-deficient black shale biofacies in which some species, for example the dwarfed *Propeamussium pumilium*, may also have had the ability to swim short distances during an adult phase (Johnson, 1984).

Family **PECTINIDAE** Rafinesque, 1815

Genus **LYRIOCHLAMYS** Sobetski, 1977

Type species.—*Pecten fissicosta* Etheridge, 1881, by original designation, Upper Cretaceous, Bedfordshire, England.

Lyrioclamys sp. indet.

Text-figs 26.15, 26.16

Material examined.—A single partial right valve, PRI 69647.

Description.—Incomplete RV small (single fragment with a length of 13.5 mm), with strong, densely packed, rounded, and slightly curved radial ribs of high relief; radial ribs observable on inner shell surface suggesting they are plicae, but it is more likely that a smooth inner shell layer is lost to diagenesis and the ribbing represents costae; with deep but narrow inter-rib furrows approximately one half the width of the ribs; ribs divide rather than intercalate; with very fine and closely spaced commarginal lirae across both tops of ribs and within inter-rib furrows; posterior flank with moderately strong and slightly curved antimarginal sculpture; cardinal area, muscle scars, auricles unknown.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Following the criteria of Waller (1991) and Waller & Marinovich (1992), the strong antimarginal sculpture of the posterior flank (Text-fig. 26.16), together with the bifurcating ribs of the RV (Text-fig. 26.15), this specimen can be confidently placed in *Lyrioclamys*. Although the anterior margin is not preserved, the antimarginal ornament is clearly positioned posterior along the disk flank with no indication of wrapping around to the inner valve surface (as in anachomata). The Gill Harbor specimen differs from other Upper Triassic pectiniids attributed to *Lyrioclamys*—including *Pecten otianus* McLearn, 1939 (Norian, British Columbia), *P. acuteauritus* Schaufhäutl, 1851 (Rhaetian, Germany) and

P. barvaricus Winkler, 1861 (Rhaetian, Germany)—in the strength and density of costae. Until more complete material which preserves skeletal hinge structure, musculature, and features of the left valve can be examined, species assignment is reserved.

Paleoecology.—Like other *Lyriochlamys* and related genera within the Chlamidae, *Lyriochlamys* sp. indet. is interpreted to be an epibyssate suspension feeder.

Pectinid gen. et sp. indet.
Text-fig. 26.17

Material examined.—A single partial ?LV, PRI 69648.

Description.—Shell small (preserved H = 9.9 mm, L = 8.9 mm), higher than long, weakly convex (W = 2.7 mm), with narrow umbonal angle (~ 70°); costate with 22 ribs (counted along ventral margin), ribs subangular in cross section and, although perhaps a diagenetic effect of coarse silicification, with crests somewhat nodose; ribs increase through intercalation; auricles incompletely preserved with only the portions immediately adjacent to valve flanks present, but too poorly silicified to determine presence of byssal notch or sinus; internal features including ligament, musculature unknown.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Given the lack of preservation of critical morphologic features of the auricles, resilifer, and coarse silicification of the specimen, assignment to any known genus or species is unwarranted. Given the general dimensions and costation pattern of the specimen, it most likely belongs to one of the several *Chlamys*-like genera such as *Granulochlamys* Allasinaz, 1972 or *Praechlamys* Allasinaz, 1972 and would therefore have possessed a byssal notch and subequal auricles typical of that group. The nature of the costae and overall shape distinguish it from other pectinoids from the Gill Harbor locality. Specifically, it differs from *Lyriochlamys* sp. indet. in its narrower umbonal angle and more densely packed and subdued radial ornamentation.

Paleoecology.—Assuming the presence of a byssal notch (see above), this specimen was likely epifaunal and byssally attached to firm substrates.

Superfamily **PLICATULOIDEA** Waller, 1978
Family **PLICATULIDAE** Watson, 1930
[emend. Hautmann, 2001a]

Remarks.—Plicatulids are represented by a number of genera that affix by their right valves and exhibit hinge elements (resilifer and resilial teeth and sockets) that shift to varying degrees downwards during ontogeny. In his diagnosis of the family, Hautmann (2001a) emended the Plicatulidae to include dextrally-cementing monomyrian bivalves which lack a byssal notch throughout ontogeny and have a fibrous resilifer that is structurally discontinuous between the two valves. At present, *Plicatula* Lamarck 1801, *Eoplicatula* Carter, 1990, *Pseudoplacunopsis* Bittner, 1895 and *Harpax* Parkinson, 1891 are recognized as belonging to the family. The latter three were originally proposed as subgenera of *Plicatula* (see below), but are here considered to be distinct and of generic rank. It should be further noted that plicatulids possess an outer shell layer of foliated calcite and inner shell layer of crossed lamellar aragonite (Carter 1990b; Hautmann, 2001a).

Carter (1990a: 223) erected *Eoplicatula* as a subgenus to accommodate *Plicatula*, whose LV resilifer lacked adjacent raised ridges and instead possessed small bourrets to laterally limit the resillium. Recognizing that several specimens in Bittner's type collection of *Plicatula imago* do indeed possess ligament support ridges and their presence or absence is variable among several other Triassic Plicatulidae, Hautmann (2001a) emended this genus to include the primary criterion of a submarginal resilifer. He further suggested limiting the importance given to the strength of the ligament supporting ridges of the LV. *Eoplicatula* differs from other Plicatulidae which exhibit a secondary horizontal ligament positioned dorsal to the hinge which may still be in touch with the primary resillium as in *Pseudoplacunopsis* Bittner, 1895 (type species *Plicatula (Pseudoplacunopsis) affixa* Bittner, 1895), or completely separated from the primary resillium as in *Plicatula* Lamarck, 1901 (type species *Spondylus plicatus* Linné, 1758). The *Eoplicatula* hinge is in many regards similar to that found in *Harpax* Parkinson, 1811 (type species *H. parkinsoni* Bronn, 1824), for which Damborenea (2002) has recently provided an emended diagnosis and lengthy discussion. As noted by Hautmann (2001a: 350), the resilial ridges in the LV of *Harpax* are even more robust than the actual crura as in *Eoplicatula*. As noted by both Hautmann (2001a: 350) and Damborenea (2002: 89), there may exist a functional relationship between the valve curvature and the position, and apparent inversion of the resilial teeth of *Harpax* when compared to those of *Eoplicatula*. An additional difference in the two ligament systems is that in *Harpax* the resilial teeth may possess striations or crenulations (e.g., Poulton, 1991; Damborenea, 2002). In *Eoplicatula*, the resilial ridges, teeth, and sockets may or may not have striae on the resilial crura of the left valve. In *Eoplicatula*, resilial striations or crenulations are not known from the type species, but have been described in the RV of *E. parvadehensis* Hautmann (2001a: 351). Additionally, *Harpax*

may also exhibit a secondary but feeble horizontal ligament on the surface dorsal to the primary triangular resilifer in the LV (e.g., *Harpax rapa* Bayle & Coquand, 1851 as described and illustrated by Damborenea, 2002, text-fig. 41b). This trait in *Harpax* is, however, not commonly present or preserved in many *Harpax* including the type species (see *H. spinosa* J. Sowerby of Damborenea, 2002, text-fig. 39h; see also Poulton, 1991, pl. 7, fig. 5).

The question of valve convexity in plicatulids is an important one and was recognized early on (Eudes-Deslongchamps, 1860). This issue was more recently considered by Lal (1996), who also brought to light the error in labeling LV and RV in the *Treatise* illustrations of *Plicatula* s.s. (Cox & Hertlein, 1969, figs C981a–d). While all Plicatulidae affix by their right valves, in *Plicatula* and *Eoplicatula* the lower RV is convex and upper LV is flat or slightly concave, whereas in both *Pseudoplacunopsis* and *Harpax*, the upper LV is convex and lower RV is planar or slightly concave. The inverse concavity among Carnian plicatulids from the Dolomites was the basis for Bittner's (1895) erection of *Pseudoplacunopsis*, yet Hautmann (2001a: 352) provided the caveat that valve convexity depends on the substrate surface to which the valves cement and is therefore not an important taxonomic character. While Hautmann's assessment of the significance of valve convexity may be valid for individuals with large attachment areas, many plicatulids exhibit very small attachment surfaces in the RV and develop through ontogeny relatively unimpeded and would therefore assume a genetically dictated growth program. The hypotheses by Lal (1996) that dextral cementation among plicatulids was not obligatory and that lower (cementing) valves, either left or right, are the more convex is not tenable given what is known about the unambiguous convexity and valve fixation within plicatuliid species and genera (as here construed).

The polarity of valve convexity among *Eoplicatula* is clear. Left valves of the type species, *Plicatula imago* (see Carter, 1990a, fig. 33) including the lectotype (Hautmann 2001a, pl. 3, fig. 4) are clearly planar to weakly concave. In *Harpax*, the reverse is true—the LV is significantly more convex than the RV. For example, convex left valves of Carnian-Norian *Plicatula hekiensis* Nakazawa, 1955 (e.g., Nakazawa, 1955, pl. 14, fig. 6; Tokuyama, 1960a, pl. 4, figs 6–9; Newton in Newton *et al.*, 1987, figs 36.1–36.11) possesses a narrow resilifer groove inserted between diverging ridges extending from the umbo ventrally into the body cavity and without a dorsal secondary ligament area.

A third area in which *Eoplicatula* and *Harpax* appear to differ is in the ornament. *Eoplicatula* are generally thicker-shelled and with strong costae bordering on plicae. Whereas in *Harpax*, the external ornament of the convex LV is typically squamose with a variable degree of low radial costae or consisting of a spinose surface.

Given this mosaic of traits shared among Triassic plicatulids, it is likely that there are close phylogenetic ties between *Eoplicatula* and *Harpax*. Although he briefly mentioned some phylogenetic relationship between these genera, Hautmann (2001a) omitted *Harpax* in his proposed phylogenetic series, with *Eoplicatula* derived from a *Persia*-like prospodylid ancestor followed by the closure of the submarginal ligament in *Pseudoplacunopsis*, which in turn gave rise to *Plicatula*. Stratigraphically, *Pseudoplacunopsis*, *Eoplicatula*, and *Harpax* are all first known from the Carnian. It would seem likely that *Harpax* was derived from *Eoplicatula* sometime in the early Carnian with the origination of the convex (free) LV and also crenulated resilifer teeth and the subsequent secondary dorsal ligament appearing soon after. Given this possibility, the evolutionary series of Hautmann (2001a) should be revised to accommodate the nearly simultaneous origin of all three plicatulid genera: *Harpax*, *Pseudoplacunopsis*, and *Eoplicatula*.

This expanded concept of both *Harpax* and *Eoplicatula* would predicate that species with a submarginal resilifer lacking a dorsal secondary ligament area in the LV and possessing smooth resilial dentition lacking crenulations are included within *Eoplicatula*. Those species that possess a feeble secondary ligament in the LV with denticulated/striated resilial crura and have a convex upper (left) valve are included within *Harpax*. Thus, the polarity of valve convexity is considered here to be of equal importance when compared to ligament systems in assigning species to *Eoplicatula* or *Harpax*.

HARPAX Parkinson, 1811 [emend. Damborenea, 2002]

Type species.—*Harpax parkinsoni* Bronn, 1824 (= *Plicatula spinosa* J. Sowerby, 1819), by subsequent designation (Bronn, 1824), Lower Jurassic, Great Britain.

Remarks.—Based primarily on Jurassic species, Damborenea (2002) thoroughly reviewed and emended *Harpax* to include plicatulids affixed by the less convex right valve. Her emended diagnosis further states that left valves have a shallow umbonal cavity with strong hinge teeth bordering a central ligament pit and with right valves with low crura adjacent to a ligament pit and a set of stronger teeth near the margin of the valve that are crenulated. These morphologic criteria are consistent with the preceding remarks under Family Plicatulidae as emended by Hautmann (2001a) and serve to discriminate between *Harpax*, *Eoplicatula*, and *Plicatula*. Hautmann (2001a) suggested that *Harpax* originated in the Jurassic, but Damborenea (2002) and more recently Ros-Franch *et al.* (2014) considered the oldest representatives of the genus to occur in the Norian. Inclusion of well-preserved forms from Arctic Canada (see below in remarks of *Harpax articulatum* n. sp.) into *Harpax* extends the range downward into the Carnian.

Harpax articulatum n. sp.

Text-figs 27.1–27.19, 29

Types and measurements.—Holotype, a LV, PRI 69649 (Text-figs 27.1–27.3); H = 25.0 mm, L = 20.8 mm. Paratypes: three LV (PRI 69652, Text-figs 27.10, 27.11; PRI 69650, Text-figs 27.4, 27.5; PRI 69653, Text-figs 27.12, 27.13) and four RV (PRI 69651, Text-figs 27.6–27.9; PRI 69655, Text-figs 27.16, 27.17; PRI 69654, Text-figs 27.14, 27.15; PRI 69656, Text-figs 27.18, 27.19). See Text-fig. 28 for graphical representation of summary statistics of measurements. All from USGS loc. M1912, Kuiu Island, Alaska from upper Norian, Hound Island Volcanics.

Other material examined.—In addition to the types, the collection consists of 34 LV and 76 RV in addition to numerous smaller fragments.

Diagnosis.—Medium-sized with strongly convex left (free) valve and planar to strongly concave right (attached) valve; umbo orthogyrate to weakly opisthogyrate; deep channel-like submarginal resilifer with strongly articulating resilial ridges and resilial sockets on LV and resilial teeth on RV; outer surface of anterior resilifer ridge of LV with faint crenulations; posterior adductor scar round, relatively high (above mid valve height) and posteriorly positioned, but well inside posterior margin; pallial line continuous, integripalliate, positioned some distance from valve margin and within leading edge of aragonite inner shell layer; valve exterior with weak radial costae, commarginal squamae and finer growth lines.

Description.—Valves moderate size for genus (maximum H = 23.3 mm, maximum L = 22.2 mm); shape variable, commonly teardrop-shaped but more rarely ovoid to posteriorly elongate-oval; beak of LV narrow, orthogyrate to weakly opisthogyrate; strongly inequivalved, LV moderately convex (maximum W = 7.3 mm) with greatest convexity mid valve height and becoming less convex in adult stages; RV smaller than LV, flat to moderately concave and in some specimens concavity quite extreme in juvenile growth stages corresponding to attachment area; attachment area of RV variable in size, most commonly quite small (< 2 mm) in adult free-living specimens to more rarely the entire RV in fully cementing forms; where not destroyed by coarse silicification, both LV and RV exterior surfaces ornamented with weak radial rounded costae separated by narrow and shallow furrows, commarginal imbricated squamae, and fine commarginal growth lines; LV hinge area concave, RV hinge area convex; resilifer submarginal, deeply concave groove expanding ventrally to form a very acute triangle, extending uninterrupted from tip of umbo into body cavity; LV resilifer channel bordered

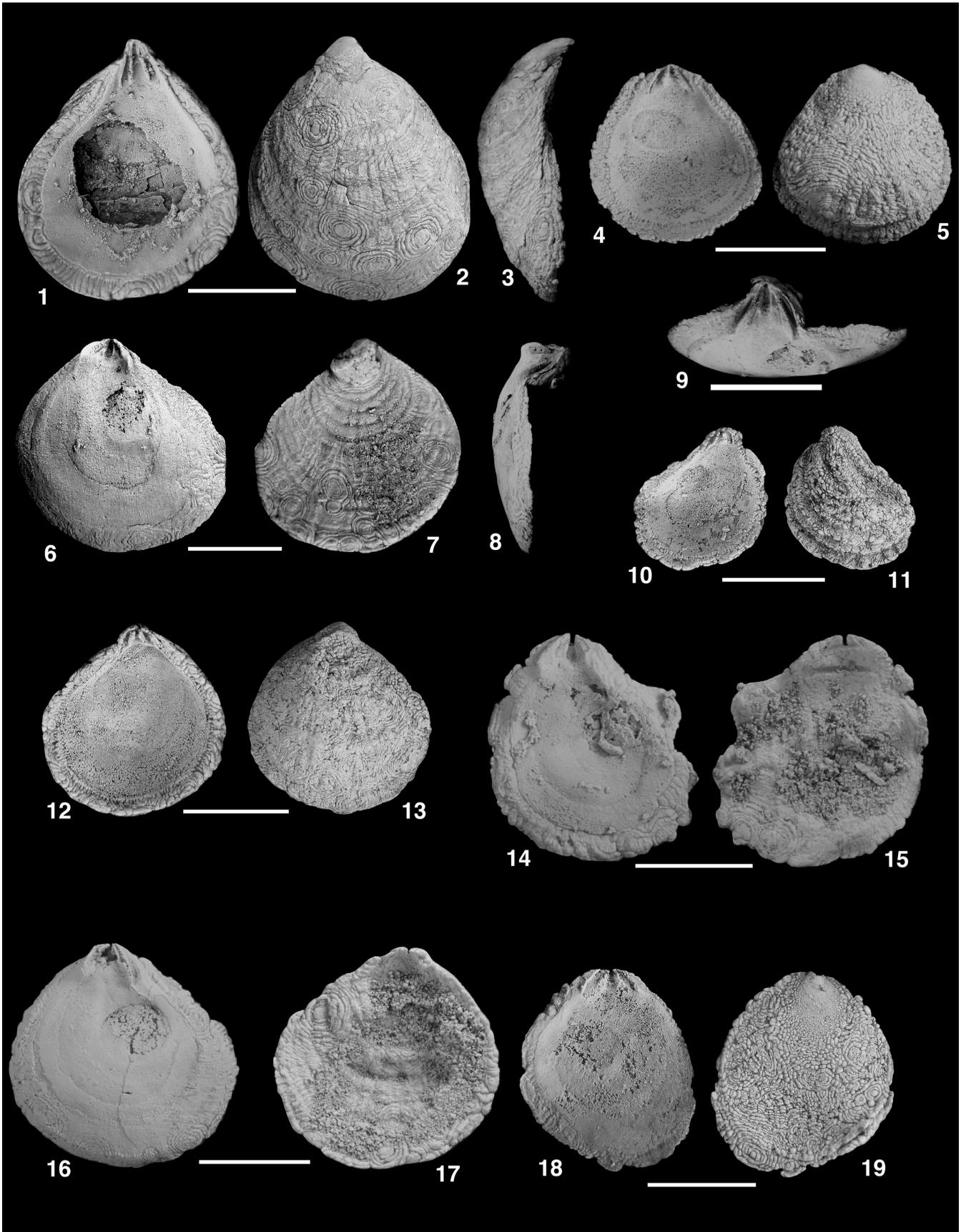
both posteriorly and anteriorly by prominent narrow raised ligament support ridges separating resilifer from the resilifer sockets which are also elongate; RV resilifer as in LV, deeply impressed, but with two subdued and small interior sockets to receive the ridges of the LV, with two prominent smooth elongate resilial teeth corresponding to resilial sockets of LV; posterior adductor scar prominent on both LV and RV, positioned near posterior margin at a distance about half the height of the valve, circular to ovate in shape, or variable size (maximum diameter = 9.2 mm); pallial line continuous, integripalliate, positioned some distance from aragonite line and valve margin; differential silicification clearly shows a discrete outer skeletal layer preserved as beekite rings which also is present along the interior margin well outside of the pallial line; an inner skeletal layer, now of finely crystalline silica but presumably representing original aragonitic mineralogy of inner skeletal layer, covers the interior valve surface to a position well outside of the pallial line and near valve margin; adductor myosctracum is usually not preserved through silica replacement.

Etymology.—Trivial name, *articulatum*, for the unique and strong articulating hinge elements.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Given the nature of the hinge with a submarginal resilifer, a convex left valve, and squamose ornament (Text-fig. 29), this species can be accommodated within Damborenea's (2002) expanded generic concept of *Harpax* and not within *Eoplicatula*, whose left valve is less convex than the right.

The new species is most similar to and likely closely related to *Plicatula perimbricata* Gabb, 1870, originally described from the Rhaetian Gabbs Formation of the New York Canyon area, Nevada. Additional specimens attributed to *Plicatula perimbricata* have been illustrated from the Rhaetian (or upper Norian) Modin Formation of the Shasta area of northern California (Sanborn, 1960, pl. 2, figs 26, 27) and the Rhaetian Sutton Member of the Parson Bay Formation of Vancouver Island (Tozer, 1963, pl. 12, figs 5–7) and have been included in faunal lists from several additional upper Norian localities including from the Alexander Terrane of Gravina Island (Berg, 1973; USGS locs M5095, M5909). Both *Harpax articulatum* and *Plicatula perimbricata* are similar in size and have convex left and concave right valves but differ in details of the hinge, shape, and external ornament. The holotype of *P. perimbricata* (Gabb, 1870, pl. 6, fig. 15a) is a LV that, unfortunately, does not preserve details of the valve interior or hinge/ligament system that still remain largely unknown. *Plicatula perimbricata*



cata is much narrower in the umbo than *H. articulatum* and exhibits more sharply defined radial and commarginal squamose external ornament. In spite of the lack of information on the hinge of *Plicatula perimbricata*, Squires & Saul (1997) suggested that, based on overall valve shape, narrow umbo, and ornament, this species may belong to *Harpax*. Like other *Harpax*, the LV of *P. perimbricata* is convex. A similar view is taken here based on newly studied *Plicatula perimbricata* collected by the author from the Rhaetian Nun Mine Member of the Gabbs Formation at Luning Draw at New York Canyon (see Laws, 1982; Taylor *et al.*, 1983) which have revealed a LV with a hinge broadly similar to that of *Harpax articulatum* but whose resilial elements are much less pronounced and do not appear to extend as deeply below the hinge into the umbonal cavity (Text-figs 30.5–30.7, PRI 69657, PRI 69658). The weaker hinge/resilial elements of *P. perimbricata* are also seen in the LV internal mold illustrated from Vancouver Island (Tozer, 1963, pl. 7, fig. 5).

In several regards, *Harpax articulatum* resembles *Plicatula hekiensis* Nakazawa, 1955 from the upper Carnian (and perhaps lower Norian) of Japan (Nakazawa, 1955; Tokuyama, 1960a) and the early Norian of northeastern Oregon (Newton *et al.*, 1987). The primary similarity is the *Eoplicatula* hinge, which possesses resilial ridges and resilial sockets in the LV and relatively strong resilial teeth (*crura*) that join at the dorsal apex of the umbo. Tokuyama (1960a: 36) noted that *P. hekiensis* from the Aso Formation of Japan possesses crenulations on the left anterior tooth (which has not been observed in either the type or undescribed collections from the Wallowa terrane). Crenulations in the resilial teeth and sockets have also been observed in undescribed collections of *Plicatula cf. P. hekiensis* Nakazawa from the Carnian Schei Point Formation of Queen Elizabeth Islands listed by Tozer (1961) and Tozer & Thorsteinsson (1964). These Arctic specimens (GSC 138684, 138685, Text-figs 30.1–30.4) exhibit the spiny exterior ornament typical of the Japanese *P. hekiensis* and younger Jurassic species within *Harpax* (e.g., *Harpax spinosa* Sowerby, 1819) and this species, like *P. perimbricata*, is here transferred to *Harpax*. It is important to note that a dorsal secondary horizontal ligament (in LV) is unknown from Japanese and Oregon specimens (as in *Harpax*), although as discussed above, may be ancestral to it.

Paleoecology.—*Harpax articulatum* attaches itself early in ontogeny to firm substrates by its planar to concave right (lower) valve (Text-fig. 13.3). In the Gill Harbor collection, it has been

found attached to *Plagiostoma scallanae* n. sp., *Cassianella cordillerana*, and even to other shells of *H. articulatum*. It is also possible that *H. articulatum*, after initially fixating by its right valve, may have become dislodged and flipped so that its left (convex) valve became the lower valve similar to the depiction of *Plicatula perimbricata* that Laws (1982) illustrated in a reclining life habit with left valves down. For *Plicatua hekiensis*, Newton in Newton *et al.* (1987) suggested a fixed right valve down on most firm substrates (e.g., spongiomorph colonies), but did not rule out the possibility of right valve-up cementing to overhanging surfaces in the reefal environment of the Martin Bridge Limestone from the Oregon locality. Given the taphonomic attributes of the Gill Harbor fauna and lack of any large framework or reefal textures in which large cavities would have existed, it is not possible to assign a cemented upward life habit to any of the *H. articulatum*.

