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MORPHOLOGY, PHYLOGENY, AND SYSTEMATIC REVISION OF GENERA IN THE DIMYIDAE (MOLLUSCA, BIVALVIA, PTERIOMORPHIA)

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ABSTRACT—Differences in the mineralogy of hinge teeth and inner shell layers in the family Dimyidae form the basis for a revision of genera. The stem genus *Atreta* (Late Triassic to Late Cretaceous) has aragonitic denticulate hinge teeth on the right valve articulating with pitted sockets on the left valve. The same arrangement is present in *Neoatreta* n. gen. (Paleocene? Miocene to Recent) but with the appearance of extensive calcitic overarching of the resilifer. In *Dimyella* (Eocene to Recent), aragonitic teeth and sockets are still present but are modified into hook shaped denticulate teeth with corresponding sockets. All three of these genera have inner aragonitic crossed-lamellar shell layers that extend well outside the pallial line. In contrast, *Dimya* (Eocene to Recent) and *Basiliomya* (Pliocene to Recent) comprise a second clade in which aragonitic hinge teeth are absent and hinge articulation is calcitic, derived from the calcitic rim. *Dimya* has only weak hinge articulation and has an aragonitic inner shell layer delimited by the pallial line; in *Basiliomya* calcitic hinge teeth are more prominent and the entire inner shell layer inside the pallial line is foliated calcite. *Diploschiza* (Cretaceous, Albian to Maastrichtian), here reinstated from synonymy with *Atreta*, is probably a precursor of the *Dimya-Basiliomya* clade based on incipient calcitic hinge teeth. Predation pressures probably drove the evolution of this cemented family from its original habitat on hardgrounds in moderately deep water into much greater depths or into cryptic habitats, including submarine caves.

New combinations are *Dimyella malnatrensis* (Corselli and Bernocchi), *D. molokaia* (Dall, Bartsch, and Rehder), *D. similis* (v. Koenen), *Neoatreta dissimilis* (Tate), *N. filipina* (Bartsch), *N. kaiparaensis* (Laws), *N. phaidra* (Woodring), *and N. plana* (Martin).

INTRODUCTION

IN VOLUME 1 of the journal *Science*, William Healey Dall (1883, p. 51) reported the discovery of the first living member of the peculiar bivalve genus *Dimya* Rouault, 1850, dredged in deep water off the Antilles by the U. S. Coast Survey steamer "Blake." Until Dall's report, the genus was known only from its type species, *Dimya deshayesiana* Rouault, 1850, from the middle Eocene of Bos d' Arros in southwestern France. As noted by both Rouault and Dall, the peculiarity of *Dimya* stems from its surprising combination of characters. Superficially, *Dimya* resembles oysters in cementing one valve to the substrate, but *Dimya* consistently attaches by its right valve, whereas oysters attach by the left. The alivincular resilium of *Dimya* is overarched apically by the medial convergence of anterior and posterior dorsal shell margins, leading to the formation of a secondary dorsal ligament composed of weak periostracum, thus resembling the condition in the Anomiidae Rafinesque, 1815, and Plicatulidae Watson, 1930. The calcitic rim of the shell is internally denticulate or ribbed, somewhat as in *Plicatula* Lamarck, 1801, and some anomiids and oysters. Unlike oysters, which have a mainly calcitic shell (except for Triassic species; see Hautmann, 2006), *Dimya* has a prominent inner, complex crossed-lamellar aragonitic layer in addition to a calcitic, mainly irregularly foliated outer layer. But it is particularly the presence of two adductor muscles throughout ontogeny that sets *Dimya* apart from other ostreoid, anomioid, and pectinoid groups, which are monomyarian throughout dissoconch ontogeny.

