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CAROLE S. HICKMAN (2021). Arcoid bivalve biodiversity during Eocene doubthouse cooling: Contrasting the active Cascadia Margin coldspot with the intracratonic Paris Basin hotspot.

Cover illustration: One of seven lots of the Eocene arcoid *Rostarca angusta* (Lamarck, 1805) in the UCMP Cloetz Collection, illustrating the abundance and size range of specimens from a single Paris Basin locality. The vial and specimens are positioned with their original label and their UCMP label on the cover image of the early 19th Century monographic description of the hyperdiverse bivalve fauna. Cover image credit: Dave Strauss.

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Arcoid bivalve biodiversity during Eocene doubthouse cooling: Contrasting the active Cascadia Margin coldspot with the intracratonic Paris Basin hotspot

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Response to the Eocene doubthouse interval of global climate cooling (53–33.5 Ma) is explored in arcoid bivalves of the families Parallelodontidae, Cucullaeidae, Arcidae, and Noetiidae. An anomalous biodiversity hotspot in the intracontinental Paris Basin of Northern Europe is contrasted with an equally anomalous coldspot at comparable latitude on the tectonically active Cascadia Margin of western North America. Reevaluation of arcoid shell morphology and an annotated glossary of shell features accompanies illustration and discussion of eight exemplar species, identifying new characters and distinguishing those with a strong phyletic signal from those representing functional convergence or developmental differences specific to size or age. Biodiversity anomalies cannot be attributed to any single factor. However, contributing factors include tectonic setting, correlates of bathymetric and sedimentary setting, sediment geochemistry, ocean gateway events, reorganization of current systems and water masses, deepening of the calcium carbonate compensation depth, patterns in the development of sea ice and polar ice storage, changes in sea level, and changes in atmospheric carbon dioxide and the carbon cycle. Opening of the Tasman Gateway and Drake Passage, thermal isolation of Antarctica, and evolution of a Pacific psychrosphere are correlated with the early appearance of cold-water molluscan taxa on the active Cascadia Margin along with the unrelated onset of arc volcanism, subduction, and geochemical changes associated with methane and sulfide seepage. Persistence of a shallow carbonate platform and proliferation of molluscan diversity in spite of global cooling is more difficult to explain, and understanding biogeographic anomalies requires additional climate proxy records. History of the western margin of North America includes an earlier Mesozoic volcanic arc and forearc basin in central and northern California with abundant basal arcoids, negating the need for westward migration out of the Tethyan region to the Cascadia Margin during the Paleogene.

Keywords: climate change, greenhouse, icehouse, Parallelodontidae, Cucullaeidae, Arcidae, Noetiidae

INTRODUCTION

During the Paleogene Period arcoid bivalve taxa achieved spectacular and enigmatic biodiversity and abundance in tropical and subtropical settings on passive continental margins and in intracratonic carbonate platform seaways. The spike in diversity is unusual because it occurred during the doubthouse interval of gradual but pronounced global cooling between the greenhouse climate maximum of the early Eocene and the beginning of the icehouse climate and dramatic faunal turnover at the close of the Eocene. The turnover event is marked by disappearance of the hyperdiverse shallow water arcoids and the first appearance of ancient basal arcoids as relict elements in deep-water settings on active continental

margins. This paper provides a comparative view of arcoid bivalve diversity during the doubthouse interval of marine climate deterioration that culminated with development of permanent polar ice caps. It is based on new observations of the hinge plate and cardinal area as character complexes that link relict deep-water arcoids from the active Cascadia margin of Washington and Oregon with arcoid taxa from the Lutetian Eocene biodiversity hotspot (point chaud) in the cratonic Paris Basin of Europe.

HISTORICAL BACKGROUND

Living and fossil arcoid bivalves have been named and studied over a period of more than two centuries,

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although relationships and phylogeny remain incompletely resolved. More recent studies of global tectonic history and climate history identify intervals of accelerated instability. These intervals raise new questions and opportunities to integrate biological and geological data. The problematic Eocene biodiversity anomaly identified here requires historical background on the biology and fossil record of arcoid bivalves as well as a brief review of how previous authors have defined the doubt-house. A clear definition of its use in this paper is specified.

Arcoid bivalves

Deep Paleozoic origins and long evolutionary history of arcoid bivalves are remarkable in part because of their persistence in difficult environments and their survival across major mass extinction boundaries. Perhaps more remarkable is their failure at major evolutionary innovation and adaptive radiation. The stigma of failure arises from rigorous demonstration of morphological constraints imposed by the design, mechanical properties, and growth of the arcoid duplivincular ligament (Thomas 1976, 1978) as well as life habit constraints imposed by the lack of fused mantle siphons that enabled the post-Paleozoic radiation of suspension-feeding heteroconch bivalves (Stanley 1975).

Unresolved conflicts in arcoid taxonomy and classification and the proliferation of family- and genus-group names reflect very different weights attached to characters and character complexes (Bieler and Mikkelsen 2006) and suspicion of rampant homoplasy (Stanley 1977, Oliver and Holmes 2006). Features of the arcoid hinge plate and dentition are the primary basis for definition of Arcoid family groups (e.g., Newell 1969) and have been used extensively in diagrams of dentition patterns (e.g., Arkell 1930a, figs. 1–14; Thomas 1976, fig. 2; Amler 1989, fig. 4), diagrammatic depictions of hypothesized hinge plate evolution (e.g., Stanley 1975, fig. 6; Thomas 1978, fig. 2; Amler 1989, fig. 5), and diagrams of ontogenetic change within species (Thomas, 1976, fig. 3; 1978, fig. 4). However there are very few synapomorphic features supporting any of the higher taxa, and anatomical features are too poorly studied and insufficiently reflected in shell morphology to be useful with extinct taxa. Using molecular data from Marko (2002), Oliver and Holmes (2006) were able to detect instances of probable monophyly as well as to identify taxa that require reevaluation. There is considerable opportunity to define and explore very specific questions in arcoid bivalve history through more refined definition and comparison of shell features.

The hinge plate of Eocene arcoid bivalves is a case in point. It arose in the course of preparing a monograph of pteriomorph bivalves from late Eocene deep-water strata of the Cascadia margin in Oregon and Washington. An unusual arcoid species in three late Eocene formations is clearly a member of the Paralleodontidae Dall, 1898, an ancient family originating in the Lower Ordovician. The Eocene species, described originally as *Barbatia gabbi* Dickerson, 1917, was subsequently designated as the type species of *Porterius* by Clark (1925) who recognized it as a paralleodontid and proposed the genus as a subgenus of the Paleozoic *Parallelodon* Meek and Worthen, 1866. Effinger (1938) subsequently treated it as a subgenus of *Cucullaria* Conrad, 1869. Paralleodontidae is widely regarded as an extinct family (Bouchet and Rocroi 2010), consistent with inference that the Eocene forms treated here were the last gasp of the family. Full treatment of *Porterius gabbi* is presented in the Keasey pteriomorph monograph (Hickman, in preparation) along with an account of many speculative references to *Porterius* in the literature by authors who had access only to the original description and Clark's inadequate illustrations. Unfortunately, there is no evidence that any of these authors borrowed or examined type material. However, the name has been accepted and used for several living and fossil species, including one from the middle Eocene (Lutetian) of the Paris Basin. It is therefore fortuitous that the University of California Museum of Paleontology (UCMP) in Berkeley has an outstanding collection of Paris Basin fossil mollusks.

Doubthouse global cooling

The term “doubthouse” refers to a dramatic interval of global instability and deterioration of Earth's climate from the Paleogene tropical “greenhouse” state to the Neogene and Quaternary “icehouse” state (Prothero et al. 2003) with permanent polar sea ice and ice sheets. Review of literature referring to the intermediate state is beyond the scope of this paper. Dates bracketing the interval vary considerably depending on the scope and kinds of data reported. Many authors have restricted the doubt-house to a narrow interval at the Eocene–Oligocene Boundary (~34–33.5 Ma) in which there was widespread marine faunal turnover (e.g., Katz et al. 2008) coinciding with the Oi1 cold temperature excursion (Zachos et al. 1996). Studies of the boundary interval have generated considerable data from temperature proxies and other paleoenvironmental parameters. Investigations of development and extent of sea ice, evidence of transient glaciations and sea level fluctuations have led some authors

to restrict the doubthouse interval to the middle Eocene (~48–41 Ma) (e.g., Dawber and Tripathi 2007, 2008, 2011, Clark et al. 2020) or to the middle and late Eocene (~48–33.5 Ma) (e.g., Fluteau et al. 2019). The doubthouse also has been defined as a broader interval of 30 million years, extending from the latest Eocene (~34 Ma) to full coverage of both polar regions by permanent ice sheets at the end of the Pliocene (~3 Ma) (e.g., Zhang 2015).

In this study doubthouse is restricted to the interval of Eocene global cooling (~53–33.5 Ma) in which arcoid bivalve biodiversity explodes in one regional setting at the same time that it contracts and almost disappears in another. It is appropriate that a globally unstable and doubtful climate state is involved in (but not solely responsible for) simultaneous regional biodiversity hotspots and coldspots. Recognizing a variable spectrum is essential to the study of climate change and oscillation. Change is not easily reduced to a uniformly gradual or progressively stepwise pattern.

MATERIALS AND METHODS

Cascadia Margin material

In addition to the original types of *Porterius gabbi*, new material includes better preserved specimens collected by the author in both the Keasey and Gries Ranch Formations as well as specimens collected by the late Harold Vokes during geologic mapping of the Keasey Formation in Oregon in the 1940s from US Geological Survey (USGS) localities housed in the Smithsonian (USNM) in Washington, D.C. Specimens collected by the author are deposited in the UCMP type collection. The species also occurs in coeval strata of the Lincoln Creek Formation in southwestern Washington. The material on which Clark based the genus *Porterius* is from a Lincoln Creek site that no longer exists (the “old log dam on Porter Creek”), a Stanford University (LSJU) specimen now in the collections of the California Academy of Sciences (CAS).

Paris Basin material

The Cloez Collection—The UCMP Cloez Collection (CLC) of Paris Basin Eocene fossils, was purchased from the estate of Dr. Charles Louis Cloez, a French chemist and avocational paleontologist. This large and carefully curated collection is remarkable in containing 1,936 Paris Basin mollusk species. It includes 608 of the 1,175 bivalve species listed by Cossmann and Pissarro (1904–1913)—effectively 50% of the described bivalve taxa, and presumably most if not all of most abundant and frequent species. Identifications are believed to have been “made

or checked” by Cossmann (Peck 1957). Locality names, species names and “code numbers” (PE), and stage/age designations for each lot are those used by Cossmann (1886–1914). Representation of small-shelled arcoid bivalve species includes lots of more than 100 specimens, enabling observations of ontogenetic change and intra-specific variation. A summary of the arcoid material in the collection follows along with the species selected for shell and hinge plate illustration and discussion.

The family Arcidae Lamarck, 1809 is represented in the Cloez Collection by 32 lots of specimens allocated to 12 species and three genus-group taxa. The family Parallelodontidae Dall, 1898, is represented by two lots allocated to two species and two genera. The family Noetiidae Stewart, 1930, is represented by 36 lots allocated to two subfamilies, three genus-group taxa, and 10 species. The family Cucullaeidae Stewart, 1930, is represented by two lots of a single species. Most of the Paris Basin arcoid species were originally described in the 19th Century under *Arca* Linnaeus, 1758, or *Barbatia* Gray, 1842, and their allocation here follows the revision of Pacaud and Renard (1995) and Pacaud (2008).

Allocation of the family Glycymerididae Newton, 1922 (controversially attributed to Dall, 1908, as Glycymeridae) has been contentious and is here considered unresolved. The free-living glycymeridids have been placed alternatively in Arcoidea Lamarck, 1809 (e.g., Vokes 1967, Amler 1999, Oliver and Holmes 2006, Bouchet and Rocroi 2010, Carter et al. 2011), Limopsoidea Dall, 1895 (e.g., Newell 1969, Stilwell 1998) or a separate superfamily Glycymeroidea Newton, 1922 (Scarlatto and Starobogatov 1979, Coan et al. 2000, Nevesskaja 2009). Paris Basin arcoids are not included in this treatment.

Shell and hinge plate illustration—Seven Paris Basin species selected for photography include two parallelodontids: *Arca adversidenta* Deshayes, 1858 (here assigned to *Porterius*) and *Arca cucullaris* Deshayes, 1829 (here assigned to *Cucullaria*, Conrad, 1869); three arcids: *Arca obliquaria* Deshayes, 1829 and *Arca interrupta* Lamarck, 1805 (both here assigned to *Barbatia* Gray, 1842) and *Arca angusta* Lamarck, 1805 (here assigned to *Rostarca* Glibert and Van de Poel, 1965); one cucullaeid: *Cucullaea crassitina* Lamarck, 1801 (type species of *Cucullaea* Lamarck, 1801); and one Noetiid: *Arca dispar* (here assigned to *Striarca* Conrad, 1862).