Superfamily **PROSPONDYLOIDEA** Ptschelinceva, 1960
Family **PROSPONDYLIDAE** Ptschelinceva, 1960

?Prospondylidae gen. et sp. indet.
Text-figs 31.1–31.4, ?31.5

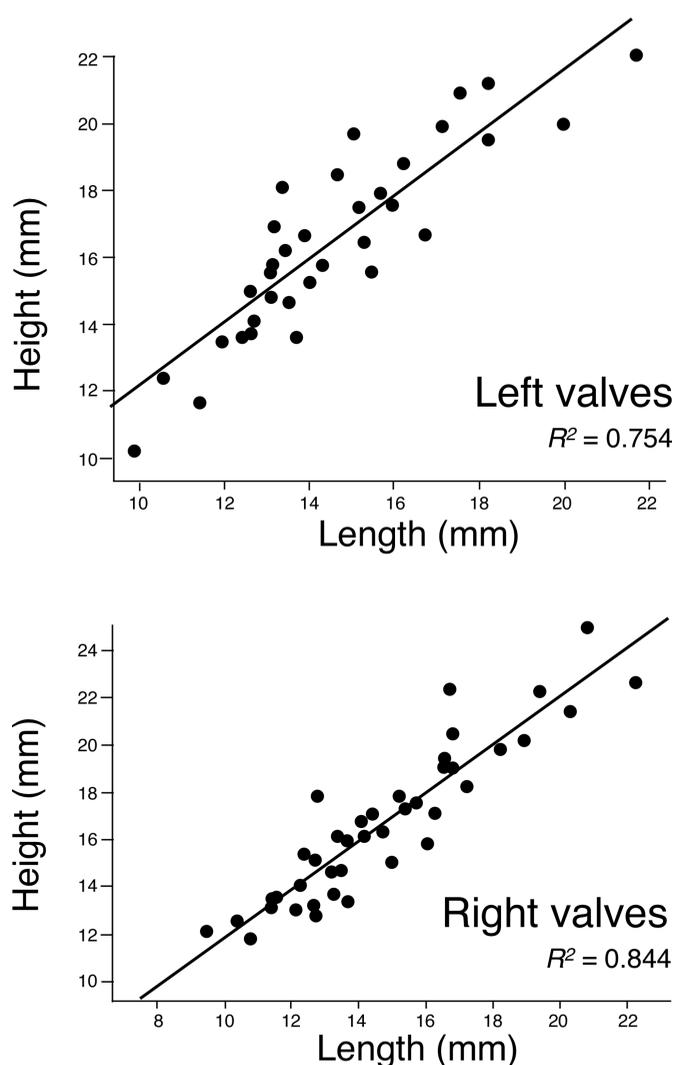
Material examined.—The collection consists of two presumably right valves (PRI 69659, UMIP 15677), and one possible LV (PRI 69660).

Description.—Valves large, strongly convex, with several broadly arched antimarginal plicae; antimarginal ribs variable and relatively coarse (rib wavelength varies from 10 to 19 mm measured at valve margin in the largest specimen) and of variable amplitude, achieving greatest height near valve margin; attachment area large (maximum diameter of attachment area = 22 mm); shell interior relatively smooth with what appears to be a preserved pallial line.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—This form is significantly different from other cementing bivalves from USGS loc. M1912. The likely presence of a pallial line suggests placement within the Prospondylidae rather than Ostreidae, which generally lack evidence of pallial muscle attachment (see Hautmann, 2001a). The very large rib wavelength (more than twice that of ?*Actinostreon* sp. A

Text-fig. 27 (at left). *Harpax articulatum* n. sp. 1–3, holotype, PRI 69649, a LV; 1, valve interior; 2, valve exterior; 3, posterior view. 4, 5, paratype, PRI 69650, a LV; 4, valve interior; 5, valve exterior. 6–9, paratype, PRI 69651, a RV; 6, valve interior; 7, valve exterior; 8, a posterior view; 9, detail of hinge. 10, 11, paratype, PRI 69652, a LV; 10, valve interior; 11, valve exterior. 12, 13, paratype, PRI 69653, a LV; 12, valve interior; 13, valve exterior. 14, 15, paratype, PRI 69654, a RV; 14, valve interior; 15, valve exterior. 16, 17, paratype, PRI 69655, a RV; 16, valve interior; 17, valve exterior. 18, 19, paratype, PRI 69656, a LV; 18, valve interior; 19, valve exterior. Scale bars = 10 mm. All from USGS loc. M1912.



Text-fig. 28. Scatter plot and least square regression of length versus height of *Harpax articulatum* n. sp. Upper plot, left valves; lower plot, right valves.

or *Noetingiconcha* sp. A) is unlike other known Triassic prospondylids and would suggest a new species. However, given the small sample size and lack of other diagnostic features of shell structure, ligament, and musculature, erection of a new species is not warranted.

Paleoecology.—Like other Prospendylidae, the Gill Harbor specimens are interpreted to be sessile and dorsally-cemented by their right valves (Text-fig. 13.2). Of particular note are the broadly folded antimarginal ribs and the steeply reaching margin situated well above the attachment area and substrate. The raised margin and broad corrugations would have elevated the commissure and feeding apparatus well above the substrate and also perhaps indicates an increased mantle surface area.

Genus *NOETINGICONCHA* Hautmann & Hagdorn, 2013

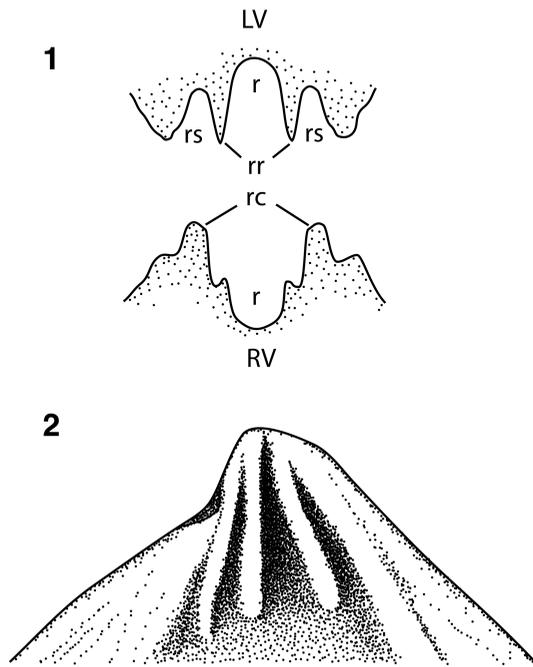
Type species.—*Noetingiconcha speculostreum* Hautmann & Hagdorn, 2013, by original designation, Middle Triassic (late Anisian), Westfalia, Germany.

Remarks.—The names *Enantiostreon* Bittner, 1901 and *Terquemia* Tate, 1867 have both commonly been applied to a variety of dextrally-cementing *Lopha*-like forms from the Middle and Late Triassic (e.g., Seilacher, 1954; Hautmann, 2001a, 2001b; Checa & Jiménez-Jiménez, 2003; Márquez-Aliaga *et al.*, 2005; Hautmann & Hagdorn, 2013). Hautmann & Hagdorn (2013) recommended assigning costate (rather than plicate), dextrally-cementing and non-byssate forms to *Terquemia* and avoiding the use of *Enantiostreon* given that internal shell characters of the type species (*Enantiostreon hungaricum* Bittner, 1901 from the Middle Triassic of Hungary) remain largely unknown. For plicate *Lopha*-like dextrally cementing forms, Hautmann & Hagdorn (2013) erected *Noetingiconcha*. *Noetingiconcha* differs from *Dentiterquemia* Hautmann & Golej, 2004, which exhibits a denticulated hinge structure, and from *Newaagia* Hertlein, 1952, which is characterized by pronounced squamose ribs. Given these criteria, likely dextral cementation, and plicate valves, the Gill Harbor specimens described below are best placed in *Noetingiconcha*. Until this present work, *Noetingiconcha* has been known only from a handful of Middle Triassic (late Anisian) species from the Muschelkalk of Germany, France, and Poland. The Gill Harbor specimens, if indeed are demonstrable *Noetingiconcha*, would significantly extend the temporal range upwards to near the Norian-Rhaetian boundary.

Noetingiconcha sp. A
Text-figs 31.6–31.13

Material examined.—The collection consists of five likely right valves (three on PRI 69661, UMIP 15678, UMIP 15679) and a single LV (PRI 69662).

Description.—Valves medium sized (maximum LV restored H = 30.0 mm, maximum RV H = 19.5 mm), of variable shape but generally circular to ovoid with moderately large attachment area on right valve and corresponding xenomorphic region on LV; left valve weakly convex to nearly flat. RV deeply convex in post-attachment shell, especially on anterior margin where growth is steeply inclined (nearly perpendicular) to the cemented substrate and much less so posteriorly where the growing margin is only slightly raised above substrate horizon (e.g., PRI 69662, Text-fig. 31.13) or, as in one specimen, even folded outward across a ledge in the substrate (e.g., UMIP 15679, Text-fig. 31.11); post-attachment shells with numerous (15–34) antimarginal plicae (rib wavelength = 1–3 mm), becoming more pronounced towards valve margin and result-



Text-fig. 29—Hinge features of *Harpax articulatum* n. sp. 1, cross-sectional area across both valves; 2, hinge structures of LV. Abbreviations: r = resiliifer, rc = resiliocardinal teeth, rr = resiliar ridges, rs = resiliar sockets.

ing in a zig-zag commissure; number of plicae appears to be a function of valve size; RV interior is relatively smooth, with one specimen (PRI 69661, Text-figs 31.6, 31.7) possessing a moderately large (diameter of long direction = 6.1 mm) ovoid posterior adductor scar positioned posteriorly and nearly abutting raised posterior and ventral margins. Ligament structure not observed.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Due to coarse replacement of skeleton, details of ligament structure are unknown. However, the position of the adductor scar of the RV (PRI 69661, Text-figs 31.7 and UMIP 15678, 31.9), together with an elevated posterior shell margin (Text-figs 31.8–31.11; see also Seilacher, 1954), confirms that these specimens were dextrally cemented and thus rightly belong in the Prospondyliidae.

Superficially, the *Lopha*-like specimens appear similar in size and shape to the several Middle Triassic specimens attributed by Seilacher (1954, figs 5a–d) to *Alectryonia* sp. and more recently by Hautmann & Hagdorn (2013, fig. 5) to *Umbostrea* sp. However, these Middle Triassic specimens attach by their left valves and rightly belong in the Ostreidae. The Gill Harbor specimens are also similar to those Newton (in Newton *et al.*, 1987) described as ?*Enantiostreon* sp. from

the lower Norian of the Wallowa terrane. However, the well-preserved Oregon specimens (complete with ligament and adductor and pallial scars) possess antimarginal ribs somewhat transitional between costae and plicate (*e.g.*, Newton in Newton *et al.*, 1987, figs 34.6, 34.7) rather than strong plicae as in the Gill Harbor specimens. Until more complete material which preserves skeletal hinge structure and musculature can be examined, species assignment is reserved.

Paleoecology.—This form is interpreted to be a dextrally-cemented suspension feeder (Text-fig. 13.1). As with the indeterminate ?prospodyliid described above, this species has well-developed marginal ribs, although the ribs of this *Noetingiconcha* are more numerous, shorter, and more tightly folded than that form, suggesting an increased benefit to marginal shell strength, but with its commissure closer to the substrate.

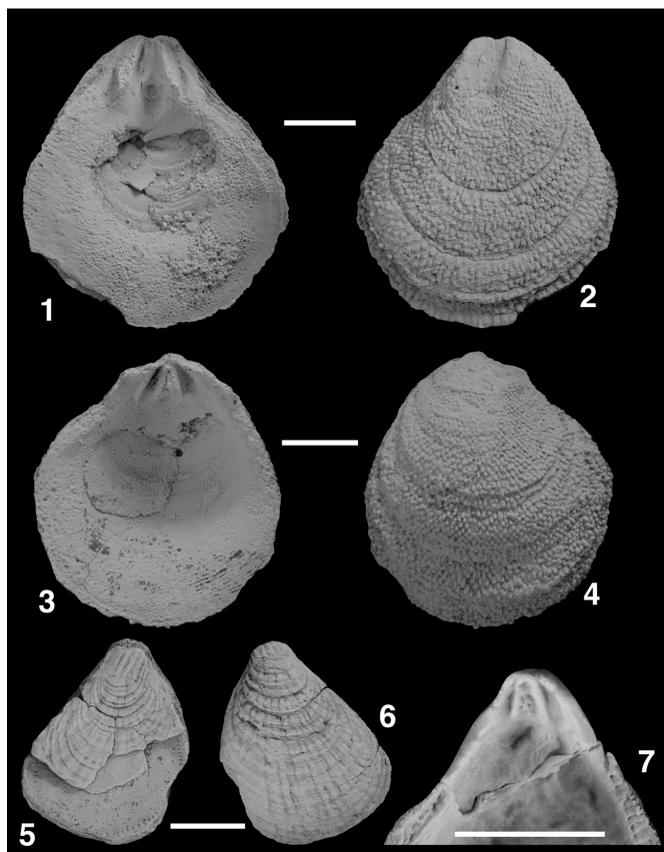
Infraclass **HETEROCONCHIA** Hertwig, 1895

Order **TRIGONIOIDA** Dall, 1889

Superfamily **TRIGONIOIDEA** Lamarck, 1819

Remarks.—A substantial body of literature exists regarding the morphology of trigonioidean bivalves and the importance of external traits (*e.g.*, surficial ornament) versus internal traits of the hinge (*e.g.*, dentition) with regard to familial and generic taxonomy and phylogeny. Cox (1952) was the first to clearly articulate the view that features of the trigonioidean hinge were more important than surficial ornament in resolving the phylogeny, and therefore taxonomy, of this diverse group, a taxonomic philosophy maintained in the *Treatise* (Cox 1969b, 1969c, 1969d). In their seminal paper, Newell & Boyd (1975) stressed that surficial ornament may be of equal importance and in certain cases take precedence over grades of dentition (schizodont, myophorian, and trigoniid) which, they hypothesized, had evolved independently. Although Cox's view was followed by some (*e.g.*, Poulton, 1979), many subsequent workers followed Newell and Boyd's approach and assigned trigonioidean genera to families based primarily upon consideration of the ornament (*e.g.*, Newton in Newton *et al.*, 1987; Cooper, 1991). Subsequently, most authorities (*e.g.*, Fleming, 1987; Johnston, 1993; Boyd & Newell, 1997) have reemphasized the importance of the hinge in classification.

Amongst the characters of the hinge that have played a role in discriminating the Myophoriidae from the Trigoniidae and Minetrigoniidae are tooth striation, presence of a hiatus between the two primary teeth of the RV, and the nature of the umbonal platform (Newell & Boyd, 1975; Fleming, 1987; Johnston, 1993; Boyd & Newell, 1997; Hautmann, 2003). Of particular interest is Fleming's (1987) monograph on Mesozoic trigonioideans from New Zealand in



Text-fig. 30. 1–4, *Harpax* cf. *H. hekiensis* (Nakazawa, 1955), Carnian Schei Point Formation, Prince Patrick Island, Arctic Canada. 1, 2, GSC 138684, a RV; 1, interior view; 2, exterior view. 3, 4, GSC 138685, a LV; 3, interior view; 4, exterior view. 5–7, *Harpax perimbricata* (Gabb, 1870), Rhaetian Gabb's Formation, New York Canyon, Nevada. 5, 6, PRI 69657, an articulated valve pair; 5, RV exterior; 6, LV exterior. 7, PRI 69658, LV interior showing hinge. Scale bars = 10 mm.

which he discussed the issue of trigoniid grade dentition in Triassic genera assigned to the Myophoriidae. Specifically, Fleming (1987) emphasized the importance of the hiatus between the two primary teeth in the RV observed in Paleozoic *Schizodus* De Verneuil & Murchison, 1844 and at least several Triassic *Neoschizodus* Giebel, 1855 (e.g., *N. thaynesianus* Newell & Boyd, 1975). Owing to the temporal gap in the presence of the hiatus (absent in most Mesozoic myophoriids but recurring in Middle Triassic–Recent trigoniids), Fleming (1987: 12) concluded that the hiatus was likely polyphyletic. The significance of the hiatus was further discussed by Johnston (1993: 107), who made additional important observations on the nature of the pedal retractor scar leading to his conclusion that both the hiatus and umbonal platform in myophoriids was not homologous to similar structures in Recent *Neotrignoia*.

The question of variability and homoplasy in tooth striation is also of considerable interest and has played a controversial role the taxonomy and phylogeny of trigonioideans. As reviewed in Boyd & Newell (1997), there exists a substantial

body of evidence demonstrating variability of the trait with respect to both strength and position on hinge teeth. The Lower Triassic species *Neoschizodus thaynesianus* is particularly illustrative in that several specimens from the type collection possess striated teeth, whereas other *N. thaynesianus* from the same sample do not. Similar variability is also known from Lower and Middle Triassic *Elegantinia* Waagen, 1906 (= *Lyriomyophoria* Kobayashi, 1954) and Middle and Upper Triassic *Gruenewaldia* Wöhrmann, 1899 (see for example Boyd & Newell, 1997; Hautmann, 2003), demonstrating the variable nature of this supposed family-level trait. Thus, Boyd & Newell (1997), influenced by the functional arguments made by Stanley (1978) and comments by Waller (cited in Boyd & Newell, 1997: 3), accepted the likelihood that dental striation may have arisen multiple times in the Trigonioidea. Boyd & Newell (1997) suggested that, at a minimum, Trigonioidea should possess striae on both flanks of tooth 2 and both flanks of tooth 3a.

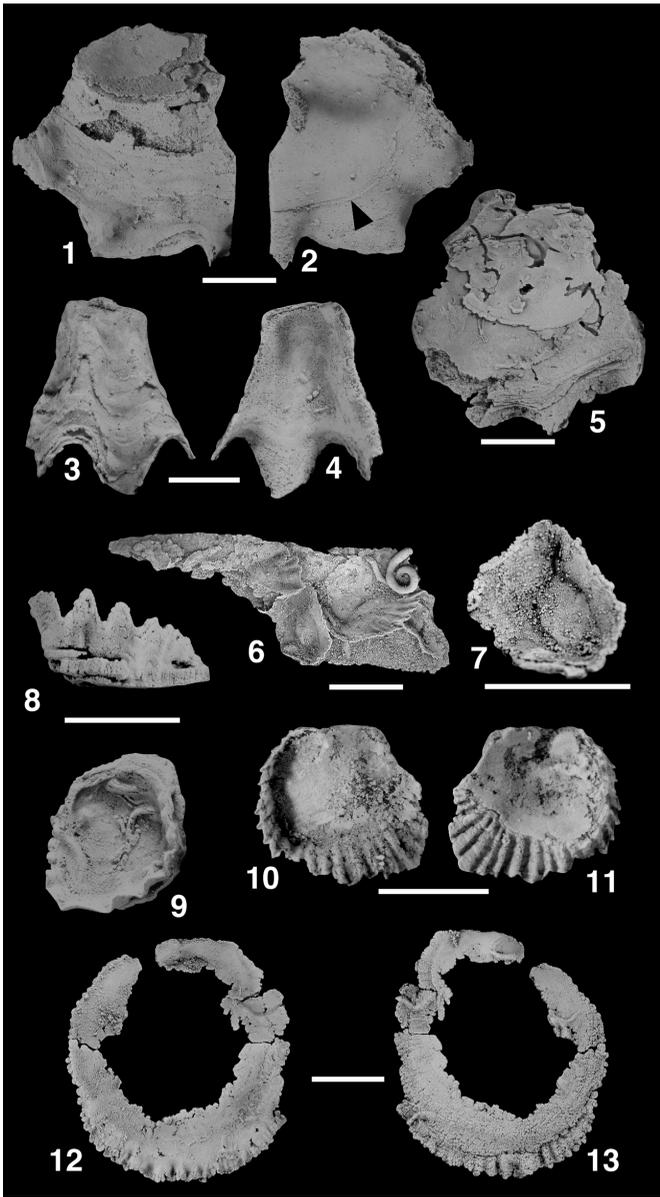
As treated here, the suprafamilial classification of early Mesozoic trigonioids generally follows that of Cox (1969b), Fleming (1987), and Carter *et al.* (2011) in placing the Myophoriidae, Minetrigoniidae, and Trigonioidea. This conservative view departs from the classification of Cooper (1991), who elevated Myophoriidae to superfamily rank to include Schizodidae (including Eoschizodidae), Myophoriidae, Pachycardiidae, and Minetrigoniidae (including Costatoriidae). According to Cooper (1991), the Trigonioidea includes several genera and family groups (e.g., *Gruenewaldia* Wöhrmann, 1889) that are now believed to be more closely aligned to the myophoriids (see Hautmann, 2003). Hautmann's (2001b) use of Myophorioidea and Trigonioidea is perhaps a more agreeable solution, but still makes it difficult to assign transitional forms (see for example both myophoriid sp. A and *Erugonia boydi* n. sp. described below, and various species attributed to *Neoschizodus* and *Gruenewaldia*). As these transitional taxa appear to occur in unrelated lineages, a polyphyletic origin of the trigoniid-grade dentition, as originally proposed by Newell & Boyd (1975), may yet show to have some validity and explanatory power.

Family MYOPHORIIDAE Bronn, 1849

Myophoriid sp. A

Text-fig. 32.1–32.8

Material examined.—In addition to the illustrated specimens—an incomplete RV (UMIP 15680, Text-figs 32.1–32.4) and two incomplete LVs (PRI 69663, Text-figs 32.5, 32.6; possibly UMIP 15681, Text-figs 32.7, 32.8)—there are two additional fragments of left valves that do not preserve any hinge elements.



Text-fig. 31. *Prospondylidae*. 1–5, *Prospondylidae* gen. et sp. indet. 1, 2, UMIP 15677, a RV; 1, valve exterior showing large attachment area; 2, interior view showing likely pallial line (identified with arrow). 3, 4, PRI 69659, a RV; 3, valve exterior; 4, interior view. 5, PRI 69660, a ?LV interior with potentially preserved inner shell layer and significant endozoan infestation. 6–13, *Noetingiconcha* sp. A. 6, PRI 69661, three encrusting RVs (along with serpulid encruster) on a large fragment of *Palaeopharus orchardi* n. sp. 7, enlarged view of one of the RVs of PRI 69661, showing PA pad. 8, 9, UMIP 15678, a RV; 8, posterior view; 9, interior view encrusted with serpulid. 10, 11, UMIP 15679, a RV; 10, valve exterior; 11, interior view. 12, 13, PRI 69662, a LV; 12, interior view; 13, exterior view. Scale bars = 10 mm. All from USGS loc. M1912.