Dall (1886) subsequently named the living species mentioned in his earlier report *Dimya argentea* and described its shell morphology and anatomy in detail. In the same year, Fischer (1886) named the family Dimyidae and described a new genus, *Dimyodon* Munier-Chalmas in Fischer 1886, from the Jurassic (Bathonian) of France, said to differ from *Dimya* in having a pair of strong hinge teeth. Although several genera and species were described in the following years (see review by Vokes, 1979), by the time of publication of the *Treatise on Invertebrate Paleontology* in 1969, only two genera in the Dimyidae were recognized (Cox and Hertlein, 1969, p. N382), *Dimyodon* and *Dimya*, with the stratigraphic range of the family extending from the Jurassic to the present day. The stratigraphic range was extended to the Upper Triassic (Carnian) with the discovery by Fürsich and Werner (1988) that the Triassic genus *Atreta* Étallon, 1862, which had previously been placed in the Plicatulidae based on the assumption that it is monomyarian, in fact has two adductor muscle scars and a pair of hinge teeth positioned precisely like those of *Dimyodon*. The dimyarian condition of *Atreta*, now regarded as a senior synonym of *Dimyodon*, had been overlooked because of the differential dissolution of aragonite relative to calcite during diagenesis. All muscle scars as well as any hinge teeth that may be formed of aragonite disappear during diagenesis under certain conditions, as in chalk facies.

The family Dimyidae is currently viewed as a low-diversity, mainly deep-water marine group consisting of five genera: *Atreta* Étallon, 1862 (=*Dimyodon* Munier-Chalmas in Fischer, 1886, and *Diploschiza* Conrad, 1866a); *Dimya* Rouault, 1850; *Dimyella* Moore, 1969; *Basiliomya* Bayer, 1971; and *Emiliomya* Corselli and Bernocchi, 1992. The oldest genus, *Atreta*, has a long fossil record that spans about 160 million years, from the Late Triassic (Carnian) through the Cretaceous (Hautmann, 2001a). *Dimya*, long regarded as the only Cenozoic representative of the family, ranges from the Paleocene to the present (Vokes, 1979), a span of about 65 million years. *Dimyella* and *Basiliomya* were both originally described as extant monotypic genera living in the tropical western Atlantic, *Dimyella* in a submarine cave off the Caribbean coast of Mexico and *Basiliomya* on the deep forereef off northern Jamaica as well as in the Bahamas. Neither genus has been reported until now from the fossil record. *Emiliomya* is also monotypic and is known only from the early Pliocene of northern Italy (Corselli and Bernocchi, 1992).

Taking these stratigraphic ranges at face value, the generic evolution of the Dimyidae would appear to have been relatively static for about 160 million years (Late Triassic to Upper Cretaceous), followed by a genus-level turnover at about the time of the Cretaceous–Paleogene boundary, then another static episode of more than 60 million years, ending with a burst of generic diversification in the Pliocene to Holocene. However, there is at present no phylogenetic concept for dimyid genera. We do not know when or where the Pliocene and Holocene genera originated, and there is no good agreement as to whether *Atreta* extends into the Paleogene or whether *Dimya* occurs below the Cretaceous–Paleogene boundary (Vokes, 1979). There is the additional problem that morphological descriptions have been either imprecise or incorrect, in some cases resulting in the misidentification of genera. That at least one of the Holocene Atlantic genera, *Dimyella*, may have a much broader geographic distribution and possibly a long fossil record is suggested by recent reports of the genus from cave faunas throughout the western Indo-Pacific (Hayami and Kase, 1996; Paulay, 2003) and by the present study, which documents its extensive distribution in the tropical western Atlantic.

In the present study I refine or introduce morphological terms that have proven to be useful for defining dimyid genera and for unraveling the evolutionary history of the Dimyidae. It will be shown that the Mesozoic stem genus *Atreta* gave rise to two monophyletic clades, both of which have living representatives. The first clade consists of *Diploschiza* (here removed from the synonymy of *Atreta* and regarded as a valid genus), *Dimya*, and *Basiliomya*. The second clade contains *Neoatreta* n. gen., and *Dimyella* (of which *Emiliomya* is regarded herein as a junior synonym). The new generic distinctions should pave the way for an eventual revision of dimyid species, both in present-day oceans as well as in the fossil record. Because members of the two major clades are extant, this study should also encourage comparative anatomical studies as well as testing of relationships by molecular genetic methods.