ARCOID SHELL FEATURES AND THE PROBLEM OF DEFINING CHARACTERS AND CHARACTER STATES

Although anatomical characters and molecular data hold promise for resolving some problems in the highly

unresolved systematics of living arcoids, the problem of pervasive homoplasy in shell features casts a very long shadow on the deep evolutionary history and relationships extending back to the Early Paleozoic. Independent origins of morphological features cannot be discounted, but there is considerable room for improvement in unmasking homoplasy by improved definition of features in terms of characters and character states. The need for better character definition and discrimination is one of the central conclusions of the review of arcoid systematics by Oliver and Holmes (2006). In particular, the widespread use of single features as defining synapomorphies of taxa should be suspect if they have a clear functional and ecological significance or, alternatively, if they are size-related or subject to change during ontogeny.

Consistency in terminology is a separate problem from character definition because different morphological terms have been used to describe the same feature. This problem persists in interpreting the extensive early taxonomic literature. MacNeil (1938) worked to achieve consistency in his systematic review of Tertiary noetiids by redefining the subfamily Noetinae and providing emended definitions of genera and species. Although the Treatise on Invertebrate Paleontology provides a long glossary of morphological terms applied to bivalves (compiled by Cox 1969), Treatise accounts of arcoid genera and higher taxa (Newell 1969) are not consistent. In many instances different terms are used to describe the same feature. Some authors have been more concerned with nomenclatural issues, classification, designation and location of type specimens, and geographic and stratigraphic distributions than with morphological terms and their illustration on specimens (e.g., Stewart 1930, Reinhart 1935, 1937, 1943). In an extreme instance of focus on taxonomic procedure and nomenclature Schenck and Reinhart (1938) devote an entire paper to an unusually lengthy morphological account of an arcoid genus and new name for its type species in order to resolve a problem of homonymy. Their stated objective is to illustrate and discuss a fine point of nomenclatural rectification that is “misunderstood by some systematists.”

Taphonomy and differential preservation of features on disarticulated fossil arcoid shells also contribute to difficulties in morphological interpretation. For example, hinge teeth and the ventral (interior) margin of the hinge plate are generally better preserved than the hinge axis (dorsal commissure) separating the dorsal margin of the hinge plate from the exterior cardinal area of ligament attachment. This is especially common in taxa with deep and narrow ophisthodontic ligament grooves. Demarcation

of the hinge axis is especially difficult beneath the beaks. This region is difficult to illuminate for photography including both the cardinal area and the hinge plate because of differences in their respective orientations. In microarcoid shells (<10 mm length) partial dissolution of hinge teeth multiplies the number of individual teeth, which appear hollow. Other distinctive features that are preserved have been overlooked and not mentioned in taxonomic description. For example, the hinge teeth in three arcoid families are microstriate in some but not all genera and species.

Features discussed and illustrated in this comparative study of Eocene arcoids are defined as follows.

Cardinal area and ligament

The exterior cardinal area of the shell is the only source of information from fossils about the distinctive proteinaceous duplivincular ligament, a synapomorphic arcoid feature. The alternating, tanned lamellar elements and weakly calcified elements of the duplivincular ligament are inserted in grooves between the beaks and hinge axis or commissure, separating exterior from the interior hinge plate and hinge teeth. The pattern of alternation is chevron-shaped in most arcoids. In fossils and some Recent taxa the cardinal region and ligament grooves are commonly corroded and poorly preserved, obscuring clear demarcation of the commissure on shells in which the hinge plate may be well preserved. Although the arcoid ligament is partially calcified (Omori et al. 1976), it is not preserved in fossils, and detailed description of the ligament is necessarily based on study of live-collected material. However, the fossil record is sufficient to identify features of the cardinal area that are used in arcoid systematics, including features originally noted by paleontologists and used in diagnosing taxa and inferring relationships. They include the distinctive vertically-striated ligament that is the autapomorphic feature defining the Family Noetiidae Stewart, 1930 as well as patterns of ligament distribution on the cardinal area that are not accepted as phylogenetically significant.

Vertically striated ligament and ligament extent—Although the vertical pattern that originated in the Cretaceous is tentatively accepted as having a single origin, computer simulations show that it is easily derived from the chevron pattern in other arcoids (Thomas et al. 2000). The possibility of multiple origins and noetid polyphyly is emphasized by Oliver and Holmes (2006) in raising a challenge for molecular testing. Within noetid genera and subfamilies there is considerable variation in the extent and distribution of the vertically patterned ligament

on the cardinal area. A narrowly zoned vertical ligament is illustrated from a well-preserved Paris Basin Eocene species. Even if ligament grooves are not well preserved, there is an extensive body of evidence that the ligament may be developed both anteriorly and posteriorly (amphidetic), or restricted beneath the beaks to either posterior (opisthodontic) or anterior (prosodontic) regions of the cardinal area. In Cenozoic arcoids with a greatly expanded posterior shell and hinge plate the ligament is correspondingly long, opisthodontic, and restricted to a very narrow and deep groove. This is especially evident if the beaks and anterior hinge plate have a correspondingly negligible cardinal area. In an interior view of such shells the hinge appears to be split.

Hinge plate and hinge teeth

The interior platform supporting the interlocking anterior and posterior series of numerous teeth and sockets of the arcoid hinge is bounded dorsally by the hinge line (commissure) and a ventral margin that ranges from straight to strongly arched. The dentition is properly referred to as pseudodont or secondarily taxodont. Taxonomic descriptions have paid considerable attention to the length and orientation of hinge teeth. Elongate posterior teeth on a strongly arched hinge plate are a diagnostic feature of the extinct Paleozoic cyrtodontids, and elongate teeth parallel to the hinge axis on a straight or weakly-arched (=gently-curved) hinge plate are the defining autapomorphy of parallelodontids. Tooth orientation also includes short vertical teeth in the center of the hinge plate, and oblique anterior and posterior teeth. Tooth shape ranges from straight to chevron- and boomerang-shaped teeth with short ventral limbs and longer dorsal limbs. Poorly organized tooth arrays and elongate thread-like teeth in one group of parallelodontids led Arkell (1930a, p. 308) to state, “the dentition seems to have been too eccentric to be of biological advantage.” He concluded that it was an “expiring effort before final extinction” (p. 309). Arkell (1930b) attributed the success of the arcoids to the mechanical advantage of numerous oblique teeth over few elongate teeth.

Counts of tooth numbers have been used many in species descriptions and tables, but comparisons of taxa are easily confounded by quantification of features that change during ontogeny. Additional features of dentition that change during development and features that are suspectly homoplasious because they satisfy paradigms for functional efficiency. They include a so-called edentulous gap at the center of the hinge plate, chevron-shaped teeth, and micro striations on hinge teeth.

Edentulous gap between anterior and posterior tooth series—The anterior and posterior sets of teeth in arcoids are not always continuous across the hinge plate. The presence of a narrow smooth region beneath the beaks, referred to as the edentulous gap, has been used as a diagnostic feature for both species- and genus-group taxa. However, it may be expressed differently (e.g., a smooth region versus one with weak vertical striations or nodules visible only under magnification on well-preserved hinge plates). Furthermore, the gap may develop only in adults or it may be present throughout ontogeny. As a developmental feature, it occurs when the ligament overgrows the hinge axis and earliest-formed teeth (Thomas 1978). Detection of developmental overgrowth in fossils requires a growth series; it has been reported in a population of 20 specimens of a small *Bathyarca* species from the Upper Cretaceous (Maastrichtian) white chalk (Heinberg 1978).

An example of a smooth gap throughout ontogeny was noted in the original diagnosis of the New Zealand Pliocene genus *Pugliarca* by Marwick (1928), who stated, “The teeth have not been obliterated by a descending area, but have never developed.”

The hinge plate has a distinctive microstructure, and Omori et al. (1976) refer not only to overgrowth but also to “demineralization” preceding overgrowth. Thus it is a feature that must be used with caution in phylogenetic inference. Several errors of interpretation are discussed below based on availability of growth series in which an edentulous gap occurs only in the largest specimens.

A special case of a very narrow separation of the anterior and posterior series of teeth occurs in species of *Deltadon* Barnard, 1962. Kamenev (2007b) provides excellent illustrations of a distinct diagonal groove separating the tooth sets and considers it a diagnostic feature of the genus.

Chevron- or boomerang-shaped teeth—Phyletic significance of peculiarly shaped teeth is questionable. Teeth with differently oriented dorsal and ventral limbs (chevron or boomerang shape) appear to contribute substantially to valve alignment and resistance to shear stress. Descriptors of unusual tooth shapes in Upper Cretaceous and Lower Paleogene cucullaeids (Zinsmeister and Macellari 1988) include deformed, contorted, distorted, and twisted. These and other unique shape descriptors require evaluation of the accompanying illustrations (or actual specimens). A peculiar oval anterior tooth complex in *Deltadon* includes teeth that bifurcate ventrally as well as a variety of simple shapes (Barnard 1962, Kamenev 2007b).

Microstriate teeth—Very fine microstriations of hinge teeth are very seldom mentioned in arcoid taxonomic descriptions. Berezovsky (2014) includes “transverse striations” in his description of the genus *Siptionella*, based on an upper Eocene species from Ukraine, but he does not illustrate the striae or treat them as in any way remarkable. Striae may not be preserved on fossils and disarticulated shells that have been subject to dissolution; they typically are not noticeable in museum specimens or figures in the literature. They are most common on the teeth of small, thin-shelled arcoids and are especially well illustrated in scanning electron micrographs of deep-water micro-arcoids (e.g., Kamenev 2007a, b).

Tooth microstructure has, in fact, been included in studies of molluscan biomineralization (Mano 1971, Omori et al. 1976). There are clear microstructural differences between the arcid hinge plate, hinge teeth, and hinge sockets. They include lamellar microstructure of striations on the lateral sides of teeth and irregular crossed-lamellar microstructure of the corresponding sockets. (Omori et al. 1976, fig.1). These observations invite biomechanical study of their functional significance as well as their taxonomic distribution and potential phylogenetic significance.

Other shell features

Features of the shell exterior and interior are difficult to define in terms of characters and character states with any utility in phyletic inference. However features that have been used in description of both living and fossil arcoids are reviewed briefly with attention to the potential for more precise definition and discrimination of phylogenetically useful data.

Size and thickness—Tables of measurements of shell features are taxonomically useful for statistical characterization within and between populations, but generally are not useful in phylogenetic assessments. Larger and thicker shells predominate prior to the Cenozoic, but thin delicate shells of deep-water taxa and the radiation of microarcoids in tropical carbonate settings are likely to reflect a combination of taphonomic bias and habitats that are not well-represented in the earlier record.

Shape—Descriptors of shell form are variable, and the most useful generalization is the distinction between the trapezoidal and ovate taxa. Shape is strongly correlated with mode of life. Shapes of free-burrowing, endobyssate and epibyssate taxa have been analyzed and quantified in detailed studies of living arcoid species (Stanley 1970) and applied successfully to ecological and evolutionary patterns in the fossil record (Stanley 1975, 1977).

Umbonal carina—Many arcoids have a prominent exterior ridge extending from the point of maximum shell convexity at the beaks to the angular break between the posterior and ventral shell margins. In the Treatise it is referred to as the diagonal ridge or posterior ridge (Cox 1969). It is most prominent on the radially-ribbed, elongate trapezoidal taxa having a height to length ratio of more than 1:1.35, and is generally useful for recognizing byssally attached epifaunal or semi-infaunal fossil forms (Stanley 1970). It is not present in the free-living ovoid glycymerids that burrow and often live in unstable sedimentary environments. In large-shelled, byssally attached arcoids on hard substrates the carina may be paired with a posterior sulcus and auricle, interpreted by Kauffman (1969) as a streamlined design for channeling flow over the posterior excurrent area to remove waste.

Beak orientation—The pointed portion of the shell proximal to the hinge axis marks the origin of shell growth. Although the beaks are typically pointed anteriorly (prosogyrous), they are sometimes distinctively opisthogyrous. Although the opisthogyrous condition is generally not taxonomically useful in diagnosing taxa or inferring relationships, it is consistent within species and is often seen in small-shelled noetiids.

Shell sculpture—Although arcoids may have smooth shells, most have at least some form of radial ribbing – continuous production of ridges and grooves of variable width and prominence. Periodic commarginal growth increments may develop ribs that interact with radial ribs to produce cancellate patterns. Shell surface patterning may be useful in diagnosing species, and rib counts are frequently reported in taxonomic descriptions and comparisons. Any evolutionary interpretation of sculpture in epifaunal arcoids must recognize that the shell surface is often invisible beneath dense periostracum.

Mode of increase in radial rib number—As shells grow, coverage of the shell with ribs becomes an ontogenetic exercise in filling space on the shell while maintaining any functional significance conferred by alternating ribs and grooves. If rib width remains the same, new ribs must be added. This can be accomplished either by the *bifurcation* or splitting of a single rib into two or by *intercalation* of a new rib to fill the space between two ribs. Although mode of increase appears in many species descriptions is specified as an absolute either or ontogenetic feature, both modes may occur on the same specimen, as noted and illustrated in the following pages. The addition of new ribs is most commonly observed during strong allometric increase in posterior shell growth, while new ribs are added less frequently (if at all) on a

uniformly expanding anterior region.