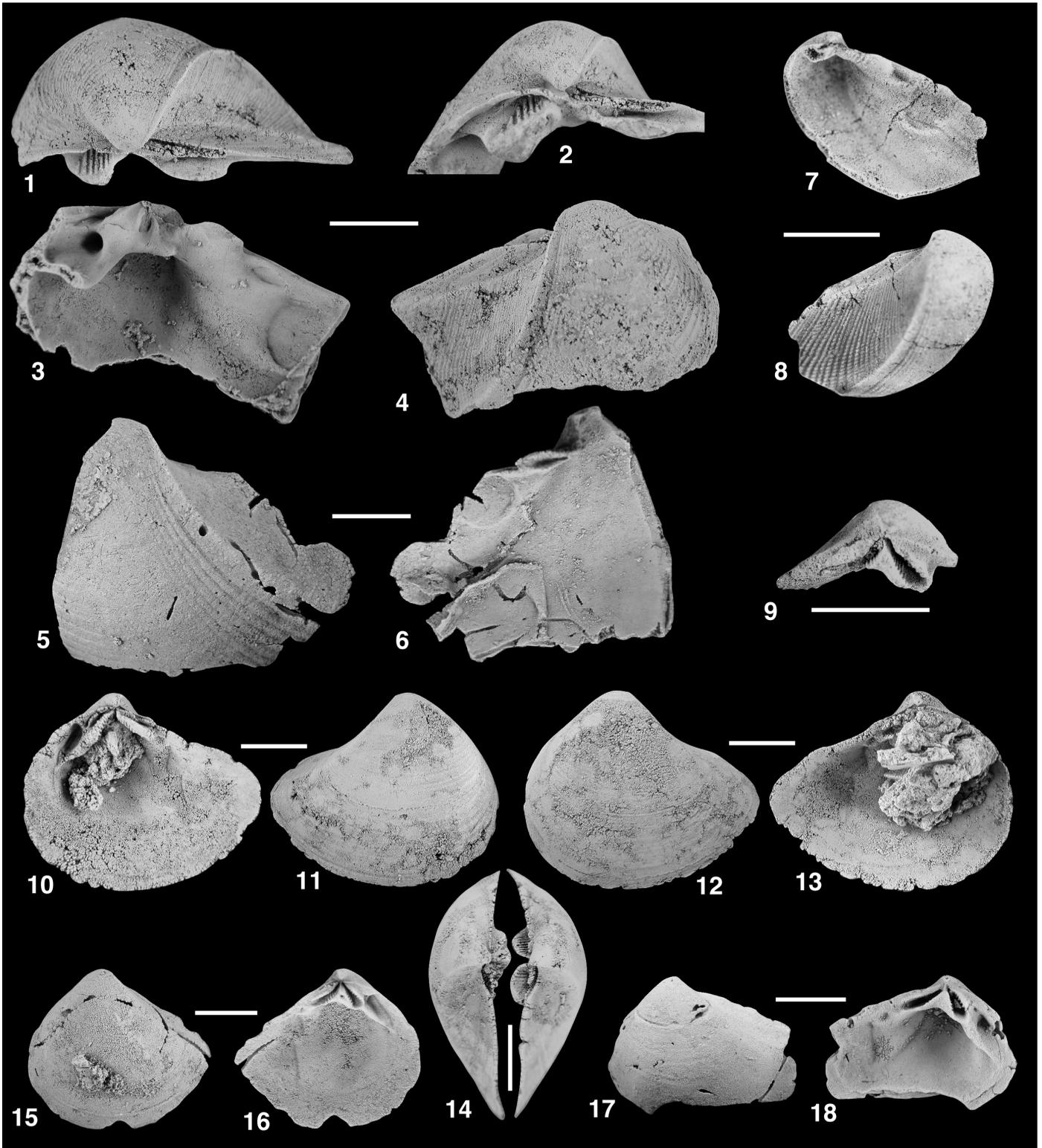
Description.—Valves large (length of LV fragment = 41.3 mm), beak incurved and prosogyrate, umbo strongly inflated (maximum width of LV = 19.3 mm); posterior hinge margin very long and straight; flank ornamented with widely-spaced concentric ornament which weakens towards posterior half of

flank, radial ribs weak and only exhibited on posterior third of flank; area well demarked from flank with sharp marginal carina and shallow ante-carinal sulcus, both carina and sulcus smooth; escutcheon crescent-shaped and long with low but noticeable escutcheon carina; area slightly concave to planar, possessing fine narrowly-spaced concentric costellae that pass uninterrupted across escutcheon carina, one specimen with weak radial ornament passing over top of concentric ornament of area (UMIP 15681, Text-fig. 32.8); RV dentition with a very robust anterior tooth (3*a*) possessing six weakly curved striae and an elongated spatula-like smooth (non-striated) posterior tooth (3*b*); teeth 3*a* and 3*b* are separated by an obvious and deeply recessed gap (hiatus) which may serve as a socket for tooth 2 of the LV; elongated socket dorsal to tooth 3*b* to receive tooth 4*b* of LV; LV with thin and elongated tooth 4*b* with striae on its underside; anterior pedal retractor scar small, circular, and very deeply recessed behind a well developed and shelf-like myophorous buttress that extends well out and over the umbonal cavity; posterior adductor scar nearly oval and well behind cardinal area; posterior pedal retractor scar small, elongate oval, and weakly impressed, situated posterior to tooth 3*b* and above and slightly anterior to posterior adductor scar.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—This form is quite remarkable in that it exhibits characters represented amongst several different Paleozoic-Mesozoic myophoriid and trigoniid genera, but also in that it possess traits described herein for the first time. Given the few specimens available, together with the fact that several important characters, particularly in the LV, remain to be described for this interesting form, I am refraining from introducing what is likely a new species and quite possibly a new genus. I consider the species to be most aligned with the Myophoriidae (*sensu* Boyd and Newell, 1997), as it is largely lacking radial ornament, possesses partial tooth striation, and has an umbonal platform between teeth 3*a* and 3*b*. The sharp marginal carina observed on this species is in itself not particularly diagnostic at the family level, as it is known from myophoriids, trigoniids, and minetrigoniids (e.g., some *Neochizodus* Giebel, 1855, *Elegantinia* Waagen, 1907 [= *Lyriomyophoria* Kobayashi, 1954 per Boyd & Newell, 1999], *Gruenewaldia* Wöhrmann, 1889, *Costatoria* Waagen, 1906, and *Minetrigonia* Kobayashi & Katayama, 1938).

Perhaps most unique about this form is the elongated shelf-like hinge platform which extends well out and over the umbonal cavity. Tooth 3*a* of the RV is remarkably bulbous and can be compared to several species with a similarly large tooth 3*a* assigned to *Procostatoria* and perhaps even *Gruenewaldia*.



Text-fig. 32. *Myophoridae* and *Erugoniidae*. 1–6, ?7, ?8, *Myophoriid* sp. A. 1–4, UMIP 15680, a RV; 1, dorsal view; 2, hinge area; 3, internal view; 4, exterior. 5, 6, PRI 69663, a LV; 5, exterior view; 6, exterior view. 7, 8, UMIP 15681, a RV; 7, interior view; 8, exterior view. 9–18, *Erugonia boydi* n. sp. 9, PRI 69664, paratype, a RV showing hinge. 10–14, holotype, UMIP 15682; 10, RV interior; 11, RV exterior; 12, LV exterior; 13, LV interior; 14, dorsal margin of conjoined valves. 15, 16, UMIP 15684, paratype, a LV; 15, exterior; 16, interior. 17, 18, UMIP 15685, paratype, a LV; 17, exterior; 18, interior. Scale bars = 10 mm. All from USGS loc. M1912.

However, the hinge characters of the LV remain largely unknown if tooth 2 is posteriorly elongated as is typical for the myophorian hinge grade, nor is it known if tooth 4*b* is striated on its dorsal side.

Paleoecology.—Like other trigonoideans (Stanley, 1978), this myophoriid is inferred to be a non-siphonate shallow, but quite active, burrower situated with its posterior margin at or slightly above the sediment-water interface (Text-fig. 13.16).

Family ERUGONIIDAE n. fam.

Type genus.—*Erugonia* Newton in Newton *et al.*, 1987: 63. Upper Triassic (lower Norian), Oregon, USA.

Included genera.—*Agonisca* Fleming, 1963 (Ladinian), *Caledogonia* Freneix & Avias, 1977 (Carnian–Norian), *Erugonia* Newton in Newton *et al.*, 1987 (lower to upper Norian), provisionally included genera and subgenera *Modestella* Hautmann 2001b (Norian and Rhaetian), and *Liotrignonia* Cox, 1952 (Lower Jurassic).

Diagnosis.—Trigonoideans with complete trigoniid dentition, orthogyrous to prosogyrous umbo, flank generally smooth, lacking prominent radial ornament, marginal carina poorly developed or absent.

Remarks.—As mentioned in the preceding discussion for the Trigonicea, it has become apparent that there are several Mesozoic genera and subgenera which possess complete trigoniid-grade dentition yet lack prominent marginal carina and external radial ornament, making confident assignment to the Myophoriidae, Trigoniidae, or Minetrigoniidae difficult. Newton (in Newton *et al.*, 1987) placed *Erugonia* into the Myophoriidae based on external morphology and noted its external similarity to the true myophoriid *Neoschizodus*. Hautmann (2001b) erected the subgenus *Modestella* (type species *Trigonia zlabachensis* Haas, 1909) for trigoniids with an opisthogyrate beak and flanks bearing commarginal ornament, but without any radial sculpture except for on the area. *Modestella* also possess a partially striated tooth 4*b* and it is therefore only provisionally included with the new family.

The erection of this new family is warranted in that the included genera all possess complete trigoniid-grade dentition and a well developed pedal retractor scar behind tooth 3*b*, and lack radial ornament (as possessed by the Trigoniidae and Minetrigoniidae) and differ from other Trigoniidae and Myophoriidae in the absence of marginal carina. As noted in the above remarks for Trigonioidea, several of these traits (particularly the dental striations) are also present to a variable extent within several established Myophoriidae and may have evolved independently.

Newton in Newton *et al.* (1987) suggested that *Erugonia* (and hence the Erugoniidae) may have originated from a myophoriid such as *Neoschizodus* Giebel, 1855. Although a *Neoschizodus* ancestor cannot be ruled out, the presence of complete dental striations, the hiatus between teeth 3*a* and 3*b*, and the pedal retractor scar behind 3*b* in the RV and corresponding socket in the LV suggest that the Erugoniidae is perhaps more closely aligned with the Trigoniidae than Myophoriidae.

Genus ERUGONIA Newton in Newton *et al.*, 1987

Type species.—*Erugonia canyonensis* Newton in Newton *et al.*, 1987, by original designation, Upper Triassic (lower Norian), Oregon.

Remarks.—Morphologic and phylogenetic considerations of *Erugonia* are provided under the preceding family diagnosis and remarks. At present, the genus is represented by two occurrences, the lower Norian of Oregon represented by the type species and the upper Norian *Erugonia boydi* n. sp. described below. Stanley (1989) included *Erugonia* sp. on a faunal list from the lower Rhaetian Sutton Member of the Parsons Bay Formation of Vancouver Island, but the specimens upon which this determination was made were never illustrated.

Erugonia boydi n. sp.

Text-figs 32.9–32.18

Type and measurements.—Holotype UMIP 15682, a silicified individual consisting of both right (Text-figs 32.10–32.11) and left (Text-figs 32.12–32.13) valves. Paratypes: PRI 69664 (Text-fig, 32.9), a RV; UMIP 15684 (Text-figs 32.15–32.16), a LV; UMIP 15685 (Text-figs 32.17–32.18), a LV. See Table 4 for complete measurement set. All from USGS loc. M1912, Kuiu Island, Alaska, from upper Norian, Hound Island Volcanics.

Other material examined.—In addition to the types, a fragmented LV and several smaller fragments contributed to the description.

Diagnosis.—Large *Erugonia*, trigonally ovate, height slightly less than length, posteriorly elongated with rounded respiratory margin; beak incurved and orthogyrous to slightly opisthogyrous; shell exterior unornamented and generally smooth; marginal carina more pronounced in juveniles and fading in later growth stages; with poorly differentiated posterior area; possessing trigoniid dentition and anterior myophorous buttress.

Table 4. Measurements for *Erugonia boydi* n. sp.

Specimen	Valve	Length (mm)	Height (mm)	Width (mm)	Remarks
UMIP 15685	LV	27.0**	29.0**	8.2	Paratype
UMIP 15682	RV	31.2	37.2	7.7	Holotype
UMIP 15684	LV	22.8*	25.1	7.7	Paratype
PRI 69664	LV	11.1*	12.2*	3.3	Paratype

* Restored measurement.

** Measurement taken from largest commarginal.

Description.—Valves large (maximum H = 31.8 mm, maximum L = 37.9 mm), moderately inflated (maximum W = 9.8 mm), trigonally ovate; longer than high (mean H/L = 0.85) and posteriorly elongated; posterodorsal margin sloping, with broadly rounded anterior margin, and more acutely rounded respiratory margin; beak incurved and orthogyrous to slightly opisthogyrous; weakly carinate with marginal carina becoming rounded in later growth stages (beyond approximately 1 cm from beak); flank with closely-spaced commarginal growth striae, radial ornament lacking; trigoniid dentition; LV with large, asymmetric chevron-shaped and striated medial tooth (2) with concave ventral surface, anterior surface of medial tooth more inclined than posterior side and dorsal surface forms an angle of approximately 80°, tooth 2 bordered above two diverging sockets sloping away from beak to receive teeth 3a and 3b of RV, teeth 4a and 4b weakly developed; RV with prominent teeth 3a and 3b diverging to form a right angle, tooth 3a dorsally concave and tooth 3b planar, teeth 3a and 3b are striated on both anterior and posterior flanks; anterior myophorous buttress thin and somewhat recessed from cardinal platform, fused with anterior tooth 3a; muscle scars fairly well preserved, with small shallow round posterior pedal retractor scar situated slightly beyond tooth 3b in RV, beyond which is impressed a larger ovate posterior adductor scar; anterior pedal retractor scar small, deeply impressed slightly dorsal to terminus of tooth 3a of RV; anterior adductor scar crescent shaped and large, situated above buttress and adjoining with anterior retractor scar at its posterodorsal extremity; pallial line not observed.

Etymology.—Trivial name, *boydi*, after Dr. Donald W. Boyd, a long-time mentor of the author, and significant contributor to our understanding of Paleozoic and early Mesozoic trigonoidean bivalves.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—This species comfortably fits within the generic concept of *Erugonia* erected by Newton (*in* Newton *et al.*,

1987) to accommodate specimens exhibiting robust trigoniid-grade dentition, yet possessing a relatively smooth exterior and lacking a well developed marginal carina. The external form of this species is remarkably similar to many of the Upper Paleozoic and Lower Triassic schizodontids and myophoriids. See for example the Permian *Schizodus wyomingensis* Newell & Boyd (1975, fig. 61) that agrees in almost every detail of shape, inflation, and ornament to the present species. Both this new species and *E. canyonensis* Newton (*in* Newton *et al.*, 1987) differ from other essentially smooth trigoniids such as *Caledogonia* Freneix & Avias, 1977 in lacking a strong marginal carina. This species can be distinguished from *Erugonia canyonensis* in that *E. boydi* is larger, exhibits greater posterior elongation, and possesses striae on both anterior and posterior flanks of tooth 3b.

Paleoecology.—*Erugonia boydi* is interpreted to be a shallow infaunal and active non-siphonate burrower by comparison to other trigonoida (see for example Stanley, 1978; Villamil *et al.*, 1998). The generally smooth valve exterior, absence of prominent carina, differentiated posterior area, and large size contrasts with the minetrigoniids described below and may suggest a burrowing position with the animal entirely below the sediment-water interface, with the posterior margin just reaching the sediment-water interface (Text-fig. 13.17).

Family MINETRIGONIIDAE Kobayashi, 1954

Remarks.—Kobayashi (1954) introduced the subfamily Minetrigoniinae to include *Minetrigonia* Kobayashi & Katayama, 1938 and *Myophorigonia* Cox, 1952. Fleming (1982) elevated this to familial rank and included his new genus *Maoritrigonia*. As discussed elsewhere (*e.g.*, Fleming, 1982, 1987), Newell & Boyd (1975) proposed the Costatoriidae, which included some genera already assigned to the Minetrigoniidae which, based upon priority of family group names, has been suppressed as a junior synonym of the Minetrigoniidae. The family is here considered to include the clade of Early Mesozoic trigonoideans possessing complete trigoniid-grade dentition and exhibiting a pronounced radial ornament across the flank and also, to a varying degree, trans-

verse, concentric ornamentation, and, in some genera, a trellised ornament of the area.

Genus *MINETRIGONIA* Kobayashi & Katayama, 1938

Type species.—*Trigonia hegiensis* Saeki, 1925, by original designation, Upper Triassic (Carnian), Japan.

Remarks.—*Minetrigonia* was introduced by Kobayashi & Katayama (1938) to include radially-ribbed trigonoidean species with a trellised ornament on the posterior area. Given that there are numerous studies, especially in the past 50 years, involving many tens of species that discuss the intricacies and variability of the external ornament of *Minetrigonia*, the remarks below focus on those from North and South America and warrant comparison to those described from the Gill Harbor locality. Cox (1952) placed *Myophoria suttonensis* Clapp & Shimer, 1911 from the Rhaetian of Vancouver Island Canada and *Myophoria pascoensis* Steinmann, 1929 from the Norian of Peru into this genus. At about the same time, Kobayashi & Ichikawa (1952) provided a lengthy discussion on the genus and also considered *M. suttonensis* and *Myophoria pascoensis* (and also *M. jaworskii* Steinmann, 1929 and *M. lissoni* Steinmann, 1929 from the same locality) as belonging to *Minetrigonia*. However, Kobayashi & Ichikawa (1952) suggested these species may belong to a separate group within *Minetrigonia* with close affinity to the west-Tethyan *Myophoria inequicostata* Klipstein, 1843. Subsequently, Fleming (1987) suggested that other Carnian species—most notably *Myophoria shoshonensis* Silberling, 1959, from Nevada, and the two Arctic species *Cardita ursina* Kittl, 1907 and *Trigonia ursiana* Böhm, 1903—could be accommodated by a somewhat broader concept of *Minetrigonia*. Newton (in Newton *et al.*, 1987) described *Minetrigonia* sp. from the lower Norian of Hells Canyon, Oregon, which has prominent radial sculpture only on the posterior margin of the flank and very faint diagonal ornamentation on a slightly concave area (see Tamura, 1995 for more recent observations on this species). Tamura & McRoberts (1993) described *Myophorigonia kobayashii* from the Carnian of Oregon that is similar in many regards to specimens here regarded as belonging to *Minetrigonia*, but differing in possessing a diagonal ornament on the flank anterior. This difficulty in interpreting the taxonomic significance of the ornament of several North American minetrigoniids (*e.g.*, *M. suttonensis*) was further articulated by Tamura (1995) who lumped them into a “*suttonensis* group” apart from *Minetrigonia sensu stricto*.

A reappraisal of the external ornament of minetrigoniid species by the author has led to the conclusion that slight differences in radial and transverse ornament on the flank are insufficient criteria for discrimination into genus-rank

groups, but do have value in discriminating species. The strategy employed herein is to conserve the original concept of *Minetrigonia*, but to accommodate those species with a radially ribbed posterior area, as well as those with a diagonal ornament across the flank. The result of this would be to keep those species of Tamura’s (1995) “*suttonensis* group” within *Minetrigonia*, as well as certain other species of *Myophorigonia* with a weakly transverse ornament (*e.g.*, *Myophorigonia kobayashii* Tamura & McRoberts, 1993). *Myophorigonia* is retained for minetrigoniids with strong radial and subordinate concentric ornamentation.

Minetrigonia newtonae n. sp.

Text-figs 33.1–33.12

Minetrigonia cf. *M. suttonensis* (Clapp & Shimer, 1911)
McRoberts in McRoberts & Blodgett, 2002: 60, pl. 1,
fig. 22.

Non *Myophoria suttonensis* Clapp & Shimer, 1911: 433, pl. 41,
figs 12–14.

Types and measurements.—Holotype, PRI 69665 (Text-figs 33.1–33.3), a complete silicified RV. Paratypes: PRI 69666 (Text-figs 33.4–33.5), a LV; PRI 69667 (Text-figs 33.6–33.7), a RV; UMIP 15686 (Text-figs 33.8–33.9), a LV; and PRI 69668 (Text-figs 33.10–33.12), a partial RV. See Table 5 for complete measurement set. All from USGS loc. M1912, Kuiu Island, Alaska, from upper Norian, Hound Island Volcanics.

Other material examined.—In addition to the five figured type specimens, the collection consists of 15 left and 14 right valves and numerous fragments.

Diagnosis.—Moderate-sized and inflated *Minetrigonia* with radial ribs crossed by concentric sculpture across entire flank; with sharp posterior carina and deep ante-carinal sulcus, area covered with very fine concentric costellae and weak transverse ribs.

Description.—Valves nearly as high as long, moderately large (maximum H = 22.8 mm, maximum L = 23.5 mm), moderately inflated (maximum W = 8.2 mm), trigonally oval; beak essentially orthogyrous to very slightly prosogyrous; umbo separated from posterior area by a distinct change in slope, respiratory margin extended posteriorly, steeply inclined and relatively straight; ornament consists of between 18–24 rounded radial ribs equally distributed across flank, posterior-most ribs adjacent to ante-carinal sulcus most prominent; concentric ornament prominent on flank and extends over radial ribs to produce bead-like projections; posterior dorsal area separated from flank by deep radial ante-carinal groove and sharp angular marginal carina radiating from beak and

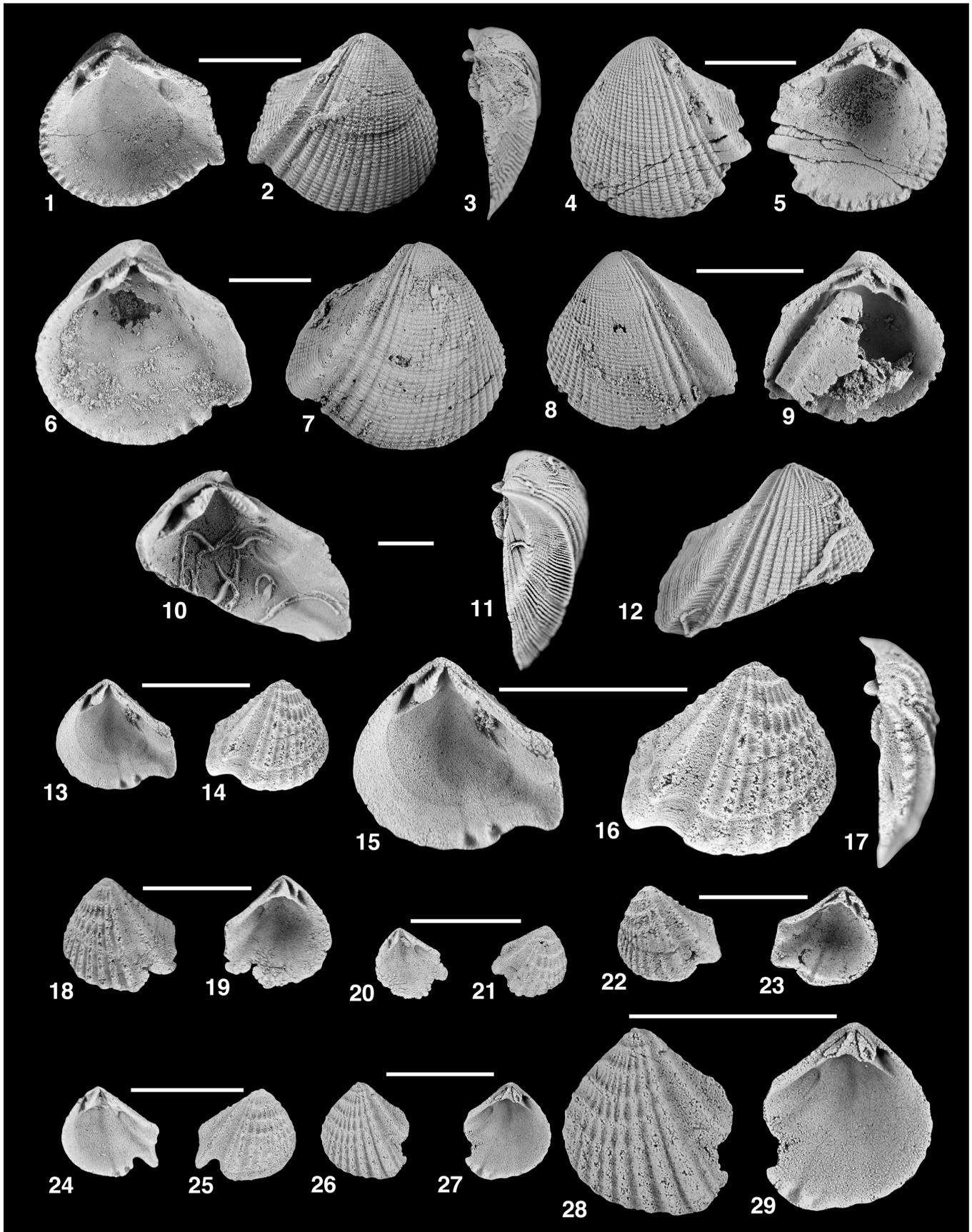


Table 5. Measurements of *Minetrigonia newtonae* n. sp.