MATERIALS AND METHODS

This study is based on collections of the Departments of Paleobiology and Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., and collections from the northern Dominican Republic on loan to the author from the Natural History Museum of Basel, Switzerland. The dentition, shell microstructures, and mineralogical boundaries on inner shell surfaces were initially studied under reflected light using a Wild M5 binocular microscope at magnifications as high as ×100. Inner aragonitic shell layers were distinguished from outer calcitic layers on the basis of reflectivity and color, the aragonitic layers generally appearing whiter, chalkier, and less translucent than the calcitic layers. Mineralogical determinations are based on the known mineralogies for particular molluscan shell microstructures as described in detail by Taylor et al. (1969), Carter (1990), and Carter and Lutz (1990). Microstructures were determined by means of scanning electron microscopy using a variety of scanning electron microscopes over a period of years, most recently a Philips XL-30 ESEM with a LaB6 electron source. Whole or fractured specimens for SEM were cleaned ultrasonically but were not etched or bleached. They were then mounted on aluminum stubs with double-sided tape and examined either with or without sputter coating with gold-palladium.

Abbreviations.—NMB=Naturhistorisches Museum, Basel, Switzerland; SAM=South Australian Museum, Adelaide; USBF=United States Bureau of Fisheries; USGS=United States Geological Survey, with reference to localities recorded in registers housed in the Department of Paleobiology, Smithsonian Institution; USNM=National Museum of Natural History (U.S. National Museum), Smithsonian Institution, Washington, D.C.; (IZ)=Department of Invertebrate Zoology of USNM; (P)=Department of Paleobiology of USNM.

MORPHOLOGY

The interior surface of the dimyid shell displays four commarginal features that are of interest for the discrimination of genera (Fig. 1): 1) the boundary separating aragonitic inner layers from the calcitic outer layer, referred to herein as the aragonite line (AL); 2) the calcitic rim (CR), extending from the aragonite line to the shell margin; 3) the pallial line (PL), a line of mantle muscle scars, commonly disjunct, connecting the two adductor scars; and 4) the denticulation line (DL), a line of denticles or pits along the distal ends of internal costellae, exposed on the calcitic rim.

The aragonite line is well outside the pallial line and close to the denticulation line in *Atreta* (Fig. 2.1, 2.2), *Diploschiza* (Fig. 2.3–2.6), *Neoatreta* n. gen. (Fig. 3.1, 3.5), and *Dimyella* (Fig. 4.2, 4.7–4.10), but is nearly coincident with the pallial line in *Dimya* (Figs. 1, 5.1, 5.6, 5.7). In *Basiliomya* there is no aragonite line, because the entire region inside the pallial line is calcitic (Fig. 6.1, 6.3). The surface inside the pallial line, whether aragonitic or calcitic, is minutely pitted or pustulose in most dimyids examined (Figs. 1, 4.2, 4.5, 5.8, 6.2). In some species, shallow pits inside the pallial line are adventitious mantle attachment scars, each floored by irregularly prismatic aragonitic myostracum. Tubules, which in some bivalves represent the projections of epithelial mantle cells into the shell inside the pallial line (e.g., in the Arcoida; Waller, 1980), possibly occur in some Dimyidae. In almost all of the dead valves dredged from the sea floor, however, microborings that may be confused with tubules are common, particularly in the aragonitic shell layers. Where aragonite extends outside the pallial line, its surface is smoother than that inside the pallial line, but its lighter color or chalkiness distinguishes it from the smooth, more reflective, silvery surface of the foliated calcitic rim. The microstructure of the aragonite, as determined by scanning electron microscopy, is irregular complex crossed-lamellar (Fig. 7.4). In the roughened area inside the pallial line, first-order lamels are commonly difficult to detect under reflected light because they are short and branching, producing a complex crossed-lamellar structure. Longer first-order lamels may in some cases be visible under reflected light at magnifications of ×50 where the aragonitic inner layer is thick, particularly in the umbonal region. The irregular microtopography of the aragonitic surface inside the pallial line suggests a high degree of calcium mobility between this area and the opposing surface of the mantle. Linear oriented crossed lamellar microstructure, such as that present in the Plicatulidae (Carter and Lutz, 1990, pl. 56A), is not present in any of the dimyids examined.