Crenulation of ventral shell margin—Marginal crenulation expressed at the growing edge of closed valves is a paradigmatic solution to keeping valves aligned in the plane of the commissure. It is inferred to act in concert with features of the hinge plate, ligament, and musculature to reduce shear. Marginal crenulation recurs in many unrelated bivalve and may be strongly expressed as interlocking valve margins.

Interior ventral crenulation—A second form of crenulation may develop between the pallial line and the growing shell margin. Interior crenulation is not visible externally when the valves are closed but can also act to reduce shear forces. The diversity of marginal crenulation patterns has been elegantly documented by Vermeij (2013). There is a possible phylogenetic signal in its expression in arcoids. In the Atlantic group of noetiid arcoids, crenulae are broad, shallow, and short in contrast to the Pacific group in which they are narrow, deep, and long (MacNeil 1938).

Faint radial lines in shell interior—Lines that are not perceptibly upraised occur in the valves of some fossil and living arcoids and are of undetermined functional, developmental, or phylogenetic significance. They are best illustrated by SEM or high-resolution photography. The microstructural basis of these lines is subject to future investigation. The lines are most prominent ventrally, immediately interior to the pallial line and occur primarily in fossil and living deep-water taxa that are suspect parallelodontids or possible parallelodontid derivatives.

Adductor muscle scars—Muscle scars of the adductors, responsible for closure of the shell, are often better preserved in fossils than the cardinal area and of features of the ligament that act in concert to enable opening of the valves.

Myophoric ridges, flanges, shelves and buttresses—Adductor muscles may be bordered by features inferred to act as additional sites of muscle attachment. However, their function cannot be demonstrated in fossils other than by analogy with comparable features in living species. Various names have been assigned to these accessory structures, and inferences of homology remain tenuous. Fine ridges may border the interior of both adductor scars or only the posterior scar. Ridges adjacent to the posterior scar may extend dorsally beneath the hinge plate. The prominent posterior “shell buttress” in cucullaeids is the only one of these accessory features to receive detailed anatomical study (Morton 1981). It is dorsal to the main posterior adductor and

provides more effective attachment for the catch muscle during contraction. There is no comparable structure associated with the anterior adductor. Oliver and Holmes (2006) considered the shell buttress to be a diagnostic feature of cucullaeids, referring to it as a “raised flange”. Fine, sharply defined ridges bordering both anterior and posterior adductors are a consistent feature in the small-shelled noetiids in the Paris Basin and may have phylogenetic significance.

Larval shell—Arcoids are presumed to have planktonic larvae with the expectation of a larval shell with both prodissoconch I and II. Unfortunately the larval shell is typically eroded, and little is known of development. However, an exceptionally large and distinctive “hat-shaped” or “collared” prodissoconch has been noted in several minute-shelled Recent arcoid species (Barnard 1964, p. 372; Kilburn 1983, fig. 29; Hayami and Kase 1996, fig. 1a, b). It also has been figured in two late Eocene species (Berezovsky 2015, fig. 5b, c)

The significance of the unusual morphology has now been documented by detailed scanning electron micrographs of hat-shaped larval shells close to metamorphosis in live-collected adult individuals (Moran 2004, fig. 5a–d). The shells occur in the mantle cavity lining, lack prodissoconch II, and provide strong inference of brooding. Although larval shells are not preserved on any of the fossil or Recent shells examined in this study, this feature warrants future study because of its implications for evolutionary biogeography because brooding is frequently associated with small body size, low dispersal potential, and rapid rates of evolution.

EOCENE ARCOID BIODIVERSITY ANOMALIES

Although arcoid bivalves were globally distributed in the Eocene their diversity and abundance differed dramatically among biogeographic regions. Genus group taxa and families were unevenly distributed, and their response to worldwide global cooling and instability during the “doubthouse” (Miller et al. 1987) interval varied geographically. This interval is bracketed by the early Eocene Climate Optimum (EECO) at 53 Ma and the dramatic terminal Eocene transition from greenhouse to icehouse earth at 33.5 Ma. Long-term cooling and intensification of the latitudinal thermal gradient was neither gradual nor stepwise. There were many fluctuations, including a minor middle Eocene climate optimum (MECO) at approximately 41.5 Ma (Bohaty and Zachos 2003). Data from detailed chemical, physical, and microfossil records suggest many interacting drivers of climate change (e.g., Retallack et al. 2004, Miller et al.

2009). Many factors have been proposed and include both marine and terrestrial. A full review is beyond the scope of this treatment. However the anomalous Eocene arcoid biodiversity coldspot in the Northeastern Pacific and the coeval hotspot in the cratonic basins of Northern Europe at equivalent latitudes suggest that differences are related to tectonic setting, sedimentary facies, rates of sedimentation, physical and chemical oceanographic change, new marine gateway openings, reorganization of global marine circulation, changes in the depth of the CCD, differences in rates of build-up of polar icecaps and sea ice, and atmospheric changes driven by evolution of terrestrial ecosystems.

Global and local drivers of change have been difficult to separate. The opening of the Tasman Gateway and origin of the Antarctic Circumpolar Current are frequently cited as the major global stimulus to growth of polar ice sheets and high-latitude sea ice (e.g., Kennett 1977, Exon et al. 2002). The gateway opening (37–33.5 Ma) was, in turn, driven by large-scale tectonic reorganization of the southern continents. Early onset of opening of the Drake Passage (ca. 50 Ma) is also implicated in Eocene global cooling (Lagabriele et al. 2009).

The dramatic anomaly between the Eocene Arcoid biodiversity hotspot in the Paris Basin and the coldspot on the Cascadia Margin of North America is consistent with the hypothesis that tempo and mode of climate deterioration were linked to events in the Great Southern Ocean that would have predictably different effects in the North Pacific and North Atlantic. The separation of Australia from Antarctica initiated development of the cryosphere and its intersection with onset of subduction and development of deep nearshore basins and thick accretionary sequences on the Cascadia margin. Shallow, tectonically stable cratonic basins in northern Europe were subject to cooling, but not to the more dramatic effects of oscillatory deepening of the CCD (Tripathi et al. 2005) or the patterns and fluctuations in ice storage at high latitudes (Miller et al. 2009).

Cascadia active margin biodiversity coldspot

Arcoid bivalves are rare, both in species diversity and abundance, in coastal Paleogene rocks of western North America. Of the two families represented in Cascadia Margin formations, there is a single parallelodontid species in the upper Eocene Keasey, Gries Ranch, and Lincoln Creek formations and six arcid species in earlier Eocene faunas. Molluscan assemblages of the middle Eocene Coaledo-Cowlitz fauna have been intensively collected for more than 100 years and are well represented in museum

collections. However there are no arcids described or reported from the Coaledo Formation (Turner 1938, Hickman personal observation). Only three arcids are known from the Cowlitz Formation (Weaver 1942), and only a single shell was recovered in a quantitative study of >3,000 specimens from eight recurring molluscan assemblages (Nesbitt 1995).

An alleged first occurrence of the Noetiid genus *Trinacria* Mayer, 1868, described as *T. willapaensis* by Clark (1925), is interesting because it occurs in an outcrop of late Eocene Keasey-equivalent beds in southwestern Washington State. However, as noted earlier by Stewart (1930) it is not a *Trinacria* and cannot be assigned with confidence to Noetiidae. Cucullaeidae was represented in the northeastern Pacific during the Cretaceous but did not survive into the Early Paleogene except in central and southern California prior to their regional extinction in the Eastern Pacific (Moore 1983).

Climate change and marine faunal change on the northeastern Pacific margin correspond with a regional shift from deltaic sedimentation in the early and middle Eocene to the onset of forearc volcanism, steepening of the continental slope, reorganization of shallow and deep current systems, onset of cold thermohaline circulation, and high latitude immigration of taxa from the northwestern Pacific (e.g., Nesbitt 1999, 2003, Hickman 2003, Scholl et al. 2003, Retallack et al. 2004).

Paris Basin cratonic biodiversity hotspot

There is a remarkable difference in the diversity of arcoid bivalves (and bivalves in general) between the Eocene of the active margin of Western North America and the interior basins of Western Europe. Paris Basin mollusk faunas have been intensively collected, studied, and systematically described and revised over a period of more than 250 years. Modern studies of these outstandingly well-preserved faunas have turned increasingly to refinement of stratigraphy, facies, and age relationships (e.g., Gély 1996, 2008) as well as correlation of fine-scale fluctuations in diversity with inferred fluctuations in temperature, sea level, salinity and other physical and chemical parameters (e.g., Huyghe et al. 2012, Dominici and Zuschin 2016).

The European basins are here defined in a strictly geographic and tectonic sense as interconnected epicontinental seas situated in the Eocene north of the ancient Tethys Sea (specifically the western portion of the modern Mediterranean Sea). The extensive carbonate platform in the Paris Basin was connected via the English Channel to both the Atlantic Ocean and North

Sea (Huyghe et al. 2012, fig. 2).

Many inter-related studies now cover the Eocene “doubthouse” interval (*sensu* Dominici and Zuschin 2016) of gradual global cooling of the Early Paleogene “Greenhouse” to the modern “Ice-House” Earth, with a permanent Antarctic ice sheet driving and reorganizing ocean circulation (Miller et al. 1987, 2009). Data are insufficient to determine the extent to which doubthouse cooling was globally gradual or step-like (Bohaty and Zachos 2003). However, it is clear that Lutetian species diversity in the Paris Basin increased in spite of cooling to one of the greatest peaks in geologic history (Huyghe et al. 2012). The Lutetian biodiversity “Point Chaud” (hotspot of French authors, e.g., Merle 2008) is not only a hot spot for mollusk species richness (>1,500 species) but includes a remarkable diversity arcoïd bivalves. Many of the arcoïds are small-shelled (<10 mm) but also common, occurring in at high abundance in many samples. They are especially well preserved and abundant in the unlithified carbonate sands of biogenic origin.

Biodiversity in other settings

Consideration of Eocene arcoïd diversity in other settings is beyond the scope of this comparison of two extremes. The rarity of arcoïds and their representation by basal taxa on Cascadia Margin suggests a relictual last stand rather than evolutionary recovery and diversification following arcoïd extinctions at the end of the Cretaceous. However, the question of whether the Paris Basin arcoïd hotspot is a singular and unique example can be answered in part by middle Eocene arcoïds of the passive margins of eastern North America. Increase in mollusk species is also documented in the Lutetian faunas of the Gulf Coast (Hansen 1988), suggesting that the Point Chaud in the Paris basin was not exclusively local (Huyghe et al. 2012). As in the Paris Basin, the best preservation in the Gulf Coast Eocene is in unlithified sedimentary units.

Minor diversity increase in the Gulf Coast Eocene and lack of diversity increase on the Cascadia Margin cannot be attributed to failure of larval dispersal out of the Paris Basin via the Tethyan Seaway. Eocene appearances of Old-World mollusks in the Gulf Coast and Northeastern Pacific and frequently are attributed to a westward current system and migratory route (e.g., Vokes 1935, 1939, Squires and Advocate 1986, Squires 2019). Potential ancestors of all of the North American arcoïds were already present in the Cretaceous. Close resemblances of many extinct fossil Paleogene taxa from the Cascadia Margin tend to be with taxa from Asia as well as taxa known only

from the Australo-Neozelandic region (Hickman 2018).

A CALIFORNIA LATE MESOZOIC PERSPECTIVE ON EOCENE ARCOID ANOMALIES

The two basal arcoïd families that barely survive into the Eocene on the active margin of the Northeastern Pacific are better understood in terms of the earlier Late Jurassic and Cretaceous forearc basin setting of the “Great Valley Sequence” in California. These Late Mesozoic parallelodontids and cucullaeids are more diverse and abundant and occur at many localities in deep-water clastic sedimentary facies. They were described and figured from the informal stratigraphic units known as the “Knoxville Series” (Upper Jurassic), “Shasta Series” and “Horsetown Beds” (Lower Cretaceous), and Chico Series (Upper Cretaceous). Faunal assemblages were collected and described originally in the late 19th Century by authors including W.M. Gabb, F.B. Meek, W.C. Merriam, T.W. Stanton, and F.E. Turner, followed by considerable revision by 20th Century taxonomists. The brief Mesozoic perspective that follows identifies three phases of documentation pertinent to Cenozoic arcoïd diversity on the Cascadia Margin of Washington and Oregon.

Taxonomic descriptive phase

Although most late 19th century arcoïds were described under *Arca* Linnaeus, 1758, it is clear from increasing use of new genus-group names and subgeneric designations that paleontologists were aware that the faunal assemblages in the Great Valley Sequence included arcoïd species now classified as parallelodontids and cucullaeids (e.g., Diller and Stanton 1894, Stanton 1895, 1896) Two significant publications during the first half of the 20th Century formalized the revised family- and genus-group allocations of these fossil arcoïds (Stewart 1930, Reinhart 1937). The early descriptive taxonomic emphasis shifted considerably during two remarkable developments and interpretive phases: plate tectonic interpretation of the Late Mesozoic Great Valley as a deep forearc basin and recognition of the “white limestones” and their fossils as ancient cold seeps.