Specimen	Valve	Length (mm)	Height (mm)	Inflation (mm)	Remarks
--	LV	17	18.7	7	--
--	LV	20.5	19.7	7	--
--	LV	21.4	19.3	7.9	--
PRI 69666	LV	19	19.4	7.4	Paratype
--	LV	14.5	15.1	4.6	--
--	LV	12	11.8	4.5	--
UMIP 15686	LV	17	14.8	5.7	Paratype
--	LV	15.7	15.2	5.4	--
--	LV	22.8	21.8	8.1	--
--	LV	23.5	22.7	9	--
--	LV	16.2	16	5	--
--	LV	21.4	20.5	6.9	--
--	LV	15	15.2	5.9	--
--	LV	17.8	16.3	5.8	--
--	LV	13.1	12.5	4.2	--
--	LV	15.1	15.5	4.7	--
--	LV	16.5	15.9	5.2	--
PRI 69665	RV	18.5	17.8	7	Holotype
--	RV	15.7	15.8	5.1	--
--	RV	17.3	17	6.1	--
--	RV	18.9	18.6	7.8	--
--	RV	16.1	16.7	5.7	--
--	RV	16.3	16.6	5.3	--
--	RV	20.5	20.2	7.6	--
--	RV	11.2	10.8	3.6	--
--	RV	21.2	21.4	7.4	--
--	RV	10.1	9.6	3.1	--
PRI 69667	RV	24	22.8	8.2	Paratype
--	RV	19.1	18.2	5.3	--
--	RV	17.7	17	6	--
--	RV	10	11	3.4	--
--	RV	11.2	11.6	3.4	--
--	RV	18.3	18.9	5.7	--

extending to posterior ventral margin; concentric ornament from flank passes across marginal carina into area; area flat to slightly concave, without medial groove, covered with finely-spaced concentric ornament, and in a few well preserved in-

dividuals, with very fine transverse sculpture; area bordered posteriorly by angular escutcheon carina; escutcheon well developed, crescent-shaped and narrow, extending from beak to the dorsal respiratory margin; hinge of trigonian grade; hinge

Text-fig. 33 (at left). Minetrigoniidae. 1–12, *Minetrigonia newtonae* n. sp. 1–3, holotype, PRI 69665, a RV; 1, interior; 2, exterior; 3, posterior. 4, 5, paratype, PRI 69666, a LV; 4, interior; 5, exterior. 6, 7, paratype, PRI 69667, a RV; 6, interior; 7, exterior. 8, 9, paratype, UMIP 15686, a LV; 8, interior; 9, exterior. 10–12, paratype, PRI 69668, a partial RV; 10, interior; 11, posterodorsal; 12, exterior. 13–29, *Myophorogonia parva* n. sp. 13–17, holotype, UMIP 15687, a RV; 13, interior; 14, exterior; 15, enlarged view of interior; 16, enlarged view of exterior; 17, enlarged view of dorsal margin; 18, 19, paratype, UMIP 15688, a LV; 18, exterior; 19, interior. 20, 21, paratype, UMIP 15689, a RV; 20, interior; 21, exterior. 22, 23, paratype, UMIP 15690, a LV; 22, exterior; 23, interior. 24, 25, paratype, UMIP 15691, a RV; 24, interior; 25, exterior. 26–29, paratype, UMIP 15692, a LV; 26, exterior; 27, interior; 28, enlarged view of exterior; 29, enlarged view of interior. Scale bars = 10 mm. All from USGS loc. M1912.

of LV with large medial triangular-shaped tooth (2), striated on dorsal limbs and slightly concave ventral surface, possessing a moderately robust anterior lateral tooth (4a) and somewhat weaker posterior lateral tooth (4b); right hinge with anterior tooth (3a) sloping at a relatively steep angle, possessing striations on both sides; posterior tooth of RV (3b) more shallowly sloping and somewhat shorter than tooth (3a), ventral surface with strong striations, dorsal surface with weak or absent striations; teeth 3a and 3b join together above an obvious gap at an angle of about 45°; muscle scars well preserved, posterior adductor scar of both valves oval and moderately large; anterior adductor scar prominent and deeply recessed and slightly above thin walled buttress; posterior pedal retractor scar small and situated slightly dorsal and anterior of posterior adductor scar; pallial line continuous, extending from posteroventral margin of posterior adductor scar around ventral margin to the anterior extension of myophorous buttress.

Etymology.—Trivial name, *newtonae*, after Cathryn R. Newton who made known the diverse Upper Triassic bivalve faunas of the North American tectonostratigraphic terranes.

Occurrence.—Here reported from the upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912) and lower Norian of the Taylor Mountains, Alaska (Nixon Fork terrane).

Remarks.—An interesting observation is that many, but not all, of the Gill Harbor specimens exhibit only partial striation on tooth 3b of the RV. Although only three of the 17 right valves show striae on the dorsal surface of tooth 3b, five of the left valves possess striated upper and lower surfaces in the posterior socket corresponding to tooth 3b of the right valve.

The Gill Harbor specimens appear to be conspecific with those illustrated by McRoberts (in McRoberts & Blodgett, 2002, figs 3.21, 3.22) as *Minetrigonia* cf. *M. suttonensis* (Clapp & Shimer, 1911). However, the large sample size of the Gill Harbor collection (34 valves, as compared to the few specimens available from the Taylor Mountain collection) permits new observations and interpretation of the hinge and ornament, suggesting they are distinct from, although closely related to, *Minetrigonia suttonensis* (Clapp & Shimer, 1911) from the lower Rhaetian Sutton Member of the Parsons Bay Formation of Vancouver Island. Although similar in size and a few other characteristics, the holotype of *Myophoria suttonensis* is represented by a single RV (Clapp & Shimer, 1911, pl. 41, figs 12–14), whose posterior area has a weak medial groove but is otherwise unornamented with concentric or radial sculpture. Additional topotype material of *Myophoria suttonensis* from Cowichan Lake illustrated by Tozer (1963, pl. 12 figs 9a, 9b) differs from the holotype

in possessing weak radial ornament on the area, but a more subdued marginal carina.

Minetrigonia newtonae is closely related to *Myophoria cairnesi* McLearn, 1942 from the Rhaetian of the Tyaughton Creek area of western B.C., Canada (Caldwallier terrane). Although *Myophoria cairnesi* can confidently be placed within *Minetrigonia*, it possesses fewer and stronger radial ribs than most other *Minetrigonia* species. Furthermore, the tubercles on the radial sculpture in *M. cairnesi* are more pronounced in the mid flank than those found on *M. newtonae*, which are of uniform strength across the entire flank. It can be distinguished from the other *Minetrigonia* in its smaller size and difference in sculpture on the area. The specimen differs from other Carnian minetrigoniids, such as *Minetrigonia kobayashii* (Tamura & McRoberts, 1993) from the Wallowa terrane, Oregon, which has a more pronounced diagonal ornament on the flank anterior.

The species can be easily differentiated from the several species of *Minetrigonia* (and *Myophorigonia*) from the South American Cordillera introduced by Steinmann (1929) and Körner (1937). *Myophoria pascoensis* Steinmann, 1929, *M. jaworskii* Steinmann, 1929, *M. lissoni* Steinmann, 1929, and *Myophoria multicostata* Körner, 1937, which are all from the same locality, are all similar in size and ornament, and quite possibly belong to a single species. These four species differ from *M. newtonae* in possessing much stronger and more widely-spaced radial ornamentation across the flank. The other Norian minetrigoniid from Peru, *Myophoria paucicostata* Jaworski, 1922, is discussed below under *Myophorigonia parva* n. sp.

Paleoecology.—Like other trigoniids (Tevesz, 1975; Stanley, 1978), *Minetrigonia newtonae* is inferred to be a non-siphonate shallow but quite active burrower situated with its posterior margin at or slightly above the sediment-water interface (Text-fig. 13.18). The well-developed posterior carina may lead to the interpretation that *M. newtonae* was oriented somewhat tangentially to the sediment-water interface, coincident to the ante-carinal groove and an exposed posterior area. As in Recent trigoniids and other burrowing bivalve groups (e.g., cardiids), radial ribbing may have served to stabilize the animal in the substrate and perhaps aid in burrowing (e.g., Kauffman, 1969; Stanley, 1970).

Genus *MYOPHORIGONIA* Cox, 1952

Type species.—*Myophoria paucicostata* Jaworski, 1922, by original designation; Upper Triassic (Norian), Peru.

Remarks.—As discussed in the remarks on Minetrigoniidae and *Minetrigonia*, *Myophorigonia* is retained for minetrigoniids with strong radial and subordinate concentric ornamentation.

Myophorignia is perhaps a lesser-known minetrioniid genus than *Minetrignia* and has a broadly similar temporal and paleogeographic distribution through the Carnian–Rhaetian of the low to mid paleolatitudes of Panthalassa (e.g., Jaworski, 1922; Tamura, 1995; McRoberts, 1997). Like *Minetrignia*, *Myophorignia* is not known from the central or western Tethys. As discussed by Ros-Franch *et al.* (2014), examples of Jurassic *Myophorignia* are not substantiated.

***Myophorignia parva* n. sp.**
Text-figs 33.13–33.29

Types and measurements.—Holotype, UMIP 15687 (Text-figs 33.13–33.17), a complete silicified RV; H = 9.7 mm, L = 10.7 mm, W = 3.4 mm. Paratypes: left valves UMIP 15688 (Text-figs 33.18, 33.19), UMIP 15690 (Text-figs 33.22, 33.23), UMIP 15692 (Text-figs 33.26–33.29); right valves UMIP 15689 (Text-figs 33.20, 33.21), UMIP 15691 (Text-figs 33.24, 33.25). See Table 6 for complete set of measurements. All from USGS loc. M1912, Kuiu Island, Alaska, from upper Norian, Hound Island Volcanics.

Other material examined.—In addition to the type specimens, the collection consists of 12 left valves and 16 right valves.

Diagnosis.—Small *Myophorignia*, with tuberculate radial ribs, sharp marginal carina, and relatively flat to concave posterior area possessing commarginal ornament passing into protruding respiratory margin; LV with triangular medial tooth and with poorly developed laterals; RV with two cardinal teeth of unequal size.

Description.—Valves small (maximum H = 11.5 mm, maximum L = 11.3 mm), weakly inflated (maximum width = 3.0 mm), trigonally suboval and strongly inequilateral, umbo essentially orthogyrous and passes into posterior area without a change in slope; respiratory margin extended posteriorly, intersecting marginal carina at nearly a right angle, steeply inclined, and relatively straight; ornament consists of about 8–10 weakly tuberculate radial ribs becoming more coarse and more widely spaced approaching posterior marginal carina, becoming obsolete near anterior margin; concentric ornament consisting of 4–6 widely-spaced step-like growth bands whose strength increases towards anterior margin of flank, with numerous fine concentric threads that pass uninterrupted from flank across ante-carinal sulcus, marginal carina, and into posterior area; posterior area separated from flank by deep and broad ante-carinal sulcus that widens towards a recessed posteroventral margin; marginal carina sharp and angular, lacking tubercles, radiating from beak and extending to posterior ventral margin; area concave, covered with finely-

spaced concentric ornament with median groove; escutcheon impressed, long, separated from area by tuberculate escutcheon carina; hinge of trigoniid grade; LV with triangular medial tooth (2), striated dorsal limbs and slightly concave ventral surface, poorly developed anterior lateral (4a) and posterior lateral (4b) teeth; right hinge coarsely preserved but with anterior tooth (3a) more shallowly sloping and shorter than anterior tooth (3b), striations not preserved on teeth 3a and 3b, but apparently present based on striations in corresponding sockets of LV, teeth 3a and 3b separated by obvious triangular recess to receive tooth 2 of LV.

Etymology.—Trivial name, *parva*, referring to its small size relative to other *Myophorignia* species.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—The morphologic features of this new species are congruent with the original concept of *Myophorignia* as introduced by Cox (1952) and later reiterated in the *Treatise of Invertebrate Paleontology* (Cox 1969d) to include small trigoniids possessing a sharp carina, ornamented with pronounced radial costae and subordinate concentric costae.

Myophorignia parva shares several characteristics with *M. paucicostata* Jaworski (1922, pl. 5, figs 9–11), which was later illustrated by Cox (1949, pl. 1, fig. 11; 1969c, fig. D71.3), especially with respect to the nature of the ante-carinal sulcus. However, the Gill Harbor specimens are smaller than the type species, have a tuberculate escutcheon carina, exhibit stronger radial sculpture, and a somewhat more pronounced concentric ornament. *Myophorignia parva* can also be compared to *Myophoria zeballos* McLearn, 1942 from the Rhaetian of Tyaughton Creek (Caldwaller terrane) and from Vancouver Island (Wrangell terrane) B.C., Canada, which can, with confidence, be placed within *Myophorignia*. *Myophoria zeballos* has a similar ornament, but achieves a much greater size: the holotype of *M. zeballos* illustrated by McLearn (1942, pl. 2, figs 6–8; GSC 9442) has a L of 29.9 mm, which is nearly twice as long as the largest *M. parva*.

Paleoecology.—As with *Minetrignia newtonae* n. sp., *Myophorignia parva* n. sp. is inferred to be a shallow but quite active burrower (Text-fig. 13.19). As noted above under *M. newtonae*, the well-developed posterior area with sharp carina suggests that some of the shell may have been emergent above the sediment-water interface.

Table 6. Measurements for *Myophorigonia parva* n. sp.

Specimen	Valve	Length (mm)	Height (mm)	Width (mm)	Notes
--	RV	7.3	7.2	2.5	--
UMIP 15691	RV	8.7	8.3	2.7	Paratype
--	RV	9.4	9.8	3	--
UMIP 15689	RV	6.4	6.8	1.8	Paratype
UMIP 15687	RV	10.7	9.7	3.4	Holotype
--	RV	8.5	8.5	2.5	--
--	RV	8.1	8.9	2.4	--
--	RV	8.1	7.9	2.1	--
--	RV	9.1	8.6	2.5	--
--	RV	7.1	7.2	2	--
--	RV	9.2	7.6	2.4	--
--	RV	9.3	9.1	2.5	--
--	RV	8	8.1	2	--
--	RV	7.9	8	2.3	--
--	RV	7.5	7.8	2	--
--	RV	7	6.9	1.9	--
UMIP 15690	LV	9.4	9.4	3	Paratype
--	LV	6.8	7.5	2	--
UMIP 15688	LV	10.1	10.5	3	Paratype
--	LV	8.6	9.4	3	--
--	LV	7.9	8.5	2.5	--
--	LV	9.5	10.1	3	--
--	LV	6.4	6.5	1.8	--
--	LV	8.6	9.2	2.7	--
--	LV	6.9	7.3	2	--
--	LV	7.5	8.8	2.4	--
--	LV	11.3	11.5	2.9	--

Order **LUCINIDA** Gray, 1854
 Superfamily **LUCINOIDEA** Fleming, 1828
 Family **FIMBRIIDAE** Nicol, 1959
 Genus **SCHAFHAEUTLIA** Cossmann, 1897

Krumbeckia Diener, 1915: 217

Type species.—*Gonodon schafhaeutlia* Solomon, 1895 (= *Gonodon ovatum* Schafhäutl, 1863) by original designation, Lower Jurassic (Sinemurian), Bavaria, Germany.

Remarks.—*Schafhaeutlia* is well represented in many Upper Triassic localities across the Tethyan and eastern Panthalassan realms (e.g., Bittner, 1895; Ichikawa, 1950; Allasinaz, 1966; Kiparisova *et al.*, 1966; Zhang *et al.*, 1979; Hautmann, 2001b). Unfortunately, nearly all of the close to 25 available names given to Upper Triassic species are based on shape and

ornament for which details of the hinge remain unknown. Most Triassic species of *Schafhaeutlia* are of moderate to large size (usually not exceeding 7 or 8 cm in length, although some can reach 9 cm in length), of moderate to pronounced convexity, and are relatively thick shelled.

A review of the genus and issues surrounding the type species was provided by Hautmann (2001b). The type species *Gonodon ovatum* Schafhäutl, 1863 from the Sinemurian Hochfellnkalk of Bavaria is unfortunately lost (Hautmann, 2001b), yet based on original illustrations (reproduced in Chavan, 1969a, fig. E19), the specimen is moderately small and possesses a distinctive robust conical cardinal dentition comprised of a *3a* and a somewhat stronger *3b* in the RV and a robust *2* in the LV. Schafhäutl's original drawing of the hinge is interpreted by Hautmann (2001b; personal communication, 2016) to consist of dorsally fused *3a* and *3b*, forming a crescent-like structure that inserts dorsally of

the central tooth 2 of the LV as found in *Krumbeckia* Diener, 1915 (type species *Krumbeckia tambangensis* Diener, 1915) and is the basis for synonymizing the two genera. In erecting *Krumbeckia*, Diener (1915: 131) remarked that it may be discriminated from *Schafhaeutlia* by its obliquely-oval shape and stronger cardinal dentition, yet Hautmann (2001b) does not consider it possible to separate them based on these criteria alone and it is clear that the strong bifid dentition of the RV in *Krumbeckia* is indistinguishable from that of some *Schafhaeutlia* as demonstrated in *S. manzavini* (Bittner, 1895) of Zardini (1981, pl. 24, fig. 7b) and *S. sphaerioides* (Boettger, 1880) of Hautmann, (2001b, pl. 30, figs 2a, 5a, 6b). It should also be noted that the massive dentition of *Krumbeckia* has led past workers to align the genus with the Megalodontidae (e.g., Cox & LaRoque, 1969), a view that can no longer be supported. Conversely, the hinge of *S. mellingi* (Hauer, 1857) from the Carnian of Austria depicted by Chavan (1969a, fig. E18.7) does not show an arched fusion of teeth 3a and 3b. In some regards, the unfused 3a and 3b in *S. mellingi*, and perhaps other *Schafhaeutlia*, is similar to that found in *Sphaeriola* Stoliczka, 1871 (type species *Sphaerium madridi* D'Archiac, 1843). Márquez-Aliaga *et al.* (2010) recognized the similarity between *Schafhaeutlia* and *Sphaeriola* Stoliczka, 1871 and commented that generally Upper Triassic species are assigned to the former and Lower–Mid Jurassic species to the latter.

A proper evaluation of the generic concept of *Schafhaeutlia* is beyond the scope of the present work. Further study is needed to characterize the variability in dentition in *Schafhaeutlia*. A conservative approach is taken here to include those species (e.g., *S. ovatum* and *S. manzavini*) with a very thick shell and dorsally fused 3a and 3b and those species (e.g., *S. mellingi* and *S. sp.* A described below) in which the two teeth diverge but are not particularly strongly fused.

Schafhaeutlia sp. A

Text-figs 34.1–34.10

Material examined.—Three RVs (PRI 69669, Text-figs 34.1, 34.2; PRI 69670, Text-figs 34.3, 34.4; PRI 69671, Text-figs 34.5, 34.6) and three LVs (PRI 69672, Text-figs 34.7, 34.8; PRI 69673, Text-figs 34.9, 34.10; PRI 69674, Text-figs 34.11, 34.12).

Description.—Shells of moderate size (maximum L = 31.6 mm, maximum H = 27.6 mm), nearly circular to ovoid in outline, slightly longer than high, shell convexity moderate (maximum W = 9.8 mm), beak opisthogyrate, situated only slightly anterior, umbo broadly inflated, elevated above disk, and variably gibbose; without lunule or escutcheon; valve exterior with closely-spaced commarginal growth lines, otherwise relatively smooth; posterior hinge with relatively long

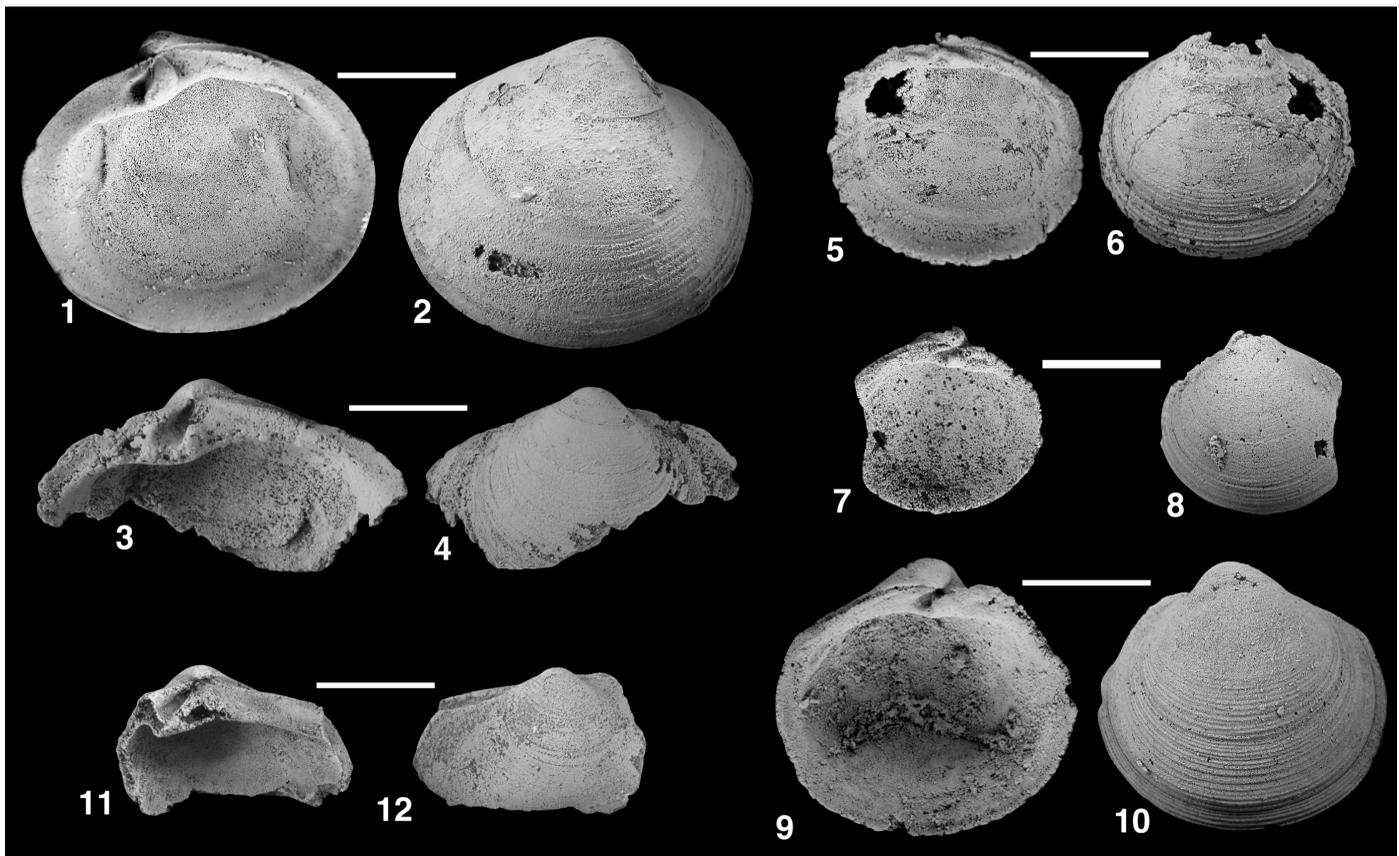
and slightly arched ligament groove with supporting nymphs; dentition somewhat variable, LV with strong peg-like opisthocline cardinal tooth (2) separated from a weak and steeply-sloping opisthocline blade-like 4b by a deep triangular socket to receive the 3b tooth of RV; RV with very strong opisthocline or orthocline 3b separated from a weak 3a by a deep socket to receive tooth 2 of LV, apex of teeth 3a and 3b converging dorsally and possibly fused, lateral teeth lacking or with a very subdued PI that forms the ventral hinge margin; pallial line continuous, integripalliate; with moderately vertically-elongated oval anterior and posterior adductor scars, with the posterior adductor scar slightly larger.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Given the distinctive dentition and general shape and ornament of the Gill Harbor specimens, they are placed within *Schafhaeutlia*. They have, however, thinner shells than is typical for the genus. Although likely, it is not possible to determine with confidence if the thin shells of the Gill Harbor specimens were due to selective silification and preservation of only the inner shell layer. Although the sample size is quite small, the hinge of the Gill Harbor specimens appears variable and there is some uncertainty regarding articulation of cardinal dentition between the left and right valves. For example, the best-preserved specimen (Text-fig. 34.1, PRI 69669, a RV) has a single blunt opisthocline tooth below the beak and two adjacent sockets, the anterior one being the more deeply recessed, whereas the two well preserved LVs (PRI 69672, Text-fig. 34.7 and PRI 69673, Text-fig. 34.9) have an overly deeply incised prosocline socket for which there is no corresponding tooth in opposing valves. In spite of this variability, the specimens are considered to represent a single species. However, examination of additional material may reveal that two species are present.