The calcitic rim is the inner surface of the outer calcitic layer along which this layer is secreted. It consists of regular foliated to complex crossed-foliated calcite (Fig. 7.2), this microstructure also forming the denticles or pits of the denticulation line. In genera where the aragonite line impinges upon the denticulation line, as in *Dimyella*, a thin inner aragonitic layer may extend over the denticles in late ontogeny. All dimyids examined lack an outermost columnar or tabular simple prismatic calcite layer such as that present in anomiids and oysters and in the early ontogeny of the right valve in most

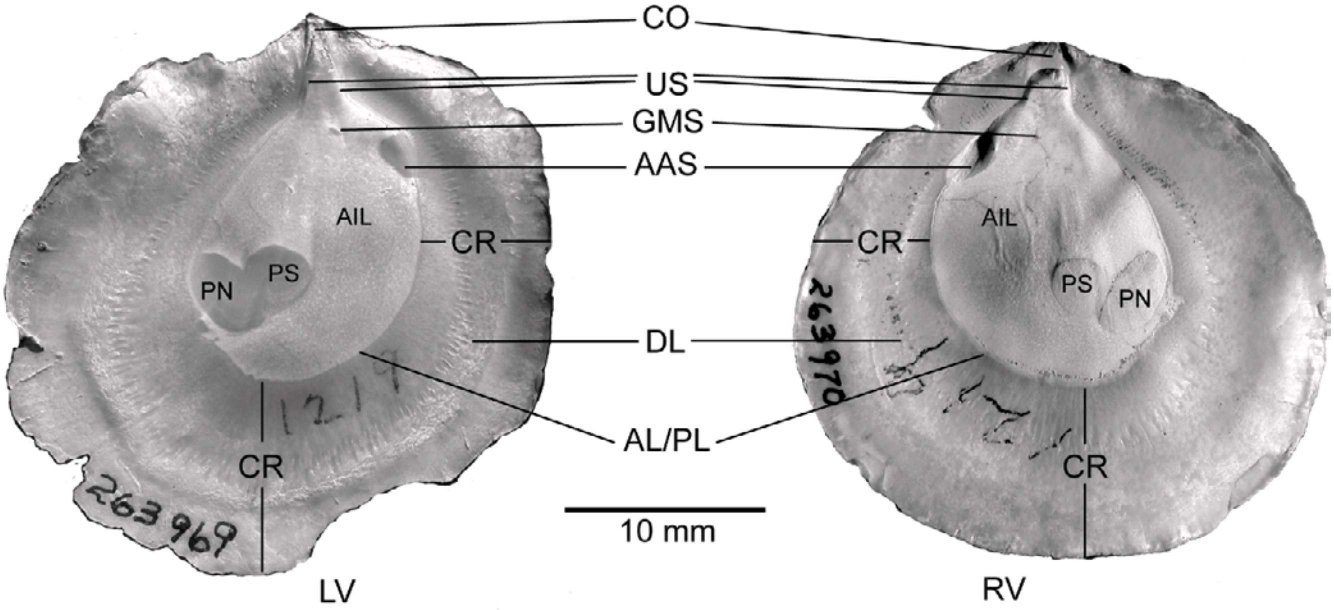


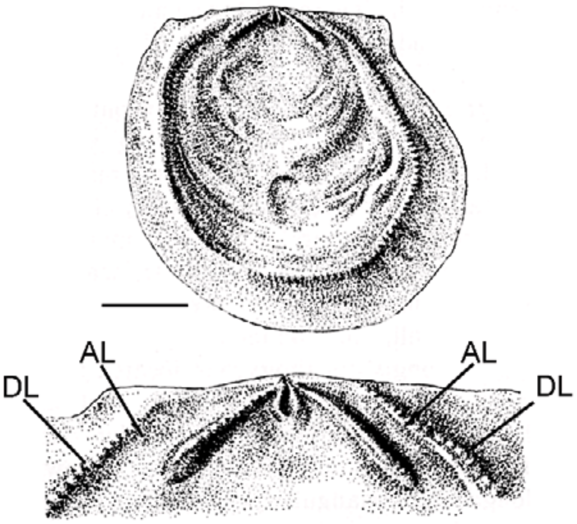
FIGURE 1—*Dimya grandis* Dall in Guppy and Dall, 1896, hypotypes of Vokes (1979), Río Amina, Dominican Republic, Gurabo Formation, showing characters mentioned in text: left valve, USNM(P) 263969; right valve, USNM(P) 263970. Abbreviations: AIL=aragonitic inner shell layer, AL/PL=coincident aragonite line and pallial line, AAS=anterior adductor scar, CO=calcitic overarch of resilifer, CR=calcitic rim, DL=denticulation line, GMS=gill muscle scar, LV=left valve, PN=posterior adductor scar (non-striate component), PS=posterior adductor scar (striate component), RV=right valve, US=umbonal shoulders.