Plate tectonic interpretive phase

The Great Valley Sequence with its isolated carbonate lenses, concretions and mounds made very little sense geologically until the structural characterization of the relationship between continental margin magmatic arcs, trenches, and the intervening deep “arc-trench gap”. A landmark paper (Dickinson 1971) established the sedimentary component for interpreting thick clastic

sequences in forearc settings. This rapidly resulted not only in a new characterization and subdivision of the Great Valley Sequence into petrologic intervals but also expanded inquiry into provenance and source terranes (e.g., Dickinson and Rich 1972). The geologic revelation rapidly connected with paleobiology via the discovery of cold seeps and unique communities fueled by geochemical energy.

Cold seep interpretive phase

The abundant and diverse fossil invertebrate faunas of the white limestones (shell coquinas in some instances) made little sense biologically until the late 20th Century discovery of chemosymbiosis. The limestones were originally thought to represent a shallow-water setting. The discovery of modern deep-water cold seeps with abundant invertebrate taxa and microbial symbionts using methane and sulfide as energy substrates immediately led paleobiologists to reexamine certain anomalous fossil assemblages. The 77 species of fossil invertebrates originally described from the white limestones (Stanton 1895) included not only parallelodontid and cucullaeid bivalves, but also two new brachiopod species and other peculiar taxa that led paleontologists back to the field and cold-seep interpretations (Campbell and Bottjer 1993, Campbell et al. 1993). Subsequent research has led to detailed geochemical and taxonomic studies beyond the scope of this treatment.

The presence of basal arcoid taxa in California Late Mesozoic active margin faunas is especially relevant to biogeographic interpretations of Cenozoic faunas of the Cascadia Margin. Some of the Late Mesozoic basal arcoids also documented from thick sedimentary sequences on the westernmost margin of British Columbia (Whiteaves 1903).

TAXONOMIC COMPARISON AND CONTRAST

Arcoid hinge plate features, along with other well-preserved features of shell illuminate the disparity in biodiversity between the Cascadia Margin of North America and the Paris Basin during the Eocene doubtouse interval (53–33.5 Ma). The two biogeographic regions are strikingly different in tectonic, sedimentary, and oceanographic setting during this interval of global cooling and climate deterioration. The arcoid biodiversity coldspot occurs on a dynamically active continental margin whereas the coeval biodiversity hotspot occurs on an epicontinental carbonate platform. Although the two regions are at the same latitude, the faunal responses are dramatically different. Taxa selected for this comparison

are listed in the Materials and Methods section with authors and dates.

Family Parallelodontidae

Persistence of the ancient parallelodontids into the Cenozoic is increasingly well accepted. New genera and species continue to be described, not only from the Eocene (e.g., *Spitionella* Berezovsky, 2014) but also the first unequivocal living parallelodontid (*Kamenevus* Valentich-Scott, Coan, and Zelaya 2020). Although several living species from the western Pacific have been assigned to *Porterius*, specimens require careful evaluation. *Arca* (*Macrodon*) *dalli* E.A. Smith, 1885, does have elongate subparallel hinge teeth, but Arkell (1930b, p. 351) argued that it is a “retrograde offshoot from *Barbatia*”. The distinction between homology and homoplasy of long subparallel teeth continues as an unresolved issue. While Oliver and Holmes (2006, p. 240–241) consider the possibility that four deep-water arcoid genera may represent living parallelodontids, they also suggest “secondary appearance of this character due to the thin nature of the hinge plate.”

Porterius gabbi (Dickerson, 1917)—*Porterius* was described and figured by Clark (1925) from the Cascadia Margin, where the type species is now known from occurrences in the Gries Ranch, Lincoln Creek, and Keasey formations. The type species was originally described by Dickerson (1917) under the genus *Barbatia*. Clark, based on advice from William Healy Dall at the Smithsonian, treated it as a relict parallelodontid. However, Clark’s description and illustrations are inadequate and misleading. Although many subsequent authors have questioned the validity of the name, none examined type material. Stewart (1930, p. 68) regarded it as a parallelodontid based exclusively on Clark’s description, suggesting that it is related to *Cucullaria* while noting that the figures are “inadequate”. Additional specimens collected by this author from the Gries Ranch Formation and upper member of the Keasey Formation assist in clarifying features of the hinge plate as well as shell features that are recognized here in two relict parallelodontids from the Paris Basin.

Porterius gabbi (Figs. 1A–E, 2A–D) is recognized here as a parallelodontid as defined by the synapomorphic hinge plate character of elongate posterior hinge teeth (Fig. 1E, pt) that are parallel to the hinge axis. These teeth are separated from the shorter and more oblique anterior teeth (Fig. 1E, at) by an edentulous gap (Fig. 1E, eg) in adult specimens, resulting from overgrowth of the hinge plate by the opisthodontic ligament and cardinal area. Demarcation of the hinge line (Fig. 1E,

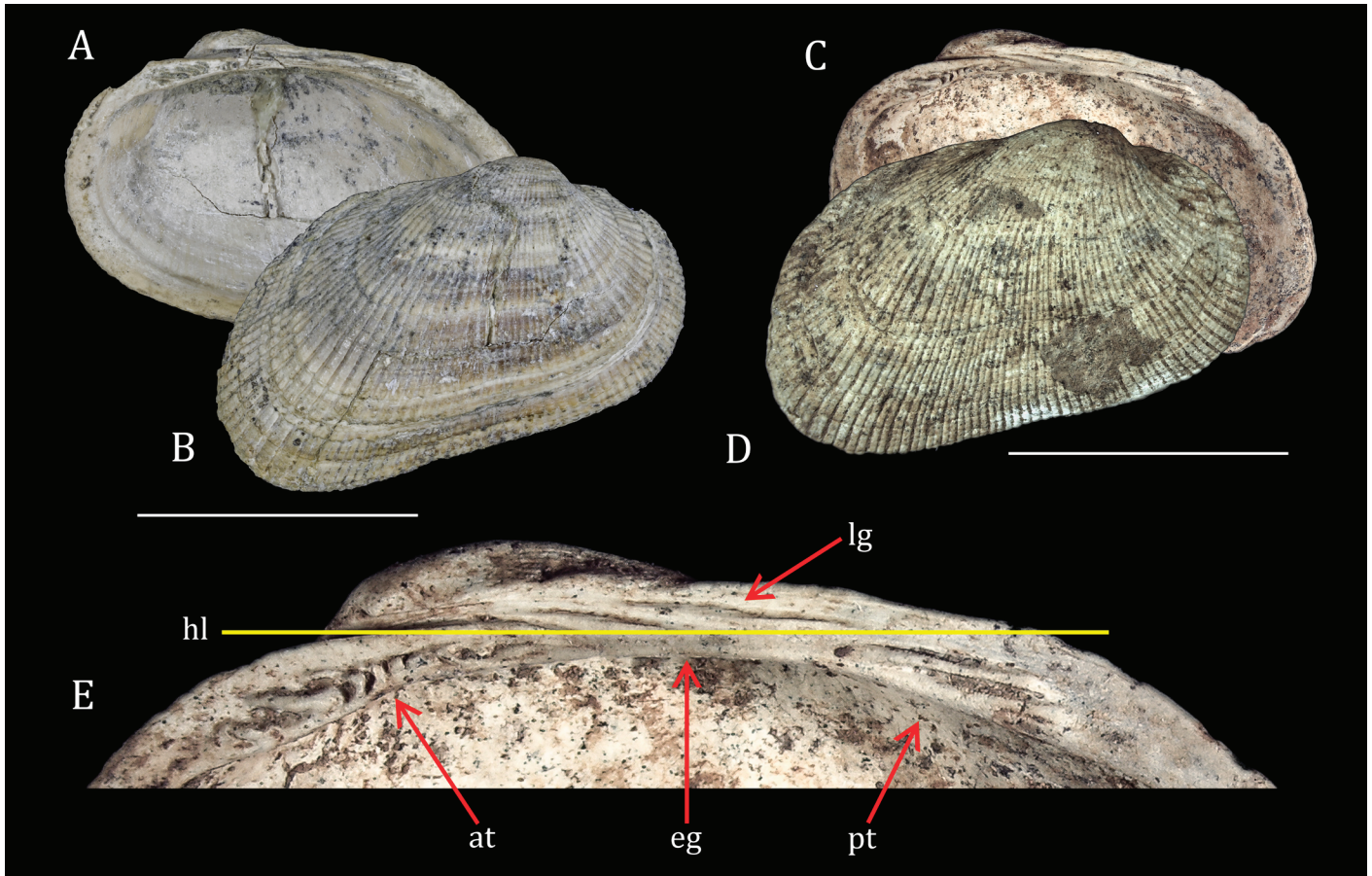


Figure 1A–E. Cascade Margin Parallelodontidae: *Porterius gabbi* (Dickerson, 1917), Keasey Formation, USGS 15518. **A.** Right valve interior view. **B.** Right valve exterior view. Gries Ranch Formation, UCMP IP 2289. **C.** Right valve exterior view. **D.** Right valve interior view. **E.** Detail of cardinal area and hinge plate of C: **at**=anterior hinge teeth, **eg**=edentulous gap, **hl**=hinge line, **lg**=exterior ligament grooves, and **pt**=posterior hinge teeth. Scale bars=10 mm.

hl) separating cardinal area from hinge plate is preservationally indistinct, and the posterior ligament groove (Fig. 1E, lg) is prominent. Juvenile specimens lack the edentulous gap. As a result of ontogenetic deepening of the narrow posterior ligament groove, the hinge region appears to be split.

Other features include microstriations of both anterior and posterior hinge teeth (Fig. 2C) and prominent radial lines in the shell interior (Fig. 2D). Adductor muscle scars are inadequately preserved to determine whether myophoric ridges are present. Shell shape is ovate-elongate, with prosogyrous beaks located far anterior to the expanded posterior portion of the shell. The shell lacks an umbonal carina. There is a slight indentation in the ventral shell margin of some shells (Fig. 1B) but no evidence of a byssal gape. Mode of life is inferred to be epibyssate in an upper bathyal community in association with giant limids, hexactinellid sponges, and terebratulid brachiopods (Hickman 1984, Fig. 7). The shell surface is coarsely sculptured by flat-topped radial ribs separated

by very narrow grooves (Fig. 1B, C). Ribs are broader on the more rapidly-expanding posterior portion of the shell (Fig. 2B) and rib number may increase either by bifurcation or intercalation. Bifurcation is more common. Comarginal growth striae are distinct but do not form ribs.

***Porterius adversidentatus* (Deshayes, 1858)**—This species from the Eocene of the Paris Basin appears to have been reallocated for the first time from *Arca* to *Porterius* by Newell (1969) in his treatment of the parallelodontids in the Treatise on Invertebrate Paleontology. Newell's figure of the critical hinge plate features is a drawing of the interior right valve of a Paris Basin specimen of *Arca adversidentata* rather than a figure of the type species from the Cascadia Margin. Newell placed this species as well as type species of *Porterius* in his "Catella Group" although there is no differential diagnoses or synapomorphic characters distinguishing the informal Treatise groups of parallelodontids.

Porterius adversidentatus (Fig. 3A–E) is similar to the Cascadia type species in having a few elongate posterior