In valve shape and ornament alone, the Gill Harbor specimens are similar to other *Schafhaeutlia* (often originally listed under *Gonodon* Schafhäutl, 1863, *Cyprina* Lamarck, 1818, or *Corbis* Cuvier, 1817) in which the details of the hinge and especially dentition remain largely unknown. For example, in general outline, they appear identical to Ladinian *Crypina cingulata* Stoppani (1860-65: 84, pl. 16, figs 20–24) and to Rhaetian *Cyprina purae* Stoppani (1860-65: 124, pl. 29, figs 5–6; see also Desio, 1929: 109, pl. 1, fig. 33).

The Gill Harbor specimens are most similar to *Schafhaeutlia americana* Cox, 1949 from the Norian of Peru (Cox, 1949, pl. 2, figs 1, 2) and the Norian and Rhaetian of Chile (Hayami *et al.*, 1977; Chong & Hillebrandt, 1985, pl. 3, fig. 1). The type specimens of *S. americana* are noticeably larger, are



Text-fig. 34. *Schafhaeutlia* sp. A. 1, 2, PRI 69669, a RV; 1, interior; 2, exterior. 3, 4, PRI 69670, a RV; 3, interior; 4, exterior. 5, 6, PRI 69671, a RV; 5, interior; 6, exterior. 7, 8, PRI 69672, a LV; 7, interior; 8, exterior. 9, 10, PRI 69673, a LV; 9, interior; 10, exterior. 11, 12, PRI 69674, a RV; 11, interior; 12, exterior. Scale bars = 10 mm. All from USGS loc. M1912.

more inflated in the umbo, and have their beaks positioned slightly more anteriorly than the Gill Harbor specimens. It is unfortunate that neither the type material for *S. americana* nor the specimens from Chile reveal the features of the hinge and dentition.

The specimens may also be compared to Carnian *Schafhaeutlia astartiformis* (Münster 1841: 87, pl. 8, fig. 24), which is similar in outline and external ornament. Well preserved specimens of *S. astartiformis* from the Carnian Cassian Formation illustrated by Bittner (1895, pl. 3, figs 3, 4) demonstrate a hinge with fused and diverging cardinal teeth in both left and right valves, unlike that of the Gill Harbor specimens. Other specimens referred to *S. astartiformis*, (see for instance Scalia, 1912, pl. 3, fig. 67; Allasinaz, 1966, pl. 54, figs 6-7; Zhang *et al.*, 1979, pl. 61, figs 27-29, 31) are likewise higher than long and have a nearly circular outline.

Several additional species of *Schafhaeutlia* may be compared to *S. americana*, but differ in their outline and position of the umbo. For example, *Schafhaeutlia mellingi* Hauer (1857: 549, pl. 3, figs 1-5; see also Wöhrmann, 1889, pl. 10, figs 4-6; Ichikawa, 1950, pl. 5, fig. 8; Kiparisova *et al.*, 1966, pl. 23, figs 3-4) is less inflated and has a lower H:L ratio greater than or equal to 1 compared to a H:L ratio significantly less than

1 for the Gill Harbor specimens. Likewise, the specimens also differ from *Schafhaeutlia nakazawi* Tokuyama (1960c, pl. 13, figs 12-14) from the Carnian of Japan, which has its umbo positioned posterior of the mid length of valves and a more rounded anterior margin. *Schafhaeutlia schafhaeutli* (Salomon, 1895, pl. 5, figs 44-45) has a larger and more rounded shell.

Paleoecology.—The life habit of lucinoideans has been discussed by several workers (*e.g.*, Kauffman, 1969; Stanley, 1970; Taylor & Glover, 2000). Although originally interpreted to be filter-feeders burrowing in soft substrates relying solely on pumping water through their two separate siphons, they are now known to also rely on sulfur-oxidizing bacteria residing in the gill filaments (Taylor & Glover, 2000). The stout and inflated shell of *Schafhaeutlia* would suggest that it was a rather shallow burrower (Text-fig. 13.24).

Order **CARDITIDA** Dall, 1889
 Superfamily **CRASSATELLOIDEA** Férussac, 1822
 Family **ASTARTIDAE** d'Orbigny, 1844
 Genus **NICANIELLA** Chavan, 1945 [emend. Gardner & Campbell, 2002]

Type species.—*Astarte communis* Zittel & Goubert, 1861, by original designation, Upper Jurassic, France.

Remarks.—Chavan (1945) considered *Nicaniella* to be a primitive Astartidae and it is differentiated from *Astarte sensu stricto* by its ventrally fading concentric folds and well-defined lunule and escutcheon (see Gardner & Campbell, 2002; Damborenea & Manceñido, 2012). *Nicaniella* can be further discriminated from Upper Triassic *Astartopsis* von Wöhrmann, 1889 (type species *Myophoria richthofeni* Stur, 1868), which has a strong posterior fold, from Triassic–Cretaceous *Praeonia* Stoliczka, 1871 (type species *Astarte terminalis* Römer, 1842), which has a distinctively quadrate outline and is more posteriorly elongated, and from *Balantioselena* Speden, 1962 (type species *Balantioselena gairi* Speden, 1962), which has a characteristic extension of the lunular margin. Given that *Astarte sensu stricto* is considered a Paleogene–Recent genus, the taxonomic status of Triassic astartiid genera is in question and in need of revision. Thus, lacking suitable alternatives, the specimens at hand of many, if not most, Triassic forms with similar morphology previously attributed to *Astarte* are best accommodated by *Nicaniella*.

Nicaniella* cf. *N. incae (Jaworski, 1922)

Text-figs 35.1–35.5, 36

- cf. *Astarte incae* Jaworski, 1922: 128, pl. 5, figs 12–14.
- cf. *Astarte appressa* Gabb. Tozer, 1963, pl. 12, fig. 21.
- cf. *Astarte* sp. Newton in Newton *et al.*, 1987: 76, figs 58, 59.
- cf. *Nicaniella?* cf. *incae* (Jaworski). Damborenea & Manceñido, 2012: 328, pl. 1, figs 22, 23.

Syntypes and measurements.—Original syntypes of Jaworski, 1922: pl. 5, fig. 12, a partial RV, H = 6.0 mm, L = 4.5 mm; fig. 13, a RV, H = 6.75 mm, L = 5.0 mm; and fig. 14, a partial LV, H = 5.5 mm, L = 5.2 mm. All three syntypes under a single catalog number: STIPB-Jaworski-25. Upper Norian, Uliachin, Peru.

Material examined.—Three partially preserved right valves (PRI 69675, UMIP 15693, and UMIP 15694).

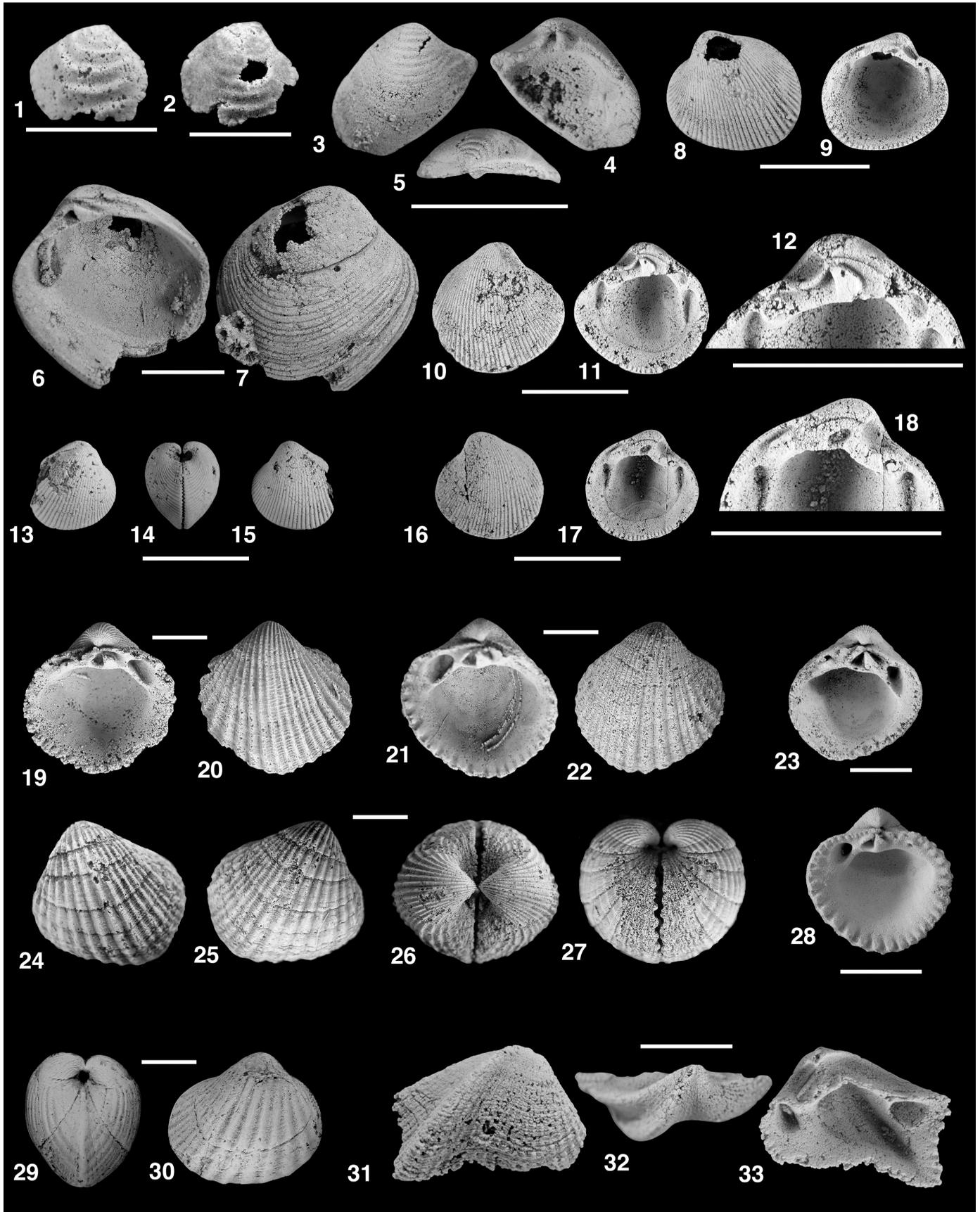
Description.—Valves small (dimensions of largest fragment: L = 9.8 mm, H = 7.3 mm), compressed (maximum W = 2.9 mm), inequilateral, subtrigonal in outline, nearly as long as high; beak rather sharp, prosogyrous; umbones broad and slightly projecting above beak; with moderately impressed lunule limited by a rounded margin; escutcheon elongated, smooth, and bordered by sharp carina; exterior with five to

seven coarse concentric regularly-spaced folds which are somewhat weaker on the posterior sector of valve and fade in strength towards the ventral margin, in cross-section dorsal sides of folds are steeper than ventral sides; hinge of RV with strong cardinal tooth (*3b*) and posteriorly and anteriorly adjacent deep cardinal sockets; weak anterior lateral (*A1*) dorsally bordered by a shallow groove. RV with a partially preserved posterior adductor scar, moderately impressed and subcircular. Given the fragmentary nature of the Gill Harbor specimens, several morphological features, including features of the LV interior and a denticulate margin can only be inferred.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Although they can be quite common, Triassic Astartidae are generally small and poorly preserved with most species being named solely on size, shape, and details of external ornament. Hinge elements are known from only few Triassic astartiid species and, apart from those attributed to *Balantioselena* Speden, 1962 and *Praeonia* Stoliczka, 1871, vary little in their strong cardinal dentition (RV with a robust *3b* and a weak or obsolete *3a* and a LV with a strong 2 and *All*).

The Gill Harbor specimens are most similar to and may be conspecific with *Astarte incae* Jaworski, 1922 from the Norian of Cerro de Pasco, Peru. Jaworski's (1922) Peruvian species, based on a partial RV (pl. 5, figs 12, 13) and partial LV (pl. 5, fig. 14), have intact hinge elements that permit meaningful comparison to those from Gill Harbor. Jaworski's RV in particular exhibits the robust and moderately steep *3b* as in UMIP 15694 (Text-fig. 35.3) from Gill Harbor. Jaworski (1922) noted that a posterior cardinal (*4b*) is absent in the LV of *A. incae*, although there exists a clear, albeit weak, receiving socket in the opposing RV in his original illustrations (pl. 5, fig. 12a) which appears to be somewhat deeper in the Gill Harbor specimen. It should be noted that Newton (in Newton *et al.*, 1987: 77) observed a posterior cardinal tooth (*4b*) on the LV in several specimens attributed to *A. incae* among the undescribed Peruvian collections at the AMNH. Another minor difference, perhaps attributable to interspecific variation, is that the Peruvian specimens appear to have a shallower lunule than those from Gill Harbor. Cox (1949: 29) listed (but did not illustrate or describe) *Astarte incae* as occurring from near La Cima Peru. Elsewhere in South America, Damborenea & Manceñido (2012, pl. 1, figs 22, 23) illustrated two specimens as belonging to *Nicaniella?* cf. *incae* (Jaworski, 1922) from the Atuel River section in southern Mendoza, Argentina. One of the Argentinian specimens, a RV (pl. 1, fig. 23), has a well-preserved hinge with a robust



cardinal tooth (3*b*) nearly identical to those of the Gill Harbor specimens (Text figs 35.4, 36).

Among North American Triassic astartids, the Gill Harbor specimens appear to be conspecific with those from the lower Norian of Oregon (Newton in Newton *et al.*, 1987, figs 58, 59). Both sets of specimens appear identical in external ornament and have a well-preserved left valve hinge that is particularly clear in one of the Oregon specimens (Newton in Newton *et al.*, 1987, fig. 58, USNM 416459). Externally similar forms were described from the mid Norian of Taylor Mountains Alaska (McRoberts in McRoberts & Blodgett, 2002, pl. 2, figs 7, 8).

These specimens differ significantly from several named *Astarte* which exhibit a significantly higher number of commarginal folds (e.g., *Astarte* sp. of Yin & McRoberts, 2006, figs 6.34, 6.36–6.41). Similarly, the present specimens differ from *Astarte andicola* Cox (1949, pl. 2, fig. 3) from the Norian of Peru in their greater number, and more narrowly spaced, commarginal folds. Given the present interpretation of *Astarte*, both of these examples should probably be transferred to *Nicaniella*.

Paleoecology.—Modern astartiids are ecologically complex with various species having quite different temperature, depth, and substrate preferences (Saleuddin, 1965). Based on it inflated valves and commarginal rugae, *Nicaniella* cf. *N. incae* is regarded as a shallow nonsiphonate burrower (Text-fig. 13.21).

Family CARDINIIDAE Zittel, 1881

Cardiniidae gen. et sp. indet.

Text-figs 35.6, 35.7

Material examined.—A single incomplete RV (PRI 69676).

Description.—RV of moderate size (L = 24.1mm, restored H = 24.8 mm), moderately inflated (W = 9.1 mm); ovate with dorsal margin; inequilateral; beak weakly prosogyrous, positioned anteriorly at approximately one-third entire L; umbo broadly rounded, extending well above hinge; lacking lunule and escutcheon; RV hinge plate narrow with curved ventral margin, with strong triangular prosocline cardinal tooth (3*b*), bordered anteriorly with deep triangular socket to receive car-

dinal tooth (2?) of the LV, with weak tuberculiform anterior lateral (AIII) on ventral hinge margin dorsal to anterior adductor scar, with elongated posterior lateral (PI) well separated from cardinal area and forming the ventral extremity posterior hinge margin; ligament opisthodontic, external, relatively short (5.5 mm), and bordered ventrally by a relatively strong nymph; adductor scars deep, ovate and subequal with anterior one being smaller and more deeply impressed than posterior scar; external surface smooth during early growth (to about 8 mm from beak), then ornamented with pronounced commarginal imbricated growth lamellae at about 0.5 mm through most of ontogeny, but becoming irregular at later growth stages.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Placement of PRI 69676 in the Cardiniidae is based on the distinctive dentition of the RV, characteristic external ornament, and valve shape. Although there are some similarities in ornament between PRI 69676 and specimens assigned to *Schafhaeutlia*, this RV is strongly inequilateral and possesses a single cardinal tooth and both posterior and anterior laterals. It differs from Upper Triassic and Lower Jurassic *Cardinia* Agassiz, 1841 [type species *C. listeri* (J. Sowerby, 1817)] in lacking a prominent lunule and escutcheon. Although much larger in size, the general parameters of the shell outline and features of the hinge appears to be very similar to Ladinian *Balantioselena* Speden, 1952 from New Zealand, but this genus too possesses a deep lunule.

Paleoecology.—Like other cardiniids, Cardiniidae gen. et sp. indet. is regarded as a shallow nonsiphonate burrower.

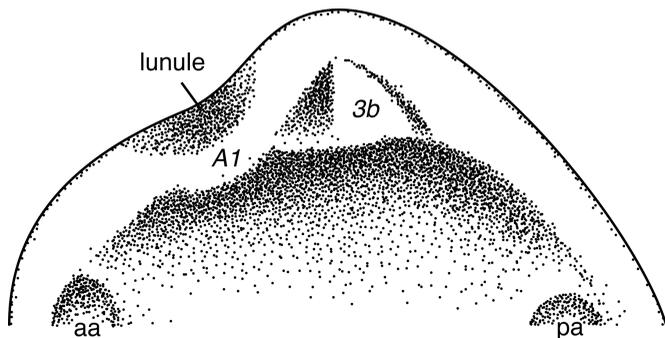
Superfamily CARDITOIDEA Fleming, 1820

Family CARDITIDAE Fleming, 1828

Genus TUTCHERIA Cox, 1946

Type species.—*Cardium submulticostatum* D'Orbigny, 1850 [= *Cardium multicostatum* Phillips, 1829], by original designation, Lower Jurassic (Pliensbachian), Yorkshire, England.

Text-fig. 35 (at left). *Carditida*. 1–5, *Nicaniella* cf. *N. incae* (Jaworski, 1922). 1, PRI 69675, RV exterior. 2, UMIP 15693, RV exterior. 3–5, UMIP 15694, a LV; 3, exterior view; 4, interior view showing details of hinge; 5, dorsal view. 6, 7, *Cardiniidae* gen. et sp. indet., PRI 69676, a RV; 6, interior view; 7, exterior view. 8–18, *Tutcheria densestriata* (Körner, 1937). 8, 9, UMIP 15695, a LV; 8, exterior view; 9, interior view. 10–12, UMIP 15696, a RV; 10, exterior view; 11, interior view; 12, detail of hinge. 13–15, PRI 69677, articulated valve pair; 13, RV exterior; 14, anterior view; 15, LV exterior. 16–18, UMIP 15697, a LV; 16, exterior view; 17, interior view; 18, detail of hinge. 19–28, *Septocardia peruviana* (Cox, 1949). 19, 20, PRI 69678, a RV; 19, interior view; 20, exterior. 21, 22, PRI 69679, a LV; 21, interior view; 22, exterior view. 23, PRI 69680, a RV exterior. 24–27, PRI 69681, articulated valve pair; 24, LV exterior; 25, RV exterior; 26, dorsal view; 27, posterior view. 28, PRI 69682, a RV exterior. 29, 30, *Septocardia arcaeformis* (Gabb, 1870), holotype, MCZ109974, articulated valve pair, Gabbs Formation, New York Canyon, Nevada; 29, posterior view; 30, RV exterior. 31–33, *Schizocardia* sp. indet., UMIP 15698, a RV; 31, exterior view; 32, dorsal view; 33, interior view. Scale bars = 10 mm. 1–28, 31–33 from USGS loc. M1912.



Text-fig. 36. Illustration of internal structures of RV of *Nicaniella* cf. *N. incaea* (Jaworski, 1922). Cardinal tooth (3b) and anterior lateral tooth (A1), aa = anterior adductor muscle scar, pa = posterior adductor muscle scar.

Remarks.—As summarized by Ros-Franch *et al.* (2014), *Tutcheria* is well known from at least the Late Triassic (Carnian) through Middle Jurassic (Aalenian). During the Norian and Rhaetian, representatives of the genus are particularly abundant from numerous shallow-water, low to mid paleolatitude localities throughout the Tethys and the margins of Panthalassa (*e.g.*, Körner, 1937; Laws, 1982; Newton in Newton *et al.*, 1987; Ivimey-Cook *et al.*, 1999; Hautmann, 2001b). It is apparently not known to occur at high paleolatitudes.

***Tutcheria densestriata* (Körner, 1937)**

Text-figs 35.10–35.18, 37

Cardium densestriatum Körner, 1937: 196, text-fig. 5, pl. 12, figs 9a–c.

Tutcheria densestriata (Körner). Cox, 1949: 30, pl. 2, fig. 8; Newton, 1986: pl. 2.1, figs 8, 9; Newton in Newton *et al.*, 1987: 69, figs 52.1–52.5; McRoberts in McRoberts & Blodgett, 2002: 61, figs 5.1–5.6.

Tutcheria cf. *T. densestriata* (Körner). Tozer, 1963, pl. 12, fig 20 a, b.

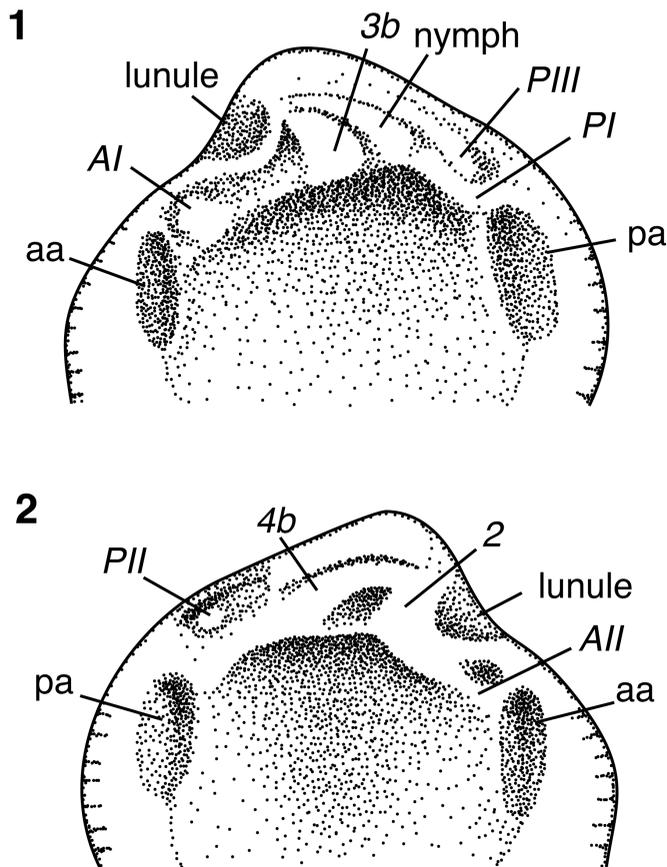
Syntypes and measurements.—Original syntypes of Körner, 1937 (pl. 12, figs 9a–c): fig. 9a, a RV, H = 18 mm, L = 19 mm, W = 6 mm; fig. 9b, a LV, H = 13 mm, L = 12.5 mm, W = 4 mm; fig. 9c, a LV, H = 11.5 mm, L = 12.5 mm, W = 3 mm.

Material examined.—The Gill Harbor collection consists of 55 mostly complete specimens (22 LV, 30 RV, and three conjoined valve pairs) plus numerous smaller fragments. Cataloged and illustrated specimens include: two left valves (UMIP 15696, UMIP 15697), one right valve (UMIP 15695), and one conjoined valve pair (PRI 69677; Text-figs 35.13–35.15). See Table 7 for measurements of Gill Harbor specimens.