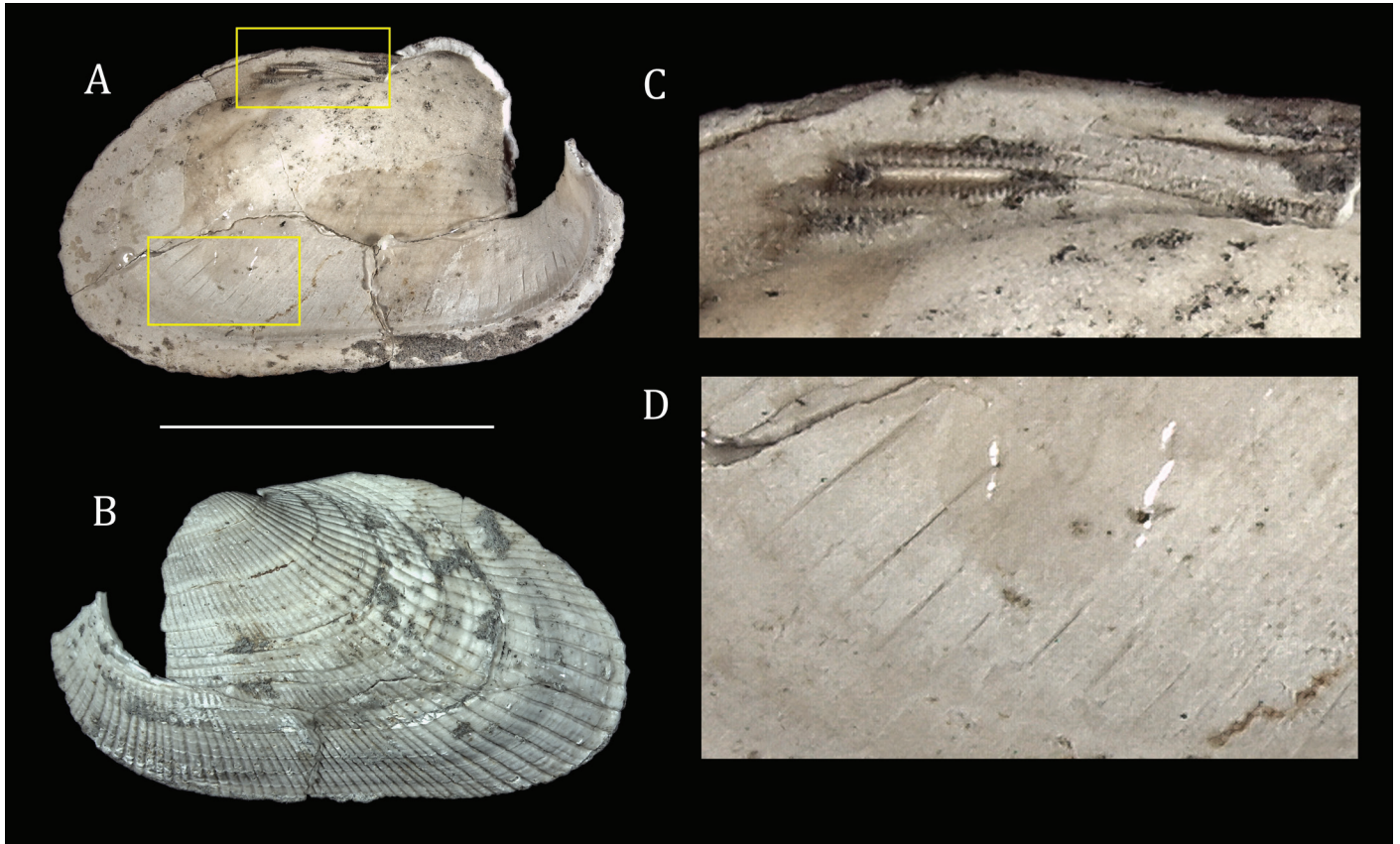


Figure 2A–D. Cascade Margin Parallelodontidae: *Porterius gabbi* (Dickerson, 1917), Keasey Formation UCMP IP 2540. **A.** right valve exterior view. **B.** Right valve interior view. **C.** Detail of hinge tooth striations. **D.** Detail of interior shell lines. Scale bar=10 mm.

hinge teeth that are parallel to the hinge line and an anterior series of shorter, more numerous, and more oblique teeth, separated from the posterior series by an edentulous gap in the largest specimens but continuous in smaller immature shells. The gap is also a result of progressive overgrowth of the central hinge plate by the opisthodontic ligament and cardinal area. The ligament groove is narrow and deep, and the hinge region has the same split appearance in this species.

Arkell (1930a, p. 307) noted the similarity of *Arca adversidentata* to many species of the arcid genus *Barbatia*. He dismissed both the shape and the tendency of some species of *Barbatia* to develop what he referred to as secondary or “mimetic” dentition, and proposed *Pseudogrammatodon* as a new parallelodontid genus based on the Paris Basin species, apparently unaware of Clark’s earlier name *Porterius*.

Other shell features shared with type *Porterius* include the lack of an umbonal carina, prosogyrous beaks situated far anterior and lack of a byssal gape or distinct indentation of the ventral shell margin (Fig. 3B). The shell surface is similarly sculptured with many flat-topped

radial ribs separated by narrow grooves (Fig. 3B). The ribs are also broader on the posterior portion of the shell. Ontogenetic increase in rib number is primarily (but not exclusively) by bifurcation. The interior surface of the shell is inadequately preserved to characterize the adductor scars or determine whether fine myophoric ridges are present. Stewart (1930, p. 68) suggested that absence of a myophoric ridges may be a diagnostic of parallelodontids, but this cannot be assessed from the material examined. Two additional features shared with the Cascadia margin species are the presence of faint but distinct interior radial lines in the shell interior to the pallial line (Fig. 3E) and interior crenulation of the ventral shell margin (Fig. 3A, D, E).

***Cucullaria cucullaris* (Deshayes, 1829)**—*Cucullaria cucullaris* (Fig. 3F–H), a second relict parallelodontid in the Paris Basin fauna, is easily distinguished from *Porterius adversidentatus* by distinctive and unusual features of the anterior hinge plate. *Cucullaria* was proposed by Conrad (1869) based on another Paris Basin species, *Arca heterodonta* Deshayes, 1860, in which the anterior and posterior series of hinge teeth are separated by a series

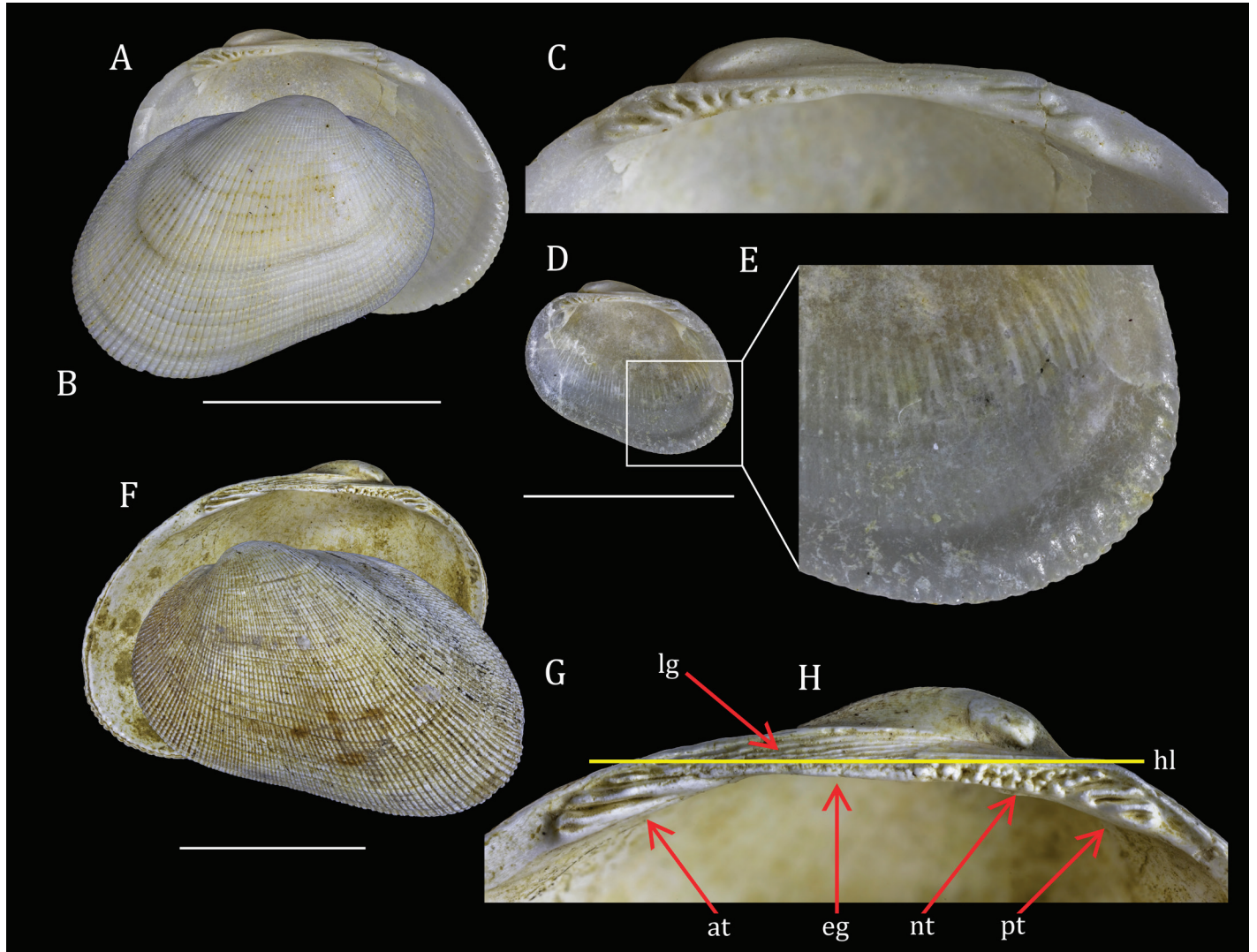


Figure 3A–H. Paris Basin Parallelodontidae: **A–E.** *Porterius adversidentatus* (Deshayes, 1858), UCMP CLC B-5399, PE110-63. **A.** Right valve interior view. **B.** Right valve exterior view of adult. Scale bar=10 mm. **C.** Detail cardinal area and hinge plate. **D.** Right valve interior view of juvenile (Scale bar=10 mm) and **E.** detail of interior shell lines and crenulate posterior margin. **F–H.** *Cucullaria cucullaris* (Deshayes, 1858), UCMP CLC B-5387, PE 110-62. **F.** Left valve interior view. **G.** Left valve exterior view. Scale bar=10 mm. **H.** Detail of cardinal area and hinge plate of **F:** **at**=anterior hinge teeth, **eg**=edentulous gap, **hl**=hinge line, **lg**=ligament grooves, **nt**=nodular teeth, and **pt**=posterior hinge teeth.

of very small teeth immediately below to the beaks. This distinctive tooth cluster has been referred to as “cardinal teeth” (Newell 1969), and is especially well preserved in *C. cucullaris* (Fig. 3H). The anterior and posterior series of teeth (**at**, **pt**) are both parallel to the hinge line (**hl**). In Fig. 3H the elongate two or three posterior teeth are separated from two or three shorter anterior teeth and the heterogeneous cluster of nodular teeth (**nt**) by an edentulous gap (**eg**). The gap is clearly generated by overgrowth of the hinge plate by the ligament groove and ligament (**lg**). Overgrowth generates the same appearance of a split hinge region characteristic of *Porterius*.

In the Treatise, Newell (1969) based his informal “Cucullaria Group” on the Eocene type of *Cucullaria*, but the

other genera he included in the group are all from the Cretaceous. The idea of a radiation of parallelodontids that barely made it into the Eocene reflects an opinion expressed by Arkell (1930a) who viewed it as an “expiring effort before final extinction” (p. 309). His conclusion is based on the dentition (figured by an inadequate diagram) as “too eccentric to be of biological advantage”.

Other shell features of *C. cucullaris* include lack of an exterior umbonal carina, prosogyrous beaks situated far anterior and lack of a byssal gape or significant indentation of the ventral shell margin. Exterior shell sculpture consists of numerous narrow radial ribs separated by narrow grooves. Unlike the sculpture in *Porterius*, regular commarginal increments intersect radial ribs to produce

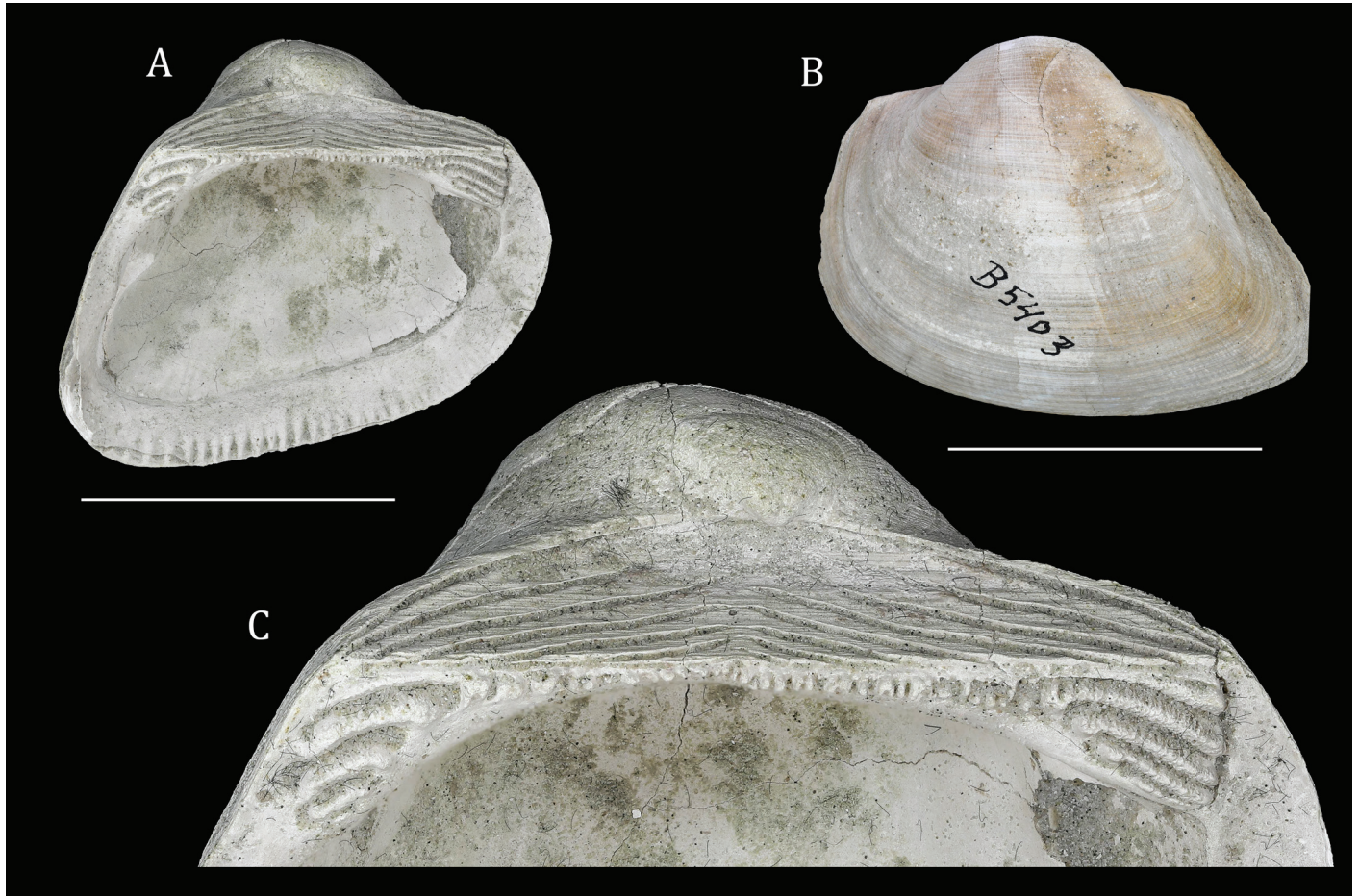


Figure 4A–C. Paris Basin Cucullaeidae: *Cucullaea crassitina* Lamarck, 1801, UCMP CLC B-5403, PE 111.1. **A.** Left valve interior view. **B.** Right valve exterior view. Scale bars=5 cm. **C.** Detail of cardinal area and hinge plate.

a fine but distinctive cancellate pattern (Fig. 3G). Increase in rib number is predominantly by bifurcation, although the origin of new ribs becomes disorganized during rapid allometric posterior expansion of the shell, with chaotic discontinuous nodulation that cannot be traced and apparent examples under microscopic inspection of discontinuous intercalations and bifurcations. The adductors are inadequately preserved to allow characterization or detection of myophoric ridges, and there is no evidence of interior radial lines. Interior marginal crenulations are absent, but exterior ribs extend beyond adjacent grooves to form very fine marginal crenulation.