Description.—Shells small (maximum L = 14.0 mm, maximum H = 14.4 mm, mean L = 8.3, mean H = 8.3), moder-

ately inflated (maximum W = 5.3 mm, mean W = 2.9 mm); as high as long (H:L = 0.9–1.1, mean = 1.0); trigonally orbicular in outline; umbone strongly prosogyrous with beak well above hinge margin; lunule very deeply impressed and bordered by weak ridge; lacking escutcheon; posterior and ventral margins evenly convex, anterior margin slightly more acutely convex than posterior; surface ornamented by densely packed radial riblets numbering between 40–50, with sub-round crests of nearly equal strength running from beak to ventral margin separated by narrow furrows, radial ornament may be intersected with widely-spaced and imbricated commarginal growth lines; pallial line continuous, integripalliate, positioned approximately 2 mm from denticulated ventral inner margin; dymyrian with moderately large and vertically-elongated oval anterior and posterior adductor scars, posterior slightly larger than anterior; scars are more deeply impressed on their dorsal margin near hinge and towards valve interior; RV hinge with a strong and posteriorly-sloping triangular cardinal tooth (3b); steeply sloping triangular nymph postero-dorsal to 3b and receiving socket for the 4b of the LV; anterior lateral (A1) short, well separated from cardinal, strongly tuberculiform and dorsally bordered by an elongate groove to receive the AII of the LV; posterior lateral (PI) weak, forming narrow ridge along ventral margin of hinge plate; PIII moderately strong, swelling near posterior extremity; with prominent and moderately deep oval recess situated between PI and PIII to receive the knob-like posterior lateral (PII) of the LV. LV hinge with a thin anterior cardinal (2) that extends to the lunular margin; thin and subhorizontal posterior cardinal (4b); posterior lateral (PII) strong, projecting and knob-like, well separated from cardinals; moderately deep recess dorsal to PII to accept expanded part of PIII of RV; anterior lateral (AII) poorly developed as part of lunular margin; with small but prominent recess ventral to the anterior extremity of AII to receive the tubercular portion of the AI of the RV.

Remarks.—The well-preserved hinges, muscle scars, and external ornament of the Gill Harbor specimens clearly place them in *Tutcheria* (see Cox 1946; Chavan, 1969c) and permit confident assignment to *Tutcheria densestriata* (Körner, 1937), originally described from the Norian of Nevado de Acrotambo, Peru. Körner's (1937) figured types and those of Newton (in Newton *et al.*, 1987, figs 52.1–52.5) from the lower Norian of Oregon show the typical dentition of this species, which is characterized by its robust triangular and steeply cardinal tooth 3b and its deeply concave lunule. This species is now well known from several additional localities in Peru. Cox (1949) illustrated the exterior of a single RV from near La Cima in central Peru and included in his synonymy specimens described, but not illustrated, by Jaworski (1922: 135) as *Cardium Héberti* Terquem from the same region. The Gill Harbor specimens also appear to agree well with the sin-



Text-fig. 37. Illustration of internal structures of *Tutcheria denestriata* (Körner, 1937). 1, RV; 2, LV. Abbreviations: cardinal dentition (3b, 2, 4b), and lateral teeth (AI, AII, PI, PIII), aa = anterior adductor muscle scar, pa = posterior adductor scar.

gle RV that Tozer (1963, pl. 12, figs 20a, b) illustrated from the upper Norian of Vancouver Island, Canada, although the hinge of the Canadian specimen is too poorly preserved for definite comparison.

Tutcheria densestriata may be compared to *T. cloacina* (Quenstedt, 1856), which is common from the Rhaetian across Northwest Europe eastward into the Northern Calcareous Alps and Carpathians and into the central Tethys (e.g., Böckh & Lóczy, 1912; Ivimey-Cook *et al.*, 1999; Hautmann, 2001b). *Tutcheria cloacina* are generally larger in size, with greater valve inflation and a much lower radial rib count (e.g., *T. cloacina* commonly possess ~ 30 radial costae compared to ~ 45 for *T. denestriata*).

Occurrence.—Here reported from the upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912). Apart from the type area and elsewhere in Peru (Körner, 1937; Cox, 1949), the species is moderately common in lower Norian strata from northeastern Oregon (Newton in Newton *et al.*, 1987), the mid Norian of central Alaska

(McRoberts in McRoberts & Blodgett, 2002) and possibly from the Rhaetian of Vancouver Island (Tozer, 1963).

Paleoecology.—Given that these small, convex and equivalved carditids have a lunule and lack a pallial sinus, they are interpreted to be shallow nonsiphonate burrowers (Text-fig. 13.22; see also Newton in Newton *et al.*, 1987; Hautmann, 2001b).

Family **PALAEOCARDITIDAE** Chavan, 1969d
[emended]

Septocardiidae Kafanov & Starobogatov in Kafanov & Popov, 1977: 61.

Original diagnosis.—Chavan (1969d: N554): “Posteriorly elongated to trigoniform, beaks orthogyrous or opisthogyrous, tending to be recurved. Hinge with high pointed 3b.”

Emended diagnosis.—Carditoidea with rounded, trigonal, posteriorly elongate to nearly equilateral shells; beaks primarily opisthogyrate to orthogyrate, rarely prosogyrate; ornamented with strong radial costae with denticulate to crenulate inner margin, possessing moderately to strong posterior carina; dentition with prominent cardinals (3a and 3b on RV and 2 and 4b on LV), posterior laterals (PI and PII), lacking anterior laterals; pallial line continuous, integripalliate; adductor muscle scars ovate, high, with anterior scar moderately to deeply impressed, separated from valve interior by internal ridge or septum of variable strength.

Remarks.—The Palaeocarditinae was introduced by Chavan (1969d) for Carditidae with a high and pointed cardinal tooth (3b) of the RV. As originally construed, the Palaeocarditinae included Upper Triassic *Palaeocardita* Conrad, 1867, Lower Devonian *Carditomantea* Quenstedt, 1929, *Pseudopis* Cox, 1946, and *Schizocardita* Körner, 1937. The subfamily was elevated to family rank in Schneider & Carter (2001) and more recently by Carter *et al.* (2011), who considered Palaeocarditidae as a paraplesion aligned to the Cardiida rather than the Carditida as interpreted herein.

Most Palaeocarditidae bear a distinctive dentition characterized by prominent cardinals (3a and 3b on RV and 2 and 4b on LV), and weak to moderately strong posterior laterals (PI on RV and PII on LV) with some species of *Palaeocardita* also possessing an additional, albeit weak, posterior lateral, PIII, on the LV). Unlike other Carditidae (e.g. *Tutcheria* Cox, 1946 and also possibly *Pseudopis* Cox, 1946), Palaeocarditidae lack anterior laterals. The similarities of the cardinal hinge elements of *Palaeocardita* to those of other *Cardita*-like heterodonts have been noted by many early workers, yet it is interesting to note that Neumayr (1891) minimized the importance of the dentition, and con-

Table 7. Measurements for *Tutcheria densestriata* (Körner, 1937).

Specimen	Valve	Length (mm)	Height (mm)	Width (mm)	H:L
UMIP 15695	LV	11.3	11.1	4.7	1
--	LV	10.9	10.7	4.1	1
UMIP 15697	LV	10.2	10.2	3.8	1
--	LV	14	14.4	5.3	1
--	LV	7.6	7.6	2.5	1
--	LV	9.6	9.4	3.4	1
--	LV	6.5	7.1	2.1	1.1
--	LV	7.5	7.4	2.2	1
--	LV	8.8	8.6	3.3	1
--	LV	6.7	6.1	2	0.9
--	LV	7	7.5	2.1	1.1
--	LV	8.1	8.6	2.8	1.1
--	RV	11.2	11.2	4	1
--	RV	11.1	11	4.3	1
--	RV	9.9	10	3.1	1
--	RV	7.1	7	2.3	1
--	RV	7.1	7.3	2.1	1
--	RV	6.5	5.8	2	0.9
--	RV	6.7	6.9	2.1	1
--	RV	7	7.2	2.6	1
--	RV	6.5	6.4	2	1
--	RV	6.2	6.4	2	1
--	RV	5.7	5.5	2	1
--	RV	6.1	5.3	1.8	0.9

sidered *Palaeocardita* within his largely edentulous (or with pseudodont) group 'Cryptodonten' (= subclass Cryptodonta of Newell, 1965 and more recent authors). *Palaeocardita* as a cryptodont is untenable given the well-documented cardinal and posterior lateral dentition. Like *Palaeocardita*, the dentition of *Pseudopsis* and *Schizocardita* Körner, 1937 (and also *Septocardia* Hall & Whitfield, 1877, as discussed below) is well known and is unlike other cryptodonts lacking true heterodont dentition.

Pseudopsis Cox, 1946 (type species *P. astonensis* Cox, 1946), a largely Lower Jurassic genus, exhibits a distinctive dentition characterized by relatively strong cardinal teeth (2, 3b, and 4b), variably strong posterior laterals (*PI* and *PII*), and a single anterior lateral present on each valve. Cox (1946: 44) introduced the genus to distinguish species with an *Opis*-like strongly bicarinate shape and external ornament which possessed a *Tutcheria*-like dentition, but with a more poorly developed *PI* tooth separating it from those species more typically representative (both internally and externally) of *Tutcheria*. He remarked on the similarity of these forms to *Astarte* and further commented that most Late Triassic species assigned to *Opis*

Defrance, 1825 (e.g., *O. ladinia* Bittner, 1865 or *O. barnensis* Stoppani, 1861) lack the prominent lateral teeth of *Pseudopsis* and *Tutcheria*. Contrary to Chavan's (1969d) placement of *Pseudopsis* into the Palaeocarditinae, the presence of the anterior laterals, which are absent in *Palaeocardita*, *Schizocardita*, and *Septocardia*, suggest this genus is better placed closer to *Tutcheria*, as originally implied by Cox (1946).

The monotypic *Carditomantea* Quenstedt, 1926, which Chavan (1969d) included in the Palaeocarditinae, is only known from the Lower Devonian of Spitsbergen. Chavan (1969d) was likely swayed by Quenstedt's (1926: 19) comparison to the cardinal dentition of Triassic *Palaeocardita* and his schematic drawing of the hinge (Quenstedt, 1926, 19–20, text-fig. 1; reproduced in Chavan, 1969d, fig. E54–3b). However, the specimens of *Carditomantea* upon which Quenstedt (1926, pl. 1, figs 1–8) erected the genus are poorly preserved molds and are not fully consistent with his written interpretation or his schematic of the hinge. The one specimen reported to possess cardinal dentition (Quenstedt, 1926; pl. 1, fig. 8, denoted with an 'H' for Hauptzahn) appears to be better explained as a preservational artifact. Further sup-

port for removing *Carditomantea* from the Palaeocarditidae can be found with Quenstedt's (1926) observation that *Carditomantea* lacks evidence of any posterior lateral dentition, which is prominent in other Palaeocarditidae and Carditidae. Additional differences between *Carditomantea* and *Palaeocardita* also can be found in musculature and sculpture. Given these observations, *Carditomantea* is better interpreted as likely possessing pseudotaxodont teeth below the beaks similar to those of several lower and middle Paleozoic praecardiids (e.g., *Maminka* Barrande, 1881 and likely also *Deltacardium* Nagel, 2006) as per Nagel-Meyers (personal commun., 2015; see also Nagel, 2006).

Schizocardita Körner, 1937 is based on several well preserved specimens from the Norian of Peru which clearly illustrate a *Palaeocardita*-like dentition. The original specimens of Körner (1937, pl. 7, figs 8a–d) show the LV with two strong cardinals (2 and 4b), the posterior of which is shorter and more blunt, and a well-developed posterior lateral tooth (*PII*). The RV of *Schizocardita* also possesses two cardinal teeth (3a and 3b), with the anterior one smaller and more oblique than the posterior, and with an elongated and slightly curved marginal posterior lateral (*PI*). The anterior adductor scar of *Schizocardita* is also moderately impressed and separated from the remainder of the interior by a low ridge or septum. Based on this dental configuration and other similarities with regards to musculature and external ornament, and following Chavan (1969d), *Schizocardita* is retained in the Palaeocarditidae.

Septocardiidae was introduced by Kafanov & Starobogatov (in Kafanov & Popov, 1977: 61) as a monogeneric family containing *Septocardia*. In their familial diagnosis, Kafanov & Starobogatov (in Kafanov & Popov, 1977) reiterated the *Treatise* diagnosis of the genus (Keen, 1969) and remarked that the family is characterized by prominent cardinal dentition (3a, 3b, and 2); other features like external ornament were also listed as characteristic of the family. As noted above, the dentition of *Septocardia* is similar in many regards to *Palaeocardita* and, as remarked by several workers (e.g., Newton in Newton *et al.* 1987), the two genera appear to be very closely related. Thus, following Schneider & Carter (2001) and more recently Carter *et al.*, (2011), the Septocardiidae is considered a synonym of Palaeocarditidae.

Genus **SEPTOCARDIA** Hall & Whitfield, 1877
[emended]

Pascoella Cox, 1949: 33.

Type species.—*Septocardia typica* Hall & Whitfield, 1877: 294 [= *Septocardia cardioidea* Hall & Whitfield, 1877], by original designation, Upper Triassic (Rhaetian), Nevada.

Original diagnosis.—Hall & Whitfield (1877: 294–295): “Shell bivalve, equivalve, inequilateral, cardiform. Hinge strong; right valve with a strong, recurving, hooked tooth under the beak, and a deep cavity below and exterior to it, which is profoundly excavated in the thickened substance of the shell. In the left valve, a large, deep cavity corresponds to the tooth of the right valve. Lateral teeth obsolete. Ligament external, situated in a groove formed by a thickened, overlapping portion of the shell posterior to the tooth and corresponding cavity. Anterior adductor muscular scar very large and deep, separated from the general cavity of the shell by a calcareous plate, or septum, extending across the anterior end of the valve on the inner side of the scar, thereby forming a distinct chamber in each valve. Posterior adductor scar much smaller, situated within the posterior cardinal margin. Pedal scars not observed. Surface of the shell marked, in the typical species, by strong, elevated, radiating ribs, with ornamented surfaces similar to many of the recent species of *Cardium*.”

Emended diagnosis.—Palaeocarditidae with impressed anterior adductor scar forming a deep cavity and separated from valve interior by strong septum; ligament groove deep and bordered ventrally with a slightly upturned nymph; dentition with strong cardinals with teeth 2 and 3b being the most prominent, with tuberculate posterior lateral tooth (*PII*); posterior adductor scar more deeply impressed than anterior scar; ornamented with pronounced radial costae, angular in cross section producing crenulated to denticulated valve margin, and transversed with fine commarginal imbricated growth lines.

Remarks.—Triassic *Septocardia* was discussed in some detail by Silberling (1959), Keen (1969), Newton (1983; in Newton *et al.*, 1987), and McRoberts (in McRoberts & Blodgett, 2002). As noted by Newton (in Newton *et al.*, 1987), and more recently Schneider & Carter (2001), *Septocardia* is closely related to *Palaeocardita*. As discussed above under the family remarks, although somewhat variable, the general parameters of dentition are similar between the two genera; therefore, the primary criterion for differentiating the two is the presence (in *Septocardia*) of the deeply recessed anterior adductor muscle scar and thick wall or septum separating the adductor cavity from the remainder of the valve interior. The question remains, however, as to how deep the anterior adductor cavity and how strong the dividing septum must be for species to be assigned to *Septocardia*. There is certainly some variability in this trait and it appears that there is a continuum in this feature between the two genera. Thus, several taxa, primarily assigned to *Palaeocardita*, appear to be transitional between the two genera. For example, *Palaeocardita crenata* Münster, 1841 and *Palaeocardita pichleri* Bittner, 1895, both from the Cassian Formation of Northern Italy (see also Zardini, 1981),

have been transferred to *Septocardia* even though the septum dividing the anterior adductor scar and valve interior is only weakly developed (see Schneider & Carter, 2001). Also included in this group of transitional forms is the common species *Cardita globiformis* Boettinger (in Verbeek *et al.*, 1880, pl. 1, figs 21–23) from the Carnian of Sumatra (see also Krumbeck, 1914, pl. 27, figs 20–25) and also the Norian-Rhaetian of Iran (Hautmann, 2001b). Additional transitional forms include *Palaeocardita buruca* Böhm, 1913 from the Norian of Timor (see Krumbeck, 1924, pl. 19, figs 28, 28 for a particularly illustrative example), and *Palaeocardita iranica* var. *multi-radiata* Hautmann (2001b, pl. 33, fig. 16, pl. 34, figs 1–6). In addition, numerous examples exist of species whose external morphology strongly suggests inclusion into *Septocardia*, but for which diagnostic internal features (dentition and deeply recessed anterior adductor scar and dividing septum) remain unknown. Among the more common species to fall into this category is *Cardita jenkinsi* Smith (1927, pl. 96, fig. 2) from the Carnian Hosselkus Limestone of northern California. Also included in this group are the multiple additional examples listed under various subspecies of *Palaeocardita buruca* (Krumbeck, 1913), and *P. singularis* (Healey, 1908), which was illustrated in Zhang *et al.* (1985, pl. 9).

***Septocardia peruviana* (Cox, 1949)**

Text-figs 35.19–35.28, 38

Pascoella peruviana Cox, 1949: 35, pl. 1, figs 9, 12a, 13, 14 (not pl. 2, fig. 5).

Septocardia typica Hall & Whitfield, 1877. Keen, 1969: N586, figs E85 1a–e (not figs E85 1f–h).

Septocardia peruviana (Cox). Hayami *et al.*, 1977: 215, pl. 29, figs 8a, b, 9a–c, 10; Chong & Hillebrandt, 1985, pl. 3, figs 4–6.

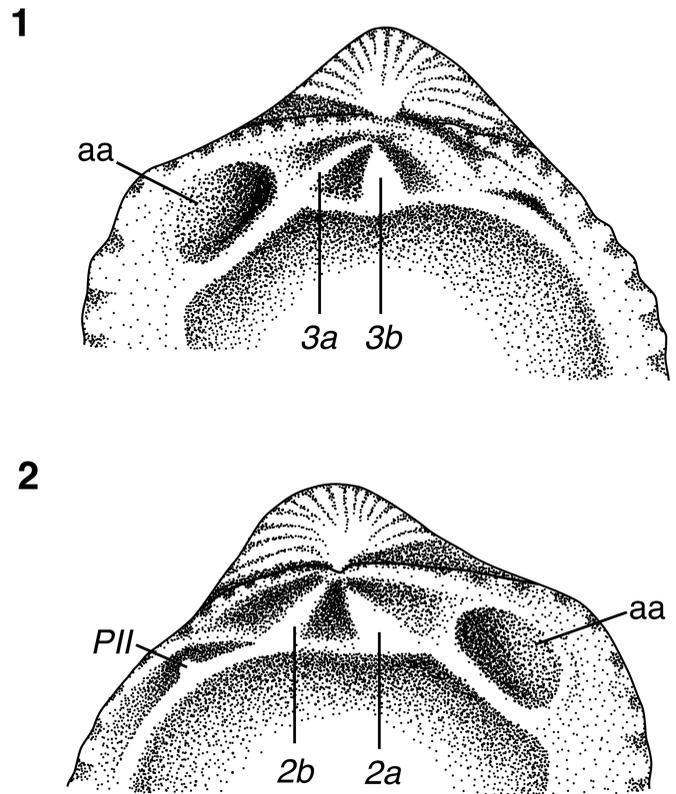
cf. *Septocardia?* sp. Silberling, 1959: 61, pl. 9, figs 1–8.

?*Septocardia* sp. Newton in Newton *et al.*, 1987: 77, fig. 60.

Septocardia cf. *S. peruviana* (Cox). McRoberts in McRoberts & Blodgett, 2002: 62, pl. 2, figs 5–14.

Holotype and measurements.—Holotype, BML 78245, a RV (Cox, 1949: 35, pl. 1, fig. 15); L = 46 mm, H = 46 mm, W = 24 mm.

Material examined.—The collection from Gill Harbor consists of 95 valves including 50 left, 44 right, and one conjoined valve pair. Cataloged and illustrated specimens include: two LV (PRI 69678, PRI 69680), two RV (PRI 69679, PRI 69682), and one conjoined valve pair (PRI 69681). In addition, numerous fragments of both left and right valves contributed to the description. See Text-fig. 39 for measurement data from the Gill Harbor specimens.



Text-fig. 38. Illustration of internal structures and dentition of *Septocardia peruviana* (Cox, 1949). 1, RV, 2, LV. Abbreviations: cardinal dentition (3a, 3b, 2a, 2b), posterior lateral tooth (Pll), aa = anterior adductor muscle pit separated from body cavity by septum.

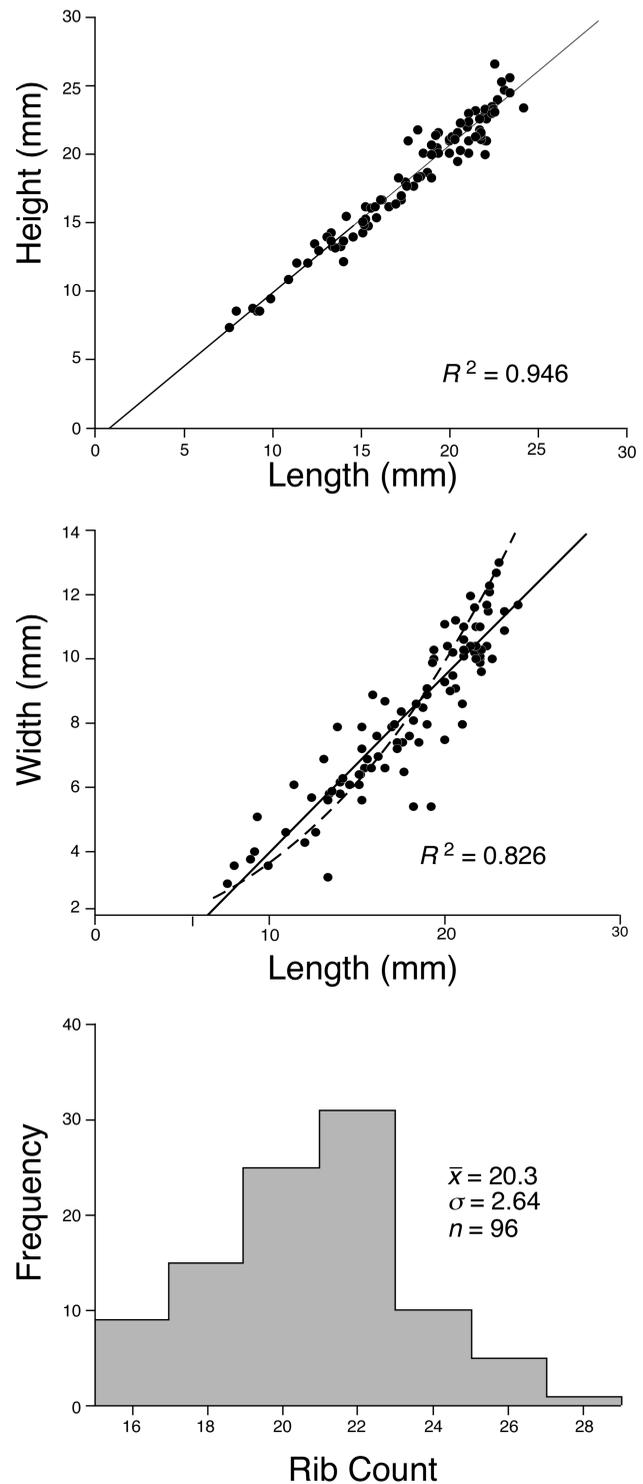
Description.—Valves moderately large (maximum L = 24.2 mm, maximum H = 26.6 mm), highly inflated (maximum W = 13.0 mm), and thick (maximum valve thickness = 3.0 mm). Equivalved and inequilateral with beak slightly anterior; oval to subquadrate in outline, nearly as high as long (mean H:L = 1.03); exterior surface ornamented by 15–28 (mean = 20.3) radial angular costae with v-shaped intercostal furrows; both costae and furrows are transversely by fine commarginal growth striae; more prominent growth lines beginning around 10 mm from beak occur at increasingly narrower intervals becoming tightly bundled at valve margin in adults; crenulate inner valve margin; hinge area sloping from beak; parvincular ligament groove short, triangular shaped, extending posteriorly from beak and bordered below by nymph, which is slightly more raised in the RV; cardinal dentition strong; LV with a robust anterior and somewhat triangular prosocline cardinal tooth (2) with two adjacent sockets, posterior one directly below beak and forward one prosocline intersecting lower hinge margin, with poorly developed elongated posterior lateral tooth or ridge extending nearly to hinge margin and terminating in a single pronounced tubercle-like process and bordered above by shallow groove; RV with two cardinal teeth (3a, 3b) converging dorsally below beak; the medial one

directly below umbo is triangular and essentially orthocline and the anterior one somewhat elongated and prosocline; anterior hinge plate with small occluding ridge on its ventral margin extending to form septum of anterior adductor cavity; pallial line continuous, integripalliate; anterior adductor scar oval, very deep, and separated from rest of valve interior by thick septum; posterior adductor scar ovate.

Occurrence.—Here reported from the upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912). Elsewhere from the Norian of Cerro de Pasco, Peru (Cox 1949); Norian and Rhaetian from Chile (Chong & Hillebrandt, 1985); lower Norian of Taylor Mountains, Alaska, Nixon Fork terrane (McRoberts in McRoberts & Blodgett, 2002); lower Norian of Hells Canyon, Oregon, Wallowa terrane (Newton in Newton *et al.*, 1987).

Remarks.—The number of well preserved specimens from Gill Harbor permits meaningful comparison with specimens Cox (1949) illustrated from Peru as *Pascoella peruviana*. The Gill Harbor specimens agree in size, shape, and external sculpture and all internal elements of the hinge. Cox (1949) described two tubercle-like depressions in the posterior hinge margin and hypothesized that these received projections that were not preserved on the left valve. The Gill Harbor specimens, however, clearly show a single such process on the left valve and receiving recess on the right. The noted similarity between the Gill Harbor *Septocardia* and those from Peru was commented on by Newton (1983). Subsequently, McRoberts (in McRoberts & Blodgett, 2002) described silicified *Septocardia* similar to the Peruvian forms from the Nixon Fork terrane from south-central Alaska. Although lacking observable valve interiors and dentition, the specimens attributed by Silberling (1959: 61, pl. 9, figs 1–8) to *Septocardia?* sp. from the upper Carnian (or perhaps lower Norian) Luning Formation of the Shoshone Mountains, Nevada (USGS locs M71, M72a) also appear similar in outline and ornament to *S. peruviana*.

This species is quite similar to *Septocardia arcaeformis* (Gabb, 1870) from Nevada. The type locality of *S. arcaeformis* is in question (Silberling, 1959), but specimens from the Rhaetian Mount Hyatt Member of the Gabbs Formation of New York Canyon, Nevada (D. Taylor, personal communication, 2006) appear indistinguishable from specimens in the type collection. Study of the original type specimens (Gabb, 1870, pl. 3, figs 9, 9a; MCZ 109974), one of which is reproduced here (Text-figs 34.29, 34.30), does not reveal the internal structures of the hinge. This specimen (MCZ 109974) and other *S. arcaeformis* from the New York Canyon locality possess fewer costae and are more posteriorly elongate than *S. peruviana*.



Text-fig. 39. Measurements and descriptive statistics of *Septocardia peruviana* (Cox, 1949) from USGS loc. M1912. Upper plot, scatter plot and least-squares regression of length versus height; middle plot, scatter plot and least-squares (solid line) and second-order polynomial (dashed line) regression of length versus width; lower plot, frequency histogram of rib count.

Septocardia peruviana can also be compared with *S. typica* Hall & Whitfield, 1877, originally described from likely mid to upper Norian strata from the Clan Alpine Range of Nevada (see Silberling, 1959, who also included *S. carditoidea* Hall & Whitfield, 1877 in this species). The syntypes of *S. typica* (USNM 12538) are represented by three small and poorly preserved specimens (two RVs and one LV). Further, the holotype of *S. carditoidea* is an articulated valve pair (USNM 12549) that, as previously noted by Silberling (1959: 59), does not match the quality or completeness of Hall and Whitfield's original illustrations (Hall & Whitfield, 1877, pl. 7, figs 25–29). Based on the syntypes and other topotype material collected by N. Silberling and S. Muller in 1952 and 1953 (unpublished USGS collections in Denver), it is clear that *S. typica* has a more rounded anterior adductor cavity that is situated in a much more ventral position and is more posteriorly elongated, with a somewhat more concave posterodorsal margin than found in *S. peruviana*. It should be noted that Keen (1969) illustrated several specimens attributed to *S. typica*, of which two valves (Keen, 1969, figs E85-1a–e) represent Hall & Whitfield's type specimens; the other two (Keen, 1969, figs E85-1a–e) are from undescribed USGS collections from USGS loc. M1912 at Gill Harbor and are removed from *S. typica* and placed in *S. peruviana*.

Outside of the Americas, there are numerous species (mostly listed under *Cardita* or *Palaeocardita*) that more correctly belong in *Septocardia* and can be compared to *S. peruviana*. For example, the LV interior of *Palaeocardita singularis* (Healey, 1908) of Zhang *et al.* (1985, pl. 10, fig. 5b) clearly shows a septum and should be transferred to *Septocardia*.

Paleoecology.—Recent carditids display a range of living habits, from free-living burrowing species to endobysate and epibysate life modes (Stanley, 1977). Like other carditids that lack a pallial sinus (*e.g.*, Stanley, 1970), *Septocardia peruviana* was likely a shallow burrower with very short siphons or lacking siphons altogether and had its commissure plane vertically oriented and its posterior margin inclined upwards (Text-fig. 13.23). Additionally, this taxon exhibits marginal crenulations which, according to Stanley (1970), is a trait that chiefly occurs in shallow infaunal or epifaunal species with spherical valves.

Genus *SCHIZOCARDITA* Körner, 1937

Type species.—*Schizocardita cristata* Körner, 1937, by original designation, Upper Triassic (Norian), Peru.

Remarks.—*Schizocardita* are quite rare in the Upper Triassic and are previously only known by the type species *S. cristata* Körner, 1937 from the Norian of Peru. The potential occur-

rence from the Norian of Alaska would extend the paleogeographic range of this genus.

?*Schizocardita* sp. indet.

Text-figs 35.31–35.33

Material examined.—A single fragmented RV (UMIP 15698).

Description.—RV trigoniform, moderately small, longer than high (maximum L of incomplete specimen = 10.7 mm, maximum H = 8.2 mm), beak orthogyrous, positioned approximately 1/3 shell length from anterior margin; posterior and anterior dorsal margins relatively straight; with pronounced posteriorly-sloping medial sulcus bordered by a rounded carina which passes into a moderately concave posterior area; cardinal area relatively broad, with concave surface, ligament opisthodontic, ligament grooves not observed; ventral hinge margin prominently overhanging deep body cavity with posterior and anterior portions joining under beak at an obtuse angle (125°); a single, straight, and relatively small anterior cardinal tooth (3a) is present sloping away from beak at a steep angle; anterior and posterior adductor scars subovate and deeply impressed with myophoric buttress; pallial line not observed; surface ornamented with numerous relatively coarse radial costae and faint commarginal growth lines.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—The Gill Harbor specimen is represented by a single incomplete RV in which the hinge is rather poorly preserved, with most details of the cardinal and lateral dentition apparently not completely silicified. The hinge bears only a single cardinal tooth of very low relief above the rather planar cardinal area. Although the Gill Harbor specimen has many of the generic traits of *Schizocardita* (especially in shape and external ornament), some significant differences of internal traits exist with *S. cristata* that may be a result of incomplete silicification or represent a new taxon. Given these uncertainties, and the fact that the Alaskan form is represented by a single specimen for which many traits, and their variability, are either unknown or poorly preserved, assignment to *Schizocardita* is only tentative.

Paleoecology.—? *Schizocardita* sp. is interpreted to be a suspension-feeding shallow burrower that was situated mostly buried with its posterodorsal margin extending exposed above the sediment-water interface (Text-fig. 13.20). Although a pallial line is not evident in the single Gill Harbor specimen, nor

in the Peruvian example, like other palaeocarditiids, members of this genus either had very short siphons or lacked siphons altogether.

Order **MODIOMORPHIDA** Newell, 1969

Superfamily **MODIOMORPHOIDEA** Miller, 1877

Family **PALAEOPHARIDAE** Marwick, 1953 [emended]

Diagnosis.—Shell equivalved, elongate, ensiform, with prosogyrous beaks situated one-fourth to one-sixth valve length from anterior margin; posterior margin rounded to truncated, dorsal margin nearly straight, ventral margin weakly convex; lunule and escutcheon distinct; surface smooth or ornamented with distinct growth lines, some genera with weak radial costae; ligament external, opisthodontic, dorsally supported by elongated nymph; dentition somewhat variable across genera, with cardinal platform possessing one or two cardinal teeth and possessing radial pseudocardinals across platform, with strong and elongated posterior lateral tooth in LV well removed from cardinal area and received by socket in RV; anterior adductor scar generally oval, deeply impressed, with myophocic buttress in some genera, posterior adductor scar shallow and positioned just below hinge approximately one-half to two-thirds valve length from anterior margin; pedal retractor scar small and deeply impressed situated behind buttress or below cardinal platform; pallial line weak and apparently integripalliate. Shell microstructure and mineralogy unknown, but likely aragonitic and consisting of at least two, possibly three, shell layers.

Remarks.—Kobayashi & Ichikawa (1951) suggested that a new monotypic family within the Unionacea should be erected for *Palaeopharus* and further speculated that *Palaeopharus* is transitional between the Pleurophoridae [= Permophoridae] and the Unionidae. Kobayashi & Ichikawa (1951) provided an excellent historical account of *Palaeopharus* and discussed at length the pseudocardinal dentition that serves as the defining criterion of this family, which suggested to them an affinity to the Unionidae and also, superficially, to *Pleurophorus* King, 1844. Marwick (1953: 69) noted the distinction of forms here regarded as true *Palaeopharus* (e.g., *P. scheii* Kittl, 1907, *P. perlongus* Böhm, 1903, and *P. maizurensis* Kobayashi & Ichikawa, 1951) from his new genus *Kalentera* and suggested, without comment, that they belong to the family Palaeopharidae; although no diagnosis or description or list of included genera in the family was given, his intent was quite clear. It should be further noted that Marwick (1953: 69) also introduced the family Kalenteridae to accommodate “*Pleurophorus*”-looking genera, including *Triaphorus* Marwick, 1953 (type species *Pleurophorus zealandicus* Trechmann, 1918) and *Kalentera* Marwick, 1953 (type species *K. mckayi*

Marwick, 1953). Marwick included his family within the Cypricardiacea without comment.

Subsequently, Kiparisova *et al.* (1966) grouped *Palaeopharus* together with *Triaphorus* Marwick, 1953, *Pseudomyoconcha* Rossi Ronchetti & Allasinaz, 1966, and *Curiona* Rossi Ronchetti & Allasinaz, 1966 into the Kalenteridae, which they placed within the superfamily Carditacea. They considered the Kalenteridae to be the senior synonym for Pleurophoridae Dall, 1895 and Permophoridae Van de Poel, 1959. Shortly thereafter, Skwarko (1967) described a unique “permophorid” from the Carnian of New Guinea and, following the examination of additional material (Skwarko, 1983), erected the genus *Somareoides* and noted its similarity in hinge dentition to *Triaphorus*. As described by Skwarko (1983: 67), *Somareoides* possesses “permophorid dentition in which 2 and 3a are attenuated.”

In the *Treatise*, Newell (1969) compared *Palaeopharus* to *Actinodontophora* Ichikawa, 1952 and noted that the later possessed massive first and last cardinal teeth. He placed both genera into his new family ?Actinodontophoridae within the Unionacea, and without recognizing Marwick’s erection of Palaeopharidae. Others have noted the similarity in the hinge of Actinodontophoridae to other Permophoridae (e.g., Böhm, 1914; Nakazawa, 1955; Nakazawa & Newell, 1968), which Fang & Morris (1997) also concluded bear little resemblance to the Unionacea (*as per* Newell, 1969) but were quite similar also to modiomorphoids. Based on priority, the Actinodontophoridae is thus considered a junior synonym of the Palaeopharidae.

Palaeopharidae is similar in many regards to Kalenteridae (including the objective synonym Permophoridae) that some workers place within the Modiomorphoidea (e.g., Damborenea, 2004). As presently understood, the Kalenteridae includes *Kalentera* Marwick, 1953, *Permophorus* Chavan, 1954 (= *Pleurophorus* King, 1844), *Curiona* Rossi Ronchetti, 1965, *Triaphorus* Marwick, 1953, and some lesser-known Early Mesozoic and Late Paleozoic genera. The Kalenteridae itself has a long, complicated history and has vacillated among several higher-level taxa, including the Carditacea (e.g., Newell, 1957; Chavan, 1969b; Cope, 1995), the Isofilibranchia (e.g., Pojeta *et al.*, 1986; Carter, 1990a), Anomalodesmata (Fang & Morris, 1997; Waller, 1998; Cope, 2000; Carter *et al.*, 2011), and Modiomorphoidea (Damborenea, 2004). A thorough review of *Kalentera* and a convincing argument in favor of positioning the Kalenteridae within the Modiomorphoidea was provided by Damborenea (2004). Damborenea supported the view earlier expressed by Fang & Morris (1977) that similarities of the hinge of Kalenteridae and carditoids was a result of convergence.

That the Palaeopharidae belong in the Modiomorphoidea remains debatable; but, for the following reasons, and follow-

ing Carter *et al.*, (2011), it is here retained until a more complete assessment of the superfamily is conducted. Membership and position of modiomorphoids is not without controversy, and therefore the discussion below will concentrate not on the superfamilial but instead on the placement of *Palaeopharus* within the Modiomorphoidea. As recognized by Fang & Morris (1997), the elongated opisthotetic ligament of modiomorphoids is positioned within nymphs and also serves as the axis of hinge rotation. Placement into the Modiomorphoidea is further strengthened if Palaeopharidae is viewed as a sister taxon to the Kalenteridae (including the Permophoridae).

Included genera.—As presently construed, the family contains the following genera: *Palaeopharus* Kittl, 1907 (Carnian-Norian, Arctic Canada, northeast Russia, Japan, and Alaska), *Actinodontophora* Ichikawa, 1951 (Permian, Japan), and tentatively, *Somareoides* Skwarko, 1967 (Carnian, New Guinea).

Genus **PALAEOPHARUS** Kittl, 1907 [emend. Kobayashi & Ichikawa, 1951]

Type species.—*Palaeopharus scheii* Kittl, 1907, by subsequent designation (Diener, 1915: 229); Upper Triassic (Carnian), Ellesmere Island, Arctic Canada.

Remarks.—Kittl (1907: 34) erected *Palaeopharus* to accommodate his new species (*P. scheii*) for very elongated and radially ornamented specimens from the Carnian of Ellesmere Island (Arctic Canada). Although his observations were based on moderately well-preserved specimens in which he adequately described both external ornament and the nature of muscle scars, the dentition of the Ellesmere material was not particularly well-preserved and thus eluded him in his erection of the genus. Kittl recognized, however, the similarity between his species and both *Pleurophorus perlongus* and *P. anderssoni* previously named and described by Böhm (1903) from Bear Island and for which the dentition was well preserved. The articulating structures of the hinge of the Arctic specimens, determined mostly from *Pleurophorus anderssoni* (Böhm, 1903, pl. 4, figs 5, 6), illustrate the presence of a weak undulatory surface suggestive of pseudocardinal dentition anterior to a single opisthocline cardinal tooth on the RV and a corresponding socket on the LV. Both of Böhm's species also exhibit a somewhat elongated tooth extending posteriorly from the cardinal platform at a very slight angle to the ventral margin of the hinge.

Nearly half a century later, Kobayashi & Ichikawa (1951) illustrated and described the new species *Palaeopharus maizurensis* from the Carnian Nabae Group of southwest Japan which clearly shows the hinge structure, providing the basis for their more robust emended diagnosis of *Palaeopharus*. This

material, taken together with well-preserved specimens of *P. paucicostatus* Nakazawa, 1955, also from the Nabae Group, provides the necessary details of the hinge permitting recognition of the variability of hinge features and the nature of the pseudocardinal dentition. As noted by Kobayashi & Ichikawa (1951: 258), the position of the pseudocardinals is somewhat variable between the Japanese species, occurring anterior to the robust cardinal tooth in *P. paucicostatus* and posterior to the cardinal tooth in *P. maizurensis*. One of the best-preserved specimens demonstrating these features is an articulated valve of *P. paucicostatus* illustrated by Newell (1969, fig. D60.5). As presently understood, the hinge of *Palaeopharus* consists of a somewhat large and generally flattened cardinal area upon which there exists one or perhaps two cardinal teeth in the RV, the anterior of which is the stronger and in some species the posterior of which is subdued or absent altogether. Between the two cardinal teeth (or behind the single tooth), the cardinal platform has radially arranged pseudocardinal denticles of variable strength and number. Additionally, the anterior adductor scar in *Palaeopharus* is deeply recessed and situated either anterior to the cardinal platform and bounded by a weak buttress, or ventral to the cardinal platform and lacking a myophorial buttress.

Palaeopharus is perhaps most closely related to Permian *Actinodontophora* (type species *Actinodontophora katsurenais* Ichikawa, 1951: 327, pl. 1, figs 15–16; see also Newell, 1969: 470, figs D60.4a–c). In addition to differences in valve outline, the primary feature distinguishing the two genera can be found in the cardinal dentition. *Actinodontophora* possesses an interesting series of radial denticles on the cardinal platform extending posteriorly from one or two strong opisthocline cardinal teeth. Ichikawa (1951: 327) referred to these denticles as subcardinal teeth and their relationship to the pseudocardinals of *Palaeopharus* seems quite likely.

Tokuyama (1958: 296) erected the subgenus *Palaeopharus* (*Minepharus*), assigning as his type his new species *Palaeopharus* (*Minepharus*) *triadicus* Tokuyama, 1958 from the lower Carnian portion of the Mine Series of Japan. As presently understood, *Palaeopharus* (*Minepharus*) is only known by its type species. This species (and by inclusion the subgenus) has strong and coarse radial and commarginal ornament, is significantly less elongated than other *Palaeopharus*, has a very deep lunule, and exhibits some significant differences in dentition. In his diagnosis of the subgenus and again in his remarks, Tokuyama (1958: 296) noted the full range of cardinal (*2b*, *3b*, *4b*) and lateral (*PII*, *AII*) dentition in which the posterior lateral is rather blunt and not elongated as in other *Palaeopharus* (compare for example Tokuyama, 1958, text-fig. 2 to Text-fig. 42). The anterior lateral *AII* of *Palaeopharus* (*Minepharus*) *triadicus* was considered by Tokuyama (1958) to be plesiomorphic to the pseudocardinals of younger *Palaeopharus*. This dentition is

idealized in Tokuyama (1958, text-fig. 2), but the corresponding illustrations of the specimens (pl. 43, figs 6–9, 11) are of rather poorly preserved internal molds in which the teeth are not all that clear. An alternative interpretation of the dental formula for *P. (Minepharus) triadicus* was presented by Cox & Chavan (1969: N580) who recognized a single cardinal tooth in the RV (3*b*), two cardinal teeth in the LV (2*b*, 4*b*), and two posterior lateral and one anterior lateral teeth. Cox & Chavan (1969: N580) elevated *Minepharus* to genus rank and questionably assigned it to the Cardiniidae Zittel, 1881. Placing *Minepharus* into the Cardiniidae was subsequently followed by Hayami (1975).

Palaeopharus appears externally like *Somareoides* Skwarko, 1983 which is only known by its type species *S. hastatus* Skwarko, 1967 from the Carnian of Papua New Guinea. The dentition in *Somareoides* illustrated by Skwarko (1983: 68, fig. 1, pl. 1, figs 2, 6, 7) is rather simple and consists of the RV anterior cardinal 3*a* sloping at approximately 45° from the beak and a rather short and nearly horizontal cardinal 3*b*. The LV of *Somareoides* has a very elongated 4*b* extending posteriorly parallel to the hinge—and a somewhat irregularly shaped, but slightly curved—2, which may be transversely striated. The anterior adductor scar of *Somareoides* is smaller and in a more anterior position than found in some *Palaeopharus*.

Included species.—*Palaeopharus scheii* Kittl, 1907 (type species), *Pleurophorus anderssoni* Böhm, 1903, *Palaeopharus buriji* Kiparisova, 1954, *Palaeopharus insertus* Kiparisova, 1960, *Palaeopharus kiparisovae* Efimova, 1966, *Palaeopharus maizurensis* Kobayashi & Ichikawa, 1951, *Palaeopharus magadanicus* Bytchkov, 1966, *Pleurophorus oblongatus* Kobayashi & Ichikawa, 1950, *Palaeopharus orchardi* n. sp., *Palaeopharus paucicostatus* Nakazawa, 1955, *Pleurophorus perlongus* Böhm, 1903, and possibly *Palaeopharus* (?) *raricostatus* Bytchkov, 1966.

***Palaeopharus orchardi* n. sp.**

Text-figs 40.1–40.4, 41.1–41.12, 42

Types and measurements.—Holotype: PRI 69683, a LV and a RV from the same individual (Text-figs 40.1–40.4). Paratypes: PRI 69687, consisting of both left and right valves of the same individual (Text-figs 41.5–41.8); PRI 69686, a RV (Text-figs 41.3, 41.4); PRI 69685, a RV (Text-figs 41.1, 41.2); PRI 69689, a LV (Text-figs 41.9, 41.10); PRI 69690 (Text-figs 41.11, 41.12), a RV. Measurements provided in Table 8.

Other material examined.—In addition to the types, the collection consists of large fragments of 11 left valves and nine right valves; of these, the cardinal areas are preserved in four right valves and two left valves. Numerous smaller frag-

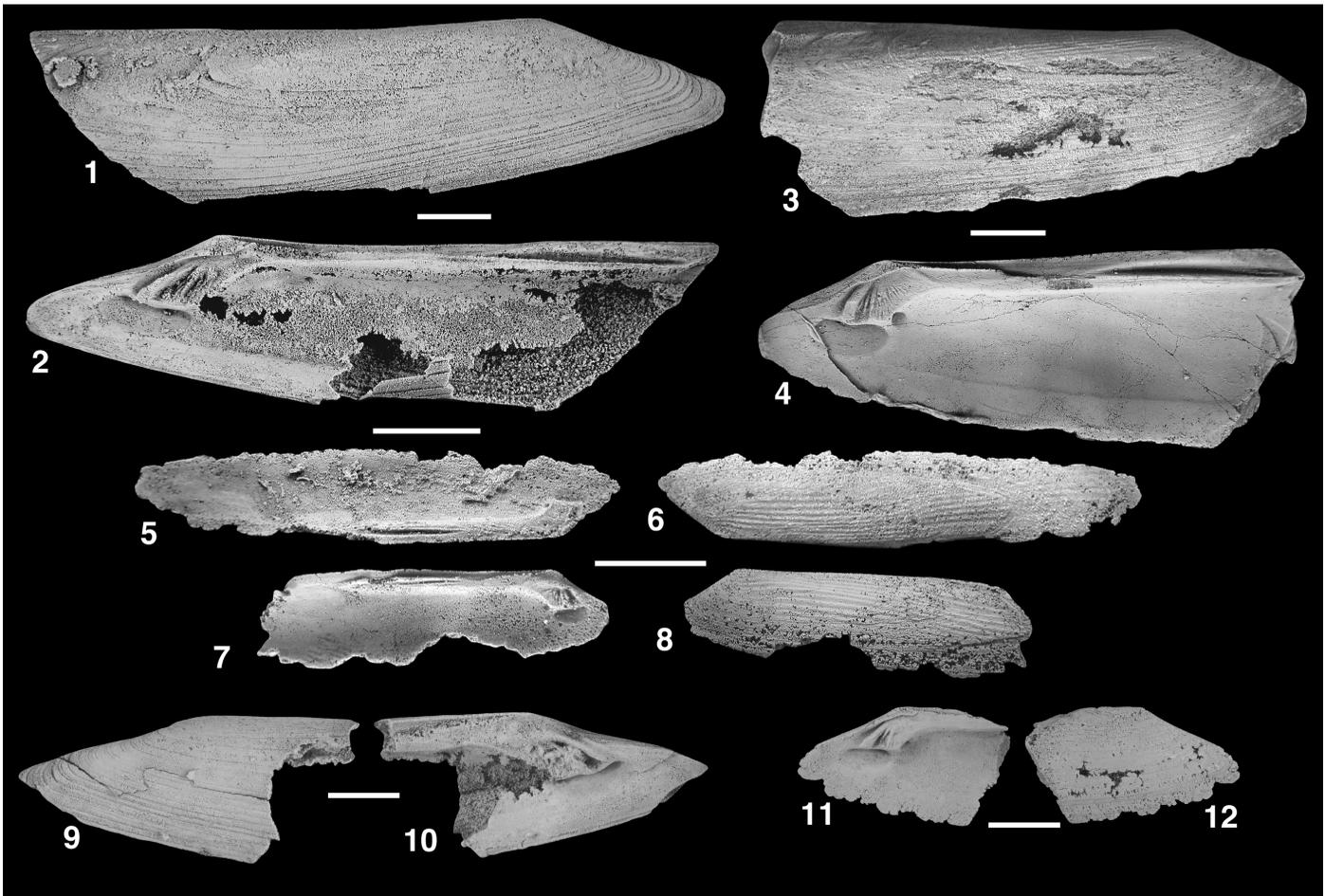
ments belonging to this species were also recovered in etched residue.