Family Cucullaeidae Stewart, 1930

Cucullaea crassitina Lamarck, 1801—This distinctive large, quadrate, thick-shelled arcoid is the sole remnant in the Paris Basin Paleocene (Thanetian) of a Mesozoic arcoid infaunal radiation that began in the Jurassic and peaked with a broad global distribution in the Late Cretaceous of >60 species. Surviving cucullaeid diversity declined precipitously during the early Paleogene and

the family had disappeared from both Europe and North America by the close of the middle Eocene. The Paris Basin species is treated here to highlight the lack of a counterpart on the Cascadia Margin. It is a contrast to the parallel decline and disappearance of parallelodontids and the relict genus *Porterius*, which persisted into the middle and late Eocene in both northern Europe and northwestern North America. Whereas the parallelodontids moved successfully into deeper and colder water during the Eocene, with offshoots arguably persisting in deep water today, the warm-water cucullaeids remained in shallow settings and contracted geographically to a tropical refugium in the Western Pacific and Indian Ocean. Although the four living cucullaeid species have retained large body size, an autapomorphic posterior myophoric buttress and infaunal burrowing mode of life, they have reduced shell thickness and other conservative morphological features of the family and moved into significantly new regions of arcoid morphospace as documented by principal component analysis (Buick 2009).

It is noteworthy that the global distribution of Cretaceous

and earliest Paleogene cucullaeids is well-documented, including species from Africa, Madagascar, New Caledonia, India, Japan, Russia and Sakhalin, Patagonian South America, New Zealand, and Seymour Island near the end of the Antarctic Peninsula (e.g., Stewart 1930, Newell 1969). There is some lack of agreement as to family placement of some Mesozoic genus group taxa such as *Nordenskjoldia* Wilckens, 1910. Newell included it in his informal “Grammatodon Group” of parallelodontids, while Zinsmeister and Macellari (1988) classify it as a cucullaeid, presenting a strong argument for clearer character definition and emphasis on features that effectively separate the two families.

Cucullaeids were well represented on the Pacific margin of North America in the Cretaceous, including the Shasta and Chico Groups and Horsetown Beds in northern California and the Nanaimo Group on Vancouver Island, British Columbia. They also were well represented and sometimes abundant in Cretaceous strata of the Atlantic and Gulf coasts (Conrad 1858,

Wade 1926, Stewart 1930). On the Northeastern Pacific continental margin, distribution contracted southward with *Cucullaea mathewsonii* Gabb, 1864, restricted to the Paleocene and Eocene from central California south to Baja California Sur and *C. morani* Waring, 1914, occurring only in the Paleocene and Eocene of Southern California (Moore 1983).

Cucullaea crassitina (Fig. 4A–C) is easily-recognized by unique features of the cucullaeid hinge plate, which include a broad central series of short vertical hinge teeth flanked by short, sub-parallel anterior and posterior short sets of well-developed, finely serrated, and effectively interlocking hinge teeth (Fig. 4C) An additional diagnostic feature is a unique massive myophoric buttress or flange projecting above the large posterior adductor scar. It is not preserved in the corroded and exfoliating shell interiors of available Paris Basin specimens. In an anatomical study of a living cucullaeid Morton (1981) has shown that buttress is a site of attachment for catch muscle, functioning mechanically to reinforce the shell

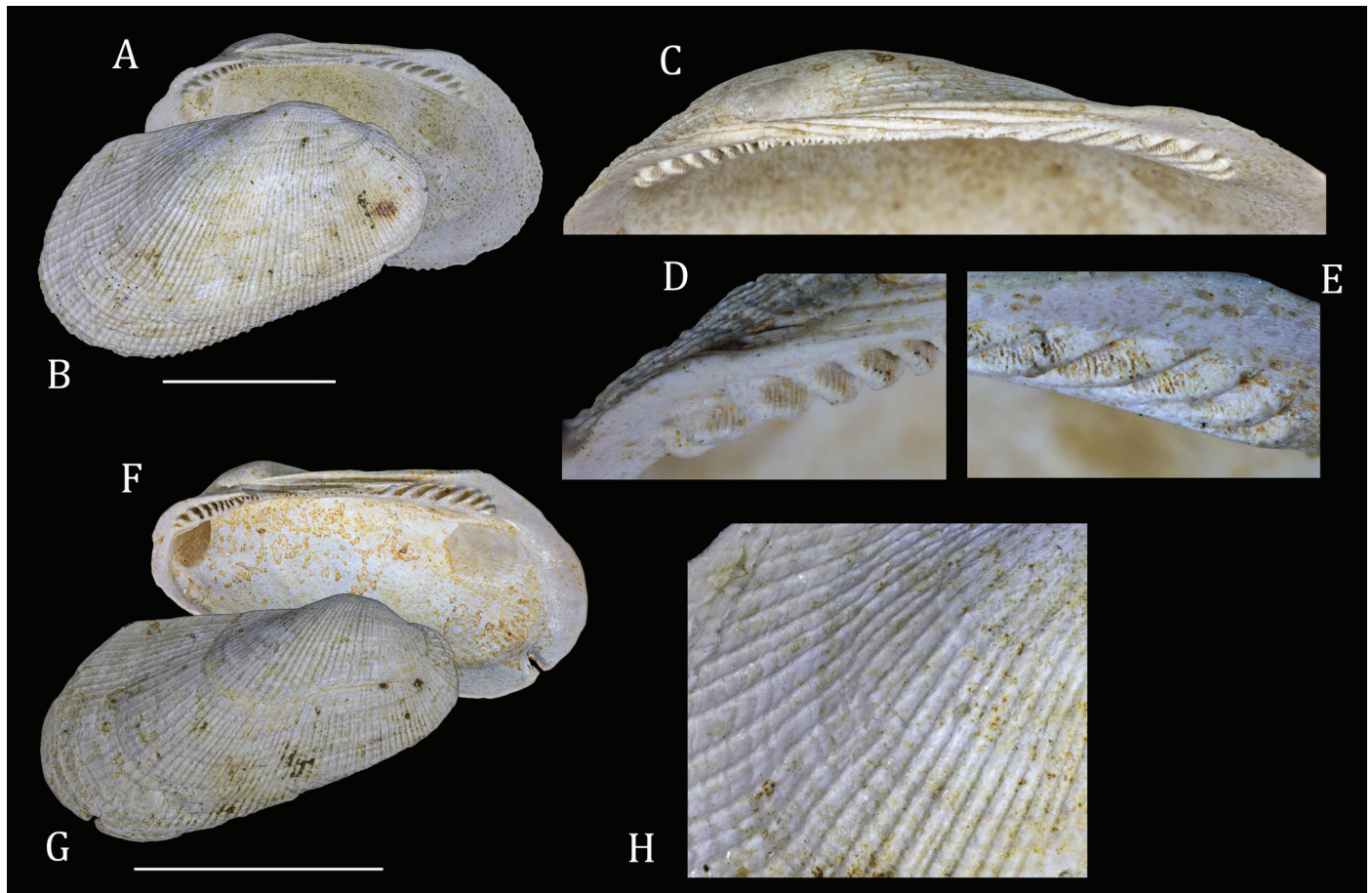


Figure 5A–H. Paris Basin Arcidae: *Barbatia obliquaria* (Deshayes, 1829). **A–E.** UCMP CLC B-5376, PE 110.33. **A.** Right valve interior view. **B.** Right valve exterior view. **C.** Detail of cardinal area and hinge plate of **A.** **D, E.** Details of microstriation of anterior and posterior teeth. Scale bar=10 mm. **F–H.** UCMP CLC B-5376, PE 110.33. **F.** Right valve interior view. **G.** Right valve exterior view. **H.** Detail of bifurcation and intercalation of radial ribs. Scale bar=10 mm.

against strong shear forces associated with a free-living, burrowing mode of life. The ligament is symmetrically amphidetic with well-preserved chevrons arranged on either side of the broad, slightly concave cardinal area above the straight hinge line and beneath small, medially-situated prosogyrous beaks (Figs 4A, C).

Shells are thick, inflated, and subtrapezoidal in shape, with a distinctive truncation of the posterior margin. Exterior shell sculpture (Fig. 4B) consists of low radial ribs with narrow interspaces and low commarginal growth increments that do not form distinct riblets. As in many cucullaeids, the interior margin of the shell is coarsely denticulate ventral to the pallial line (Fig. 4A).

Family Arcidae Lamarck, 1809

***Barbatia (Barbatia) obliquaria* Deshayes, 1829**—*Barbatia (Barbatia) obliquaria* (Fig. 5A–H) is one of three Paris Basin arcids treated here to highlight the extraordinary diversity of species currently assigned to the genus *Barbatia* Gray, 1842. The systematics of this genus is contentious and far from resolved, in spite of considerable efforts by both paleontologists and neonatologists. Oliver and Holmes (2006) were unable to find any phenotypic support for monophyly, and molecular analyses indicate polyphyly (Marko 2002, Feng et al. 2015). However, there was clearly an explosion of abundance and species diversity of the *Barbatia* morphotype in the interconnected epicontinental carbonate basins of northern Europe. In the Paris Basin there are 38 nominal species in three subgenera (Pacaud and Le Renard 1995) including 18 species from the Lutetian biodiversity hotspot (Pacaud 2008). Eleven nominal species are recorded from a middle Eocene fauna in Ukraine where *Barbatia* is the most diverse of 76 bivalve genera (Berezovsky 1997). A larger set of 29 arcoid species is elegantly illustrated and described from the revised middle to upper Eocene “Mandrokova Fauna” in Ukraine (Berezovsky 2015). Well-preserved *Barbatia* material has been described and figured from faunas in southern England, Belgium and Germany. In contrast, only five species of *Barbatia*, based on very few specimens, are known from the active Cascadia Margin of western North America.

Barbatia obliquaria is easily assigned to the *Barbatia* morphotype of small to minute (length typically <20 mm), relatively thin-shelled, ovate-elongate arcids with small prosogyrate beaks near the rounded anterior margin and a long, obliquely-expanded posterior margin. The opisthodontic ligament groove is narrow, resulting very little separation of the beaks. The hinge plate (Fig. 5A, C, F) is gently curved and narrow with oblique anterior and

posterior series of teeth of the same form separated by a region of numerous short denticles oriented perpendicular to the hinge line. The short denticles are beneath the long ligament groove, but have not been eliminated to form an edentulous gap, even in the largest specimen observed (n=16, length range=9–29 mm). The short anterior and longer posterior teeth are microstriate (Fig. 5D, E). The shell exterior (Fig. 5B, G, H) lacks a distinct umbonal ridge and is finely sculptured with numerous low, thin radial ribs with narrow interspaces and thin incremental ribs that become more conspicuous toward the ventral margin, where they produce a faintly cancellate pattern as they intersect radial ribs. The shell interior lacks radial lines. The posterior adductor scar is circular and larger than the narrower anterior adductor (Fig. 5F). There is no interior or marginal crenulation of the valves. There is no ventral emargination or byssal notch, although shells were probably attached throughout life by a weak byssus and nestling in rubble. This is consistent with observation of a growth interruption in the posterior ventral margin of one of the shells (Fig. 5F, G).

***Barbatia (Barbatia) interrupta* Lamarck, 1805**—*B. interrupta* (Fig. 6A–G), a different thin-shelled *Barbatia* morphotype, occurs at many localities in the Lutetian of the Paris Basin as well as in the Lutetian Eocene of the Selsey Formation in England, where Wood (1871) noted minor differences in shell outline in the British Museum’s Edwards Collection. The major feature that has been used to differentiate the species is the pronounced interruption of dentition in the central hinge plate beneath the beaks (Fig. 6A, B), as well as the strongly oblique orientation of both posterior and anterior series of hinge teeth, which are effectively parallel to the hinge in some specimens (Fig. 6B, C). Teeth in both series are strongly microserrate (Fig. 6C). In contrast to *B. obliquaria*, the ventral margin of the shell has a shallow byssal embayment (Fig. 6D) and coarser exterior radial ribs (Fig. 6D), which extend beyond the narrower interspaces to crenulate the ventral margin (Fig. 6E). Commarginal elements are less prominent, appearing primarily as growth pauses. The interior margin of the shell is strongly crenulate outside the pallial line. Inside the pallial line, the shell has prominent radial lines, and the posterior adductor scar is narrow and elongate rather than circular.

There is considerable intraspecific variation in the specimens examined, and one lot in the Cloez collection is apparently misidentified. Individuals of the same size, although identical in shape differ in hinge plate features: on close examination there is no interruption of dentition in the central hinge plate, where a long series of small

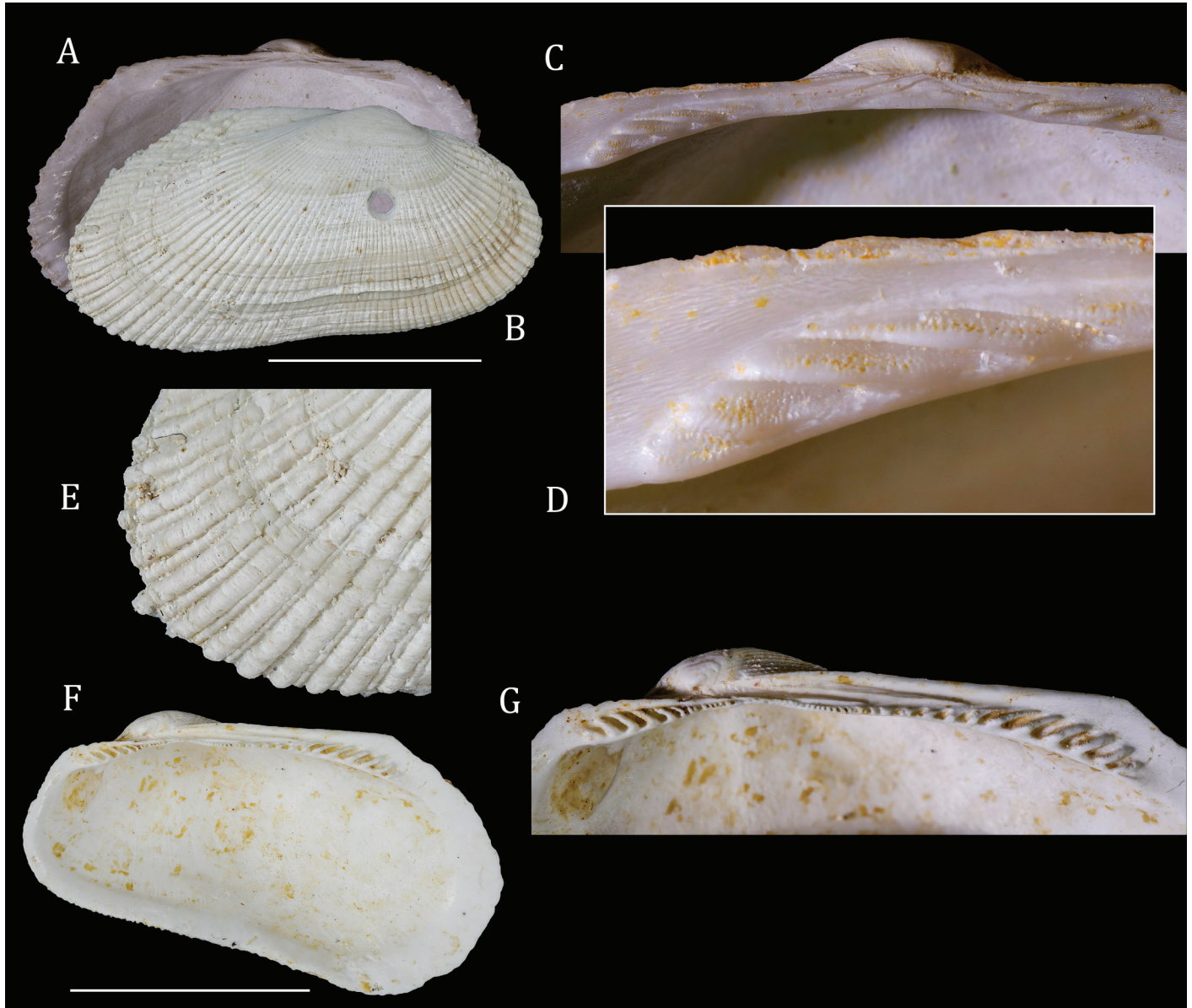


Figure 6A–G. Paris Basin Arcidae: *Barbatia interrupta* (Lamarck, 1805), A–E. UCMP CLC B-5363, PE 110.29. **A.** Left valve interior view. **B.** Detail of cardinal area and hinge plate. **C.** Detail of microstriate posterior hinge teeth. **D.** Right valve exterior view, **E.** Detail of posterior radial ribs. **F, G.** UCMP CLC B-5387, PE 110.29 (specimen misidentified as *B. interrupta*). **F.** Right valve interior view. **G.** Detail of cardinal area and hinge plate with uninterrupted dentition. Scale bars=10 mm.

vertical teeth separate the anterior and posterior oblique boomerang-shaped teeth (Fig. F, G).

Rostarca angusta (Lamarck, 1805)—Also a small, thin-shelled arcid, this Paris Basin species has been treated for more than two centuries under *Barbatia*. Cossmann (1887) treated it, along with four other species under the subgenus *Plagiarca* Conrad, 1875, based on a species from the Cretaceous of North Carolina. Glibert and Van De Poel (1965) cited a number of morphological distinctions as a basis for introducing the new subgeneric name *Rostarca* for five Paris Basin taxa, designating *Barbatia angusta* as the type species. There was no intent

to treat *Rostarca* as a Paris Basin endemic, because they included an Eocene species from Pakistan that shares the primary defining features: extremely elongate trapezoidal shape and faint radial and comarginal sculpture. Their “diagnosis” is detailed, and *Rostarca* is treated here a distinct genus.

Rostarca angusta (Fig. 7A–D) is a phenotypic extreme among arcoids in its narrow trapezoidal shell form, with a disproportional posterior length, sub-parallel dorsal hinge and ventral margin, and pronounced angulation at the juncture of the posterior and ventral margins. The beaks are distinct, sharply pointed and closely opposed

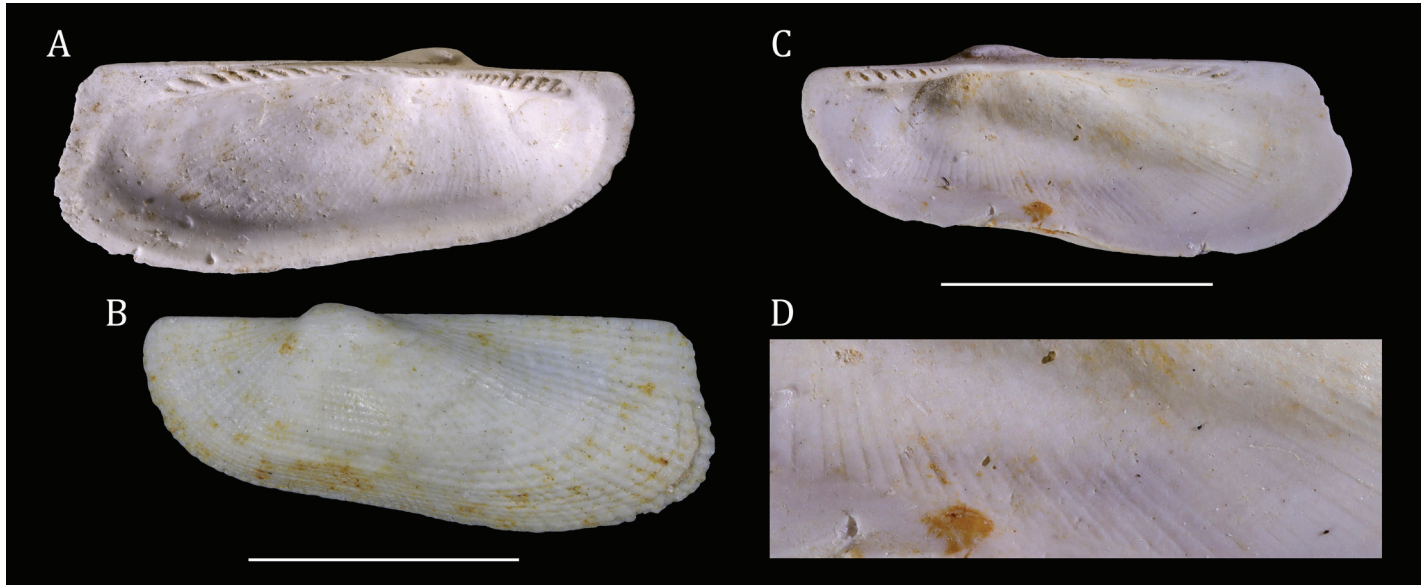


Figure 7A–D. Paris Basin Arcidae: *Rostarca agusta* (Lamarck, 1805), UCMP CLC B-5391, PE 110.40. **A.** Left valve interior view. **B.** Left exterior view. **C.** Right valve interior view. **D.** Detail of interior shell lines. Scale bars=5 mm.

on either side of a long, narrow opisthodontic ligament groove. The ligament groove is shallow and the ligament does not completely overgrow the hinge plate beneath the beaks, leaving a series of small vertical denticles between the anterior and posterior tooth series (Fig. 7A). There are as many as 16 oblique posterior teeth and 12 shorter and less oblique anterior teeth (Fig. 7A, C). There is no evidence of tooth microserration in the material examined. The small, circular anterior adductor scar and larger posterior scar are faintly preserved and lack myophoric ridges. The most striking feature of the interior is the series of radial lines (Fig. 7D), also conspicuous in parallelodontids and some other arcoid taxa. Although exterior sculpture (Fig. 7B) is weakly developed, the pattern is faintly cancellated by intersection of fine radial and commarginal ribs. Very shallow indentation of the ventral margin is consistent with a semi-infaunal epibyssate nestling mode of life.

Family Noetiidae Stewart, 1930

Although the family was present worldwide the Late Cretaceous, the Paleogene faunas of Paris Basin provide the only evidence that they were ever a prominent faunal element. Noetiids are not present in Eocene faunas of the Cascadia margin. However three species have been described from Paleocene and early to middle Eocene of southern and middle California. They were described between 1864 and 1927 from finer-grained offshore mudstone facies and were never abundant faunal elements in the tropical Paleogene fauna of the northeastern

Pacific. Although type specimens are not well preserved and there are few subsequent collections, Moore (1983) provides a detailed summary and illustrations of the California material.