Diagnosis.—Moderately large *Palaeopharus*, posteriorly elongate, lunule weak, with well-developed cardinal platform possessing a single prominent and anteriorly sloping cardinal tooth in RV received by socket in LV behind cardinal tooth, cardinal platform with radiating series of pseudocardinal teeth; ornament generally smooth with commarginal growth lines and very weak radial ornament present on the upper angular sector extending from beak to posterodorsal margin.

Description.—Shell enisiform; moderately large and greatly posteriorly elongate (maximum L = 14.47 cm, maximum H = 2.83 cm), beak prosogyrous, slightly raised, positioned approximately one-eighth of shell length from the anterior margin; dorsal margin generally straight; posterodorsal angle gently sloping at approximately 38°; ventral margin broadly convex so that the greatest height is near the middle of the valves; posteroventral margin sharply rounded, forming an acute angle of ~ 73°; lunule weak and invaginated in front of beak; anterodorsal margin sloping away from beak and forming a subangular anterior margin of about 40° with the anteroventral margin; conjoined and closed valves with narrow gape of about 3.0 mm on posterior half of shell; broad triangular-shaped cardinal platform below beak with prominent denticles (= pseudocardinal teeth) on both valves situated behind a single opisthocline cardinal tooth on right valve (3*b*?) and corresponding socket on left valve; ligament opisthodetic, parivincular, situated wholly posterior to cardinal area; clearly segregated into lower fibrous layer and upper lamellar layer by narrow ridge; lower fibrous layer extending from beak to posterior adductor scar, bordered below by thin ridge-like nymph; upper lamellar ligament extending well beyond fibrous part and terminating slightly behind and above posterior adductor scar, with strong elongated but slightly arched nymph most prominent and almost tooth-like in the left valve at a length approximately two-thirds the distance from beak to posterior adductor scar and with corresponding groove in right valve; isomyarian, posterior adductor scar oval, moderately large (maximum L dimension = 17.4 mm), positioned at mid-length of shell, dorsally situated and abutting against posterior end of ligament groove; anterior adductor scar bean-shaped, dorsally concave, and elongated horizontally, moderately large (maximum dimension = 11.5 mm), situated ventral to cardinal platform and slightly in front of beak; small circular pedal retractor scar deeply recessed and situated posterior of anterior adductor scar and adjacent to and slightly behind cardinal platform; pallial line faint, integripalliate, about 8 to 10 mm from ventral margin; exterior surface uniformly covered with commarginal growth lines;



Text-fig. 40. *Palaeopharus orchardi* n. sp. Holotype, PRI 69683. 1, 4, RV; 1, exterior, 4, interior. 2, 3, LV; 2 exterior, 3, interior. Scale bar = 10 mm. From USGS loc. M1912.



Text-fig. 41. *Palaeopharus orchardi* n. sp. 1, 2, paratype, PRI 69685, a RV; 1, exterior, 2, interior. 3, 4, paratype, PRI 69686, a RV; 3, exterior, 4, interior. 5-8, paratype, PRI 69687; 5, RV interior; 6, RV exterior; 7, LV interior; 8, LV exterior. 9, 10, paratype, PRI 69689, a LV, 9, exterior, 10, interior. 11, 12, paratype, PRI 69690, a RV; 11, interior, 12, exterior. Scale bars = 10 mm. All from USGS loc. M1912.

weak radial ribs present on upper angular sector, extending from beak to posterodorsal margin.

Etymology.—Trivial name, *orchardi*, after Michael J. Orchard, significant contributor to Triassic conodont biochronology and member of the 2003 field party to Keku Straight.

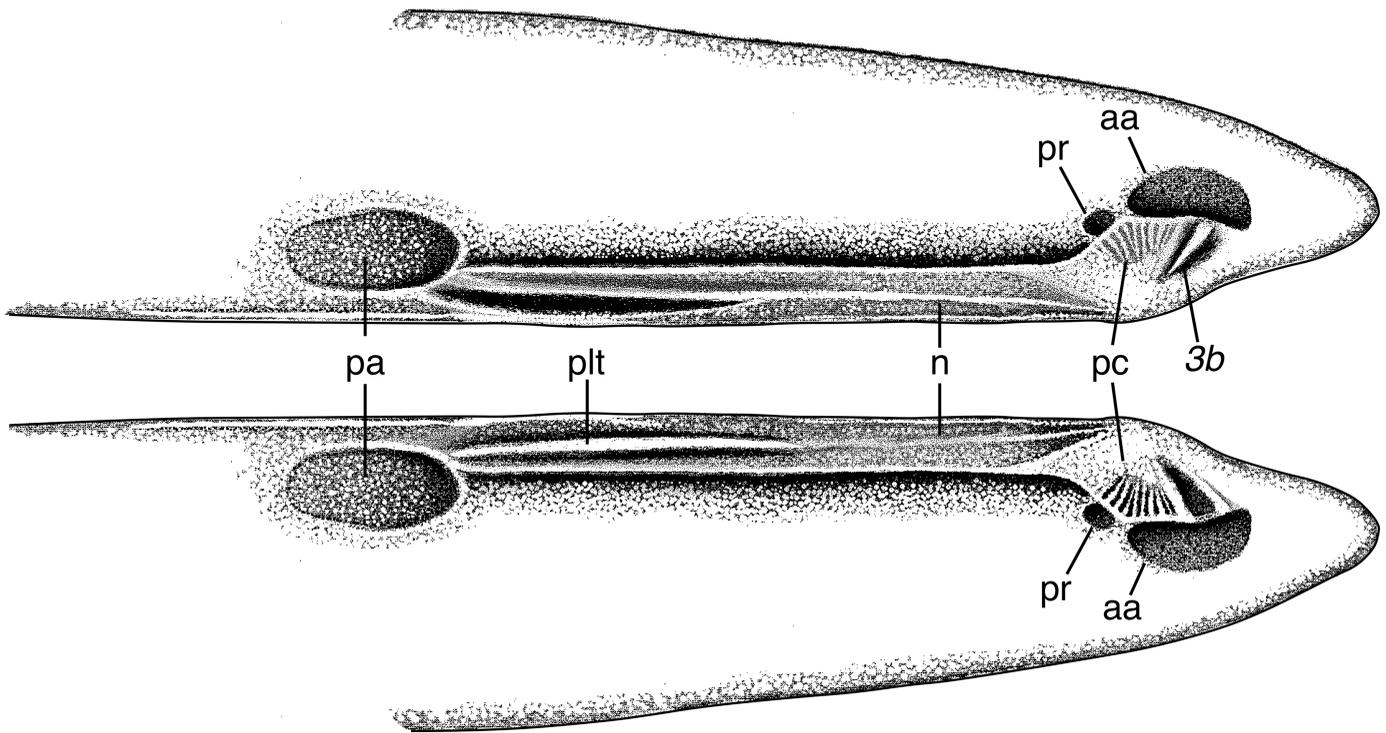
Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—Although several species of Triassic *Palaeopharus* are known from Japan, and mostly high paleolatitude localities in Arctic Canada, Svalbard, and Russia, apart from the single listing in Berg (1973: 24) from the upper Norian Chapin Peak Formation of Gravina Island, Alaska (USGS locs M5095, M5909), this is the first reported occurrence of this genus from the Americas and also from a such low paleolatitude. The well-preserved valve interiors of this new species

permit discrimination from the nearly identical external features of *Somareoides hastatus* (Skwarko, 1967, 1983) from the Carnian of Papua New Guinea.

It is unfortunate that the type species, *Palaeopharus scheii* Kittl (1907: 34, pl. 3, figs 1-4), is poorly preserved and that the entire shell margin is not preserved, nor are most of the features of the cardinal area and dentition. However, Kittl's reconstruction of shell form suggests that the beak is located about one-sixth the shell length from the anterior end. The shell expands somewhat in height towards the posterior end, reaching its maximum at about two-thirds length. The anterodorsal margin is significantly more sloping than *P. orchardi*. The anterior adductor scar is visible in one of Kittl's figures (1907, pl. 3, fig. 2) and appears to be elongate and bean-shaped as in *P. orchardi*, but is situated more anterior with respect to the cardinal platform.

Other high-paleolatitude species differ from *Palaeopharus orchardi* in significant ways, both in shape and in external ornament. *Palaeopharus anderssoni* (Böhm, 1903: 45, pl. 4,



Text-fig. 42. *Palaeopharus orchardi* n. sp. Illustration of hinge and muscle scars in RV (upper) and LV (lower). Abbreviations: aa = anterior adductor scar, pr = anterior pedal retractor scar, pa = posterior adductor scar, n = nymph, pc = pseudocardinals.

figs 4-7, 9, 10) exhibits much stronger radial ornament than *P. orchardi*. Like other species, this species' anterior insertion scar is more rounded and ventrally recessed into the cardinal platform and slightly more anterior than *P. orchardi*. *Palaeopharus perlongus* (Böhm, 1903: 46, pl. 4, figs 1-3, 8) exhibits somewhat stronger radial ornament, which is especially pronounced in the "carina" and extends slightly below the carina and is even observable in the valve interior. The beak is even more anterior (less than one-tenth the length of the shell) than *P. orchardi*.

Palaeopharus maizurensis Kobayashi & Ichikawa (1951) has its beak positioned about one-fourth to one-fifth the shell length from the anterior end. *Palaeopharus orchardi* also lacks the chevron sculpture found in *P. maizurensis* Kobayashi & Ichikawa, 1951 and some other *Palaeopharus* (e.g., *P. anderssoni* Böhm, 1902).

Several species of *Palaeopharus* from northeastern Russia, none of which preserve details of hinge dentition or other internal features, may be compared to *P. orchardi*. *Palaeopharus buriji* Kiparisova, 1954 (pl. 34, figs 5, 6; see also Kiparisova *et al.*, 1966: 184, pl. 32, figs 1-10, pl. 33, figs 1-3) and *Palaeopharus oblongatus buriji* Kiparisova, 1954 in Kiparisova (1972: 101, pl. 14, figs 1, 2) have much more pronounced radial ornamentation extending below the lateral carina on the valve flank and which reaches to the ventral margin at some distance in front of the posterior margin, and has its beak situated at a more posterior position (at about one-fifth

the shell length from the anterior end). *Palaeopharus incertus* Kiparisova, 1960 (pl. 24, fig. 16; see also Kiparisova, 1972: 103, pl. 14, figs 3, 4) is similar to *P. buriji*, but the valves expand to a maximum height towards the posterior margin and the beak is situated at about one-sixth the shell length. Likewise, *P. magadanicus* Bytchkov, 1966, illustrated in Kiparisova *et al.* (1966, pl. 33, figs 8, 9) exhibits a greater valve expansion towards the posterior (as in *P. buriji*), but is otherwise similar, especially in external ornament, to *P. orchardi*.

Paleoecology.—Infaunal mobile suspension feeder. A non-sinuate pallial line suggests this species was a shallow burrower with short siphons or lacked a functional siphon (Text-fig. 13.25). The deeply recessed anterior pedal retractor scar situated posterior to the cardinal platform and lack of evidence for a strong posterior pedal retractor requires the foot to have been situated closer to the anteroventral margin.

Order **CARDIIDA** Férussac, 1822

Superfamily **TELLINOIDEA** de Blainville, 1814

Family **TANCREDIIDAE** Meek & Hayden, 1865

Genus **TANCREDIA** Lycett, 1850

Type species.—*Tancredia donaciformis* Lycett, 1850, by subsequent designation (Meek & Hayden, 1865: 95), Middle Jurassic (Bajocian), Gloucestershire, United Kingdom.

Table 8. Measurements of *Palaeopharus orchardi* n. sp.

Specimen	Valve	Length (cm)	Beak (from Ant) (cm)	Height (cm)	Remarks
PRI 69683	LV	14.47*	1.99 (LV), 1.98 (RV)	2.83	Holotype
PRI 69687	LV	4.61*	0.62 (LV), 0.63 (RV)	0.93 (LV), 0.91 (RV)	Paratype

* Restored measurement.

Remarks.—Tancrediids are very poorly known from the Triassic and apart from a few named species of questionable taxonomic affinity to *Tancredia*, they have only appeared on faunal lists without illustration or description. Ros-Franch *et al.* (2014) concluded that all Triassic *Tancredia* were of doubtful affinity to true *Tancredia* and listed the earliest known occurrence as Sinemurian. Jurassic species of *Tancredia* are quite distinct from one of the few described supposed tancrediids from the Triassic, *Sakawanella triadica* Ichikawa (1950: 245) from the Carnian of Japan. *Sakawanella* possesses two internal ridges that are absent in *Tancredia* and thus reaffirm their separation at the generic level.

***Tancredia norica* n. sp.**
Text-figs 43.1–43.15

Types and measurements.—Holotype: PRI 69692; RV, H = 28.7 mm, partial L = 44.3 mm; LV, H = 28.4 mm, partial L = 48.1 mm. Paratypes include three left valves (PRI 69691, UMIP 15699, and UMIP 15702) and two right valves (UMIP 15700 and UMIP 15701).

Other material examined.—In addition to the types, the collection consists of 6 partial RVs and 5 partial LVs and numerous additional smaller fragments.

Diagnosis.—Moderately large *Tancredia*, subtrigonal, equivalved and strongly inequilateral, with beak medial or slightly posterior and posterior carina; with sharply truncated posterior margin and large posterior gape; narrow lunule, dentition as in other *Tancredia* with strong cardinal teeth *4b* and *2* in RV, and *3a* and strong triangular *3b* in LV; with well to moderately developed adductor scars and tall but shallow pallial sinus; largely smooth or with faint commarginal growth lines.

Description.—Shells moderately large size (maximum L = 57.2 mm, maximum H = 31.5 mm), subtrigonal, equivalved and strongly inequilateral, moderately inflated maximum W = 10.9 mm); beak medial or situated slightly posterior of mid length of valve; posterodorsal margin steeply sloping towards truncated posterior margin; anterodorsal margin less steeply inclined towards rounded anterior margin; ventral margin convex; lunule narrow; large heart-shaped posterior gape (measured on opposing valves PRI 69692 with W = 14.3 mm

and H = 11.2 mm); with weak posterior carina extending from beak to ventral part of posterior gape delimiting a posterior area surrounding gape; ligament external, opisthodontic, received by narrow groove extending to truncated posterior gape margin; LV with nearly horizontal and elongated *4b* and very strong and projecting *2*; RV with strong triangular *3b*, and separated from weak opisthocline *3a* by a deep triangular socket to receive the *4b* of the LV; anterior adductor scar oval, moderately impressed, positioned just ventral to anterior hinge and extending nearly to posterodorsal margin, in early ontogeny, the anterior adductor is more deeply impressed and separated from main valve interior with a buttress or septum; posterior adductor scar irregular shaped, somewhat oval, its dorsal extremity below the gape margin and extending in a ventral direction to form a steeply inclined and narrowly linear impression; exterior surface with numerous tightly-spaced commarginal growth lines.

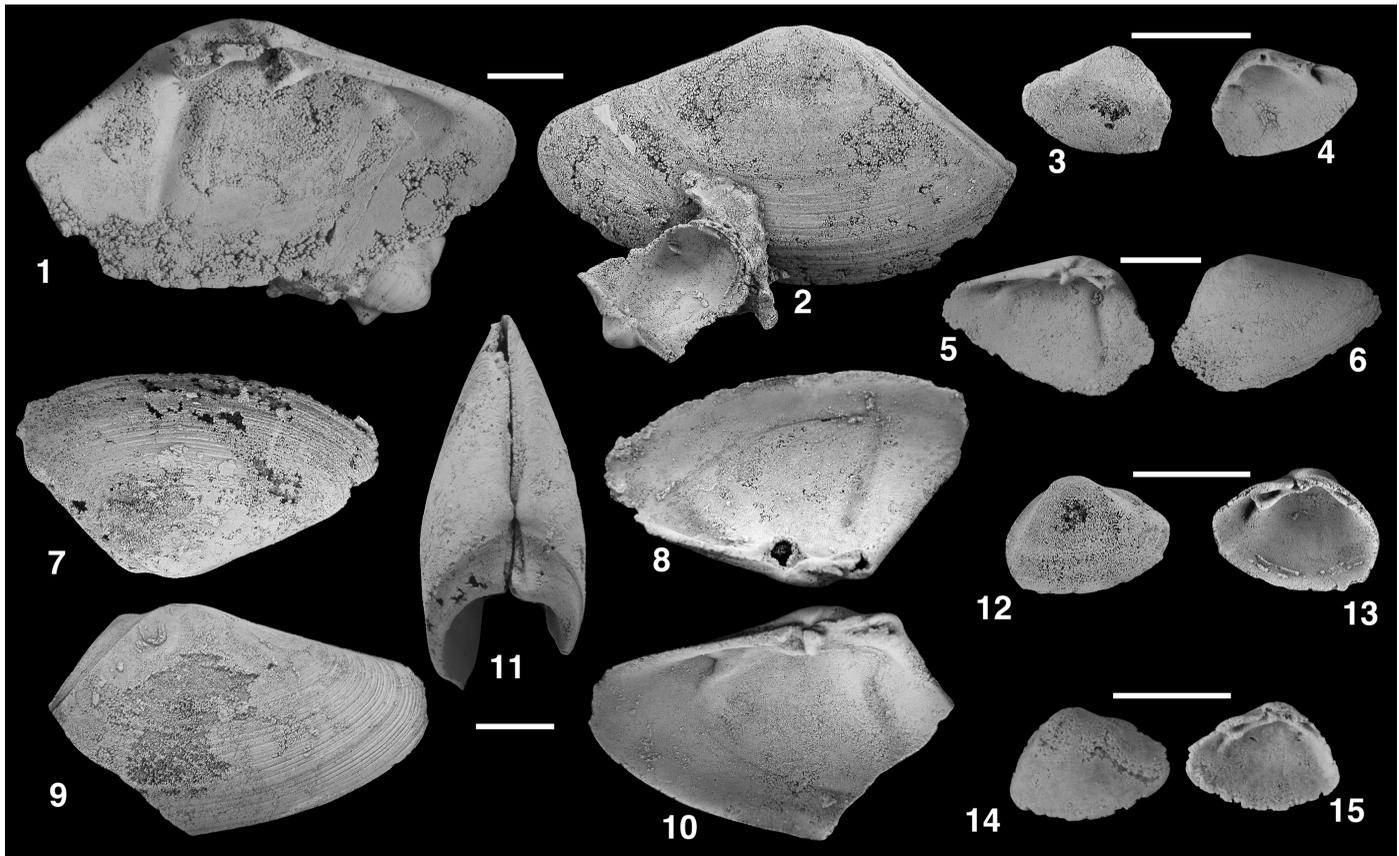
Etymology.—Trivial name, *norica*, referring to its only known occurrence in the Norian stage and also in reference to its being the oldest demonstrable representative of the genus.

Occurrence.—Upper Norian (*Gnomohalorites cordilleranus* ammonoid Zone) Hound Island Volcanics, Gill Harbor, Kuiu Island, Alaska (USGS loc. M1912).

Remarks.—The specimens under consideration are assigned to *Tancredia* based upon their distinct dentition, valve shape, and very large posterior gape.

Tancredia has been reported from several Norian and Rhaetian localities in Siberia (Kiparisova *et al.*, 1966; also listed in Kurushin, 1990; Polubotko & Repin, 1990; Kazakov & Kurushin, 1992). The two named species of *Tancredia* from Siberia are represented by small, poorly preserved internal molds lacking features of the hinge and dentition and comparisons with *T. norica* can only be made on external features and shell outline. *Tancredia tuchkovi* (Kiparisova *et al.*, 1966, pl. 35, figs 8–10) has a much more equant shape and also has a more pronounced umbo that extends further above the hinge than *T. norica*. Conversely, *Tancredia explicata* (Kiparisova *et al.*, 1966, pl. 35, figs 11–13) appears much more compressed and elongated than *T. norica*.

Although several small bivalves attributed to *Tancredia* have been described from the Triassic of the Germanic Basin



Text-fig. 43. *Tancredia norica* n. sp. 1, 2, paratype, PRI 69691, a LV; 1, interior, 2, exterior. 3, 4, paratype, UMIP 15699, a LV; 3, exterior, 4, interior. 5, 6, paratype, UMIP 15700, a RV; 5, interior, 6, exterior. 7–11, holotype, PRI 69692; 7, 8, a RV; 7, interior, 8, exterior; 9, 10, a LV; 9, exterior, 10, interior; 11, dorsal view of conjoined valve pair showing large posterior gape. 12, 13, paratype, UMIP 15701, a RV; 12, exterior; 13, interior. 14, 15, paratype, UMIP 15702, a RV; 14, exterior; 15, interior. Scale bars = 10 mm. All from USGS loc. M1912.

and western Tethys, none can be shown to demonstrably be placed in the genus. For example, the types of both *Tancredia beneckeii* Philippi (1898, pl. 6, fig. 12) and *Tancredia triasina* Schaubert (1857, pl. 7, fig. 1) are external molds lacking valve interiors and hinge elements and thus preclude definitive assignment to the genus. Additionally, those from the Rhaetian—including *T. ditmarii* Martin (1865, pl. 3, fig. 7) from the Côte-d'Or region, France and *T. sinemuriensis* Martin described by Fischer-Ooster (1869, pl. 2, fig. 8) from the Rhät-Sandstein of the Bern region, Switzerland—are also external molds lacking valve interiors and hinge elements and thus preclude definitive assignment to the genus.

It is interesting to note that Stanley (1989) lists the presence of *Tancredia* from the Rhaetian Sutton Member of the Parsons Bay Formation at Lake Cowichan in southern Vancouver Island. These bivalves were, unfortunately, never illustrated or described, but occur in association with a taxonomically diverse scleractinian-sponge dominated reefal facies. Although the Vancouver specimens remain to be studied, given the similarity of associated fauna between the Sutton Member (Wrangell terrane) and the Gill Harbor (Alexander terrane) faunas, it is entirely possible they could represent the

same taxon. Regardless, the presence of *Tancredia* at the Gill Harbor locality demonstrably extends the range of *Tancredia* to the Norian and suggests that the genus may have had its origin within the Panthalassa realm prior to migrating into northwest Europe by Jurassic time.

Paleoecology.—It is likely this species was a facultative mobile infaunal burrower (Text-fig. 13.26). The very large posterior gape suggests large siphons, but the tall and shallow pallial sinus observed on the Gill Harbor specimens suggests a burrowing habit that was not as deep as other Tellinoidea or other well preserved Jurassic and Cretaceous species (Fürsich, 1982; Stiller, 2006). It is also interesting to note that some Jurassic *Tancredia* have been associated with reduced paleosalinities (Holmden & Hudson, 2003).

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