Arcopsis dispar (Deshayes, 1858)—Deshayes' species (Fig. 8A–D) also has been treated under *Striarca* Conrad, 1862, a genus group based on a Cretaceous species from Tennessee, and *Arcopsis* Koenen, 1885, is sometimes treated as a subgenus of *Striarca*. It is treated here as a distinct genus based on the narrow, triangular ligament with vertical grooves (Fig. 8B, D) in contrast to the longer, less restricted ligament in *Striarca*. However the genera share cardinal areas with a triangular amphidetic ligament beneath sharply defined prosogyrous beaks, features considered diagnostic of the family. Noetiids are one of the few higher taxa of arcoid bivalves that can be defined by a synapomorphy (Oliver and Holmes 2006); and in molecular analysis they cluster as a monophyletic group (Feng et al. 2015), in contrast to disturbingly separate clades in a polyphyletic Arcidae (Marko 2002). However, some species of *Arcopsis* and *Barbatia* in the Paris basin faunas are superficially similar in minute shell size, shape and cancellate exterior sculpture (Fig. 8A, C). *Arcopsis dispar* is one of the most abundant of the minute-shelled arcoids in the Cloez collection, and the two specimens illustrated here are from a lot of >500 shells covering a range of shell size classes from a single shell with a length of <2 mm to shells in the 7–8 mm range. Ten percent of the valves have small naticid drill holes. There is no byssal gape although a weak indication

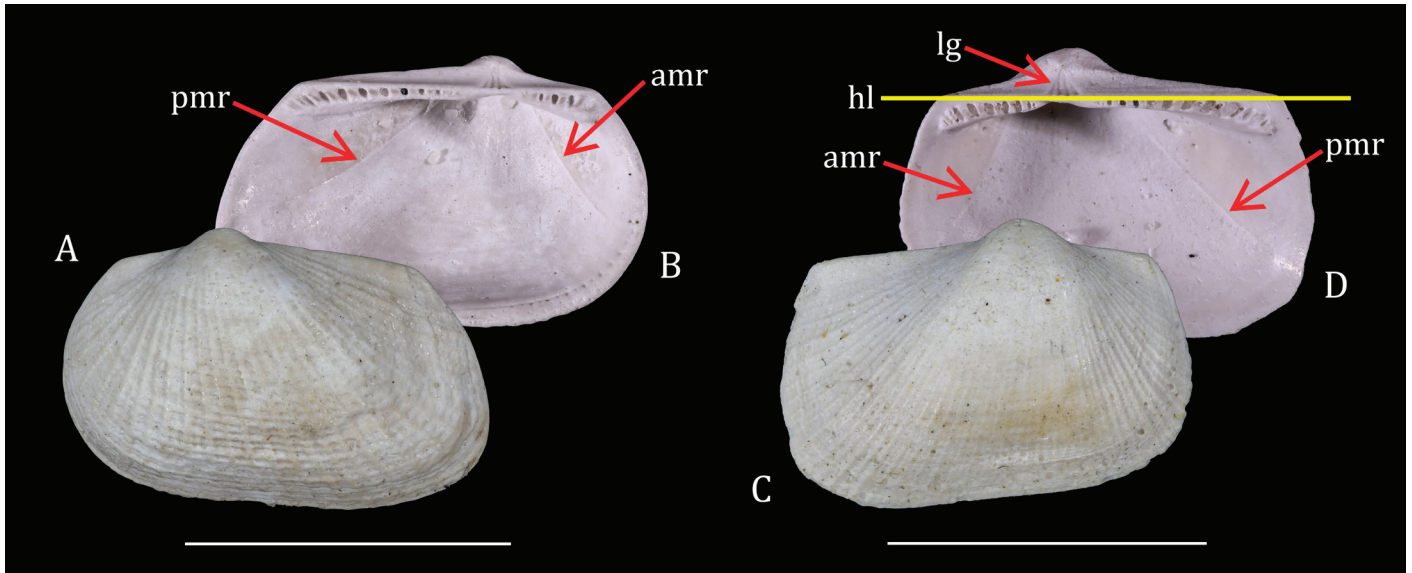


Figure 8A–D. Paris Basin Noetiidae: *Striarca dispar* (Deshayes, 1858), UCMP CLC B-5377, PE 110-51. A, B. Exterior and interior views of a left valve. C, D. Exterior and interior views of a right valve: **amr**=anterior myophoral ridge, **hl**=hinge line, **lg**=ligament grooves, and **pmr**=posterior myophoral ridge. Scale bars=5 mm.

of a byssal emargination, shell shape and sedimentology (medium grained glauconitic sand with calcareous fragments adhering to shell interiors) are consistent with a semi-infaunal mode of life, attached by a few weak byssal threads to individual sediment grains or undersides of larger pieces of rubble.

The strongly inflated valves of quadrate to rhomboidal outline provide a distinctive shape contrast to the more elongate small-shelled species of *Barbatia* that are also frequent in the Paris Basin Eocene. The beaks are widely separated by a shallow, weakly concave and well-demarcated cardinal area and distinct hinge line. Shell exteriors may, however, be very similar in the development of fine cancellate sculpture (Fig. 8A, C). Valves become increasingly inequilateral during growth, with more rapid posterior expansion, but they never achieve the exaggerated posterior elongation common in the *barbatia*-form arcids. The cardinal area is typically well preserved on shells and is slightly convex and smooth on either side of the small triangular ligament. The hinge line (Fig. 8B, D) is straight, and the ventral margin of the hinge plate is weakly arched. Hinge teeth are short, straight, and vertical to weakly oblique, with 12–13 teeth in the posterior series and 7–8 in the shorter anterior series of the largest specimens.

A feature of the shell interior that is consistent in *Arcopsis* and other noetiids is the thin, sharp myophoric ridge bordering the interior of both anterior (Fig. 8B, D amr) and posterior (Fig. 8B, D pmr) adductor scars. The ridges continue dorsally beneath the hinge plate to the

beaks. Lack of conspicuous crenulation of the ventral shell margin is partly a consequence of the weak surface sculpture combined with preservational corrosion, but the interiors of the best-preserved shells have distinct crenulation between the pallial line and ventral margin and a puckered pallial line (Fig. 8B). There is no evidence of the interior radial lines frequently observed in both parallelodontids and arcids.

Arcopsis dispar does not occur in Lutetian faunas of the Paris Basin but is abundant in earlier Paleogene (Yressian and Thanetian) assemblages from similar unconsolidated sedimentary facies. A comparative analysis of Lutetian species diversity in lithified and unlithified sedimentary facies by Sanders et al. 2015 revealed a “huge loss” of small-shelled species in the lithified facies, which the authors attribute to taphonomic bias.

SUMMARY AND CONCLUSIONS

The doubtouse interval of Eocene global climate and dramatic atmospheric and oceanic cooling between 53 and 33.5 Ma is one of the most dramatic periods of climate instability in Earth history. Increasingly detailed data of many kinds show that temperature decline was neither steady or stepwise during transition from an ice-free tropical greenhouse world to an icehouse world with polar icecaps, reorganized thermal and chemical structure of oceans, ocean gateway openings, and reorganized ocean currents and circulation patterns. This is also an interval of biological reorganization recorded worldwide in well-preserved marine mollusk assemblages. An

extraordinary surge in marine molluscan biodiversity in the intracontinental Anglo-Parisian Basin of Northern Europe contrasts with an equally anomalous decline at equivalent latitude on the northeastern Pacific margin of North America. Arcoid bivalves provide an exceptionally good illustration of opposing coeval trends in Eocene diversity and abundance.

Eight Eocene species from the families Parallelodontidae, Cucullaeidae, Arcidae and Noetiidae are illustrated and discussed in an evaluation of (1) arcoid shell morphology, taxonomy and systematics and (2) geologic and paleoclimatic data bearing on the problem of anomalous and contradictory faunal responses during the doubt-house interval.

Comparative morphology, taxonomy and systematics

Phenotypic features have been treated differently in living and fossil arcoids, and there is a long history of taxonomic research that is restricted either to living taxa or extinct fossil taxa. Although diagnoses and descriptions of living and fossil species often take the same format in systematic and faunal monographs, morphological terminology is not consistent. This study provides a new taxonomic foundation.

Based on detailed morphologic observations, arcoid features are redefined and standardized in a glossary distinguishing characters that have an apparent phylogenetic signal from those rich in functional information and suspect homoplasy and those that change during development, as illustrated in large populations. Examples of synapomorphic characters are most distinctive on the interior hinge plate and features of the hinge teeth, and exterior features of the cardinal area, ligament and ligament grooves. Homology of accessory structures for muscle attachment (ridges, flanges, shelves, buttresses) is inferred by new distinctions in their placement and special features. Examples of features of predominantly developmental significance include shell shape that change during allometric growth, such as extreme elongation of the posterior portion of the shell and patterns of addition of sculptural elements during shell growth. Functional features, which often are homoplastic, include mechanisms that resist stress and promote valve alignment. Examples include commissural crenulation of the ventral shell margin and interior crenulation that is not visible at the commissure. Noted here for the first time in many arcoids are microscopic striations on hinge teeth, inferred to promote effective frictional alignment of the hinge.

Comparative geology and historical biology

Major conclusions that bear on the anomalous biodiversity between the northern European hotspot and northwestern American coldspot are based many kinds of data. These data are extracted from the actual stratigraphic record of the fossiliferous rocks in both regions, reconstructions of tectonic, bathymetric, and sedimentary settings, inferences of physical and chemical oceanographic conditions, reconstructions of ocean currents and changes in marine gateways affecting larval dispersal and geographic patterns, and potential biases in fossil preservation.

Tectonic setting—An active margin plate convergence, subduction, and arc volcanic setting compared with an intraplate epicontinental setting provide a first order basis for comparing biodiversity patterns. Low diversity on active margin forearc basins and high diversity in stable epicontinental basins establish a framework for investigating many individual physical, chemical, and biotic factors associated with each setting.

Bathymetric and sedimentary setting and facies—There is a clear association of heightened diversity in the Paris Basin with shallow-water depth facies, biogenic carbonate sediments, low rates of sediment accumulation, poor or no lithification, and absence of features indicative of hostile geochemistry (e.g., hypoxic conditions, sulfide or methane emissions). Low diversity on the Cascadia Margin is associated with outer shelf or slope depths, clastic sedimentation, thick sedimentary sequences and strong lithification, and discrete or diffuse seepage of methane or sulfide.

Gateways, currents and dispersal—The Paris Basin is not a local anomaly, because elevated diversity is also noted on the passive margins of the western Atlantic and Eocene of the Gulf Coastal Plain. However, westward dispersal out of the Paris Basin cannot explain taxonomic originations in families and genera that were already present in the New World during the Late Mesozoic. Eocene current system reorganization, gateways, and barriers to dispersal are not well understood at this time.

The active Cascadia Margin coldspot of arcoid biodiversity reflects a puzzling lack of Paleogene genera and species of Arcidae and Noetiidae, the families that dominate arcoid assemblages in the Paris Basin. The occurrences of relict Parallelodontidae and Cucullaeidae, families that disappear from the Eastern Pacific margin during the Paleogene, is preceded by a well-documented record of both families and potential progenitors in the Great Valley Sequence record of an earlier active margin in Central and Northern California. In both ancient

volcanic arc settings, there is geologic and geochemical evidence of deep water and unique cold-seep environments.

Physical and chemical oceanographic factors—Reorganization of ocean currents, development of a two-layered ocean with a cold bottom layer (psychrosphere) beneath a warmer thermosphere, changes in the depth of the CCD, ice accumulation leading to polar icecaps and significant sea ice at high latitudes are highly likely to have produced different regional effects. Changes in ocean current systems in the North Pacific have been accepted as the source of introduction of Asian taxa into the Northeastern Pacific. There is longstanding evidence for dispersal of some Paleogene Tethyan genera to the northeastern Pacific, and dispersal must continue to be investigated case by case rather than as origin and expansion of entire biotas.

Taphonomic factors—Taxonomic diversity in the Paris Basin especially high in thin, poorly-lithified bioclastic beds, while taxonomic diversity is low in the thick, strongly-lithified siliciclastic sequences of the Cascadia Margin. Although rates of accumulation and compaction clearly affect some aspects of preservation, in situ articulated shells are more common in the thick siliciclastic sequences, and preservation of original shell microstructure is typically excellent in unweathered specimens. Taphonomic factors affecting biodiversity merit greater attention but so do factors affecting quality of preservation.

FUTURE DIRECTIONS

Understanding historical patterns of arcoid bivalve biodiversity and evolutionary radiation must be grounded in systematics and an integration of living taxa with an extraordinarily long fossil record. Oliver and Holmes (2006) confronted the immense task of bringing greater resolution to the classification and relationships of living arcoids, emphasizing the need for better character definition and unmasking of the rampant homoplasy that has plagued recognition of monophyletic family- and genus-group taxa. Their list of phenetic challenges for living arcoids is long, and their critical evaluation of detailed anatomical data suggested that anatomy, as well as shell morphology, is strongly linked to mode of life. At least for the biologist, alternative hypotheses of relationship can be tested with molecular data. The evidence thus far is consistent with multiple parallel evolutionary radiations and is especially exciting to a paleobiologist confronting enigmatic biogeographic patterns during intervals of profound change in global climate.

The conclusions presented here provide considerable opportunity to treat living and fossil arcoids together as an exemplary taxon with an unusually deep evolutionary history. The arcoid shell is rich in features that merit more critical study. For paleontologists, it is important to break down the traditional barriers between the Paleozoic, Mesozoic, and Cenozoic eras. This is a tall order, but arcoids crossed major mass extinction boundaries and developed novel functional and developmental strategies. They confronted long intervals of global change in their geologic and tectonic environments, linked with changing oceanographic and atmospheric conditions. Chemical proxies for the drivers of global change are increasingly refined. Coeval differences between the Cascadia Margin at the inception arc volcanism and subduction and the carbonate platform of the Paris Basin can be specified as different sets of linked parameters. These, in turn, can be explored with respect to the contrasting functional, ecological, constructional, and phyletic responses.

There are several avenues of future research that can bring the Recent together with the fossil record of arcoids. For example, the microarchitecture of the biomineralized shell is conservative relative to many of the traditional shell features employed in taxonomy. Microarchitectural differences noted above in the calcium carbonate of the hinge plate, hinge teeth, and hinge sockets can be studied equally well in living and fossil taxa and need not remain largely unnoticed in the literature of materials science and skeletal biomineralization. A second example explored above is in the realm of arcoid larval and developmental biology, using the larval shell to distinguish between taxa with planktonic development and those that brood and the association of brooding with small body size and dwarfing that apparently has recurred within some lineages. A third example, not explored above, is respiratory physiology and the ability to persist in hypoxic or dysoxic geologic settings. Hemoproteins have been noted in both Arcidae and Noetiidae, together sometimes referred to as blood cockles. Characterization of oxygen-binding proteins in basal bivalve groups with a long geologic history may have as yet unrecognized phyletic potential as well as a role in their persistence. These are speculative examples intended to stimulate curiosity in basic research at a time of increasing emphasis on applied science.

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