Pectinoidea (Waller, 1978). In fresh Recent dimyid shells, particularly in *Dimya argentea* Dall, 1886, reflected light deeply penetrates the foliated calcite, giving it a silvery sheen. This led some early students of the Dimyidae (e.g., Dall, 1886; Bartsch, 1913) to refer to this layer as nacreous, a term now reserved for a specific aragonitic microstructure (Carter, 1980, p. 81) not known to be present in this family. In fossils that have undergone some weathering, the calcitic rim is generally grayish, compared to the lighter hue and common chalkiness of the aragonitic inner layer and the muscle scars. In some Recent shells, some areas on the inner surface of the calcitic rim of the right valve appear non-reflective and chalky, as in the syntypes of *Dimya argentea* (e.g., USNM(IZ) 64101). Examination by scanning electron microscopy of similar chalky areas in *Dimya lima* Bartsch, 1913, revealed an open calcitic microstructure (Fig. 7.3) similar to that of the chalky layers of oyster shells (Margolis and Carver, 1974, fig. 1E, 1F; Carriker, 1996, p. 137–140).

The calcitic rim is broadest midventrally, narrowing dorsally along the anterior and posterior margins, and the denticles of the denticulation line become more closely spaced in the dorsal region in most species (Figs. 1, 2.5, 5.3, 5.4). The exceptions are in *Basiliomya* (Fig. 6.1, 6.4), where denticles are widely spaced around the entire denticulaton line, and in *Dimyella* (Fig. 4.3, 4.6, 4.7), where denticles maintain close spacing even midventrally. In some dimyids, exemplified by *Dimya grandis* Dall in Guppy and Dall, 1896, the inner margin of the calcitic rim along the aragonite line in the dorsal region forms umbonal shoulders (US) where it drops off steeply to the aragonitic surface in the umbonal cavity (Fig. 1). In fossils having thick aragonite in the umbonal region, the differential dissolution of the aragonite relative to the more resistant calcitic rim also produces steep umbonal shoulders, which in some cases may actually be undercut where calcitic secretion extended over the outer edge of the aragonitic layer, exemplified by some specimens of *Atreta* and *Diploschiza* (Fig. 2.6).

The denticulation line is invariably on the calcitic rim, but its position on the rim relative to the aragonite line and shell margin is variable among genera. In *Dimyella*, the calcitic rim is particularly narrow, with both the denticulation line and the aragonite line nearly at the shell margin (Fig. 4.7). Denticulation conveys shear resistance when the valves are closed, because the denticles of one valve, usually the right valve, penetrate corresponding pits on the other valve, usually the left, although both denticles and pits may be present on the same valve. The growth tracks of the denticles or pits form antimarginal riblets or grooves on the inner shell surface. Where the calcitic rim is broad, deposition of foliated calcite may quickly fill in behind a denticle or pit so that no elongate tracks of a riblet or groove remain on the inner shell surface, although the microstructural track may be visible in transmitted light within the calcitic layer. If the track of the denticle or pit is not covered, then an internal riblet or groove forms on the inner surface of the outer calcitic layer, marking the migration of the denticles or pits during ontogeny. In some fossil dimyid shells from which aragonite has been dissolved, the riblets are plainly visible across most of the inner surface of the exposed calcitic layer, as in Mesozoic specimens of *Atreta* and *Diploschiza* (Fig. 2.5). The pits of the denticulation line may have raised edges, in which case their ontogenetic migration tracks appear as closely spaced pairs of fine lines, usually on the left valve.

The pallial line in most dimyids is a variably disjunct line of small muscle scars that abuts the ventral margin of the anterior adductor scar and may or may not be confluent with the posteroventral margin of the posterior adductor scar. The line is nearly continuous in *Dimya* (Figs. 1, 5.6, 5.7) but is coarsely disjunct in *Basiliomya* (Fig. 6.1, 6.4). Many past descriptions of dimyids have confused the pallial line with either the aragonite line or the denticulation line, even though in some cases the pallial line may be well inside of these, as can be seen in Recent *Neoatreta filipina* (Bartsch, 1913) (Fig. 3.1) and *Dimyella* (Fig. 4.7). There has also been confusion about the position of the posterior adductor scar (specifically, the posterior component of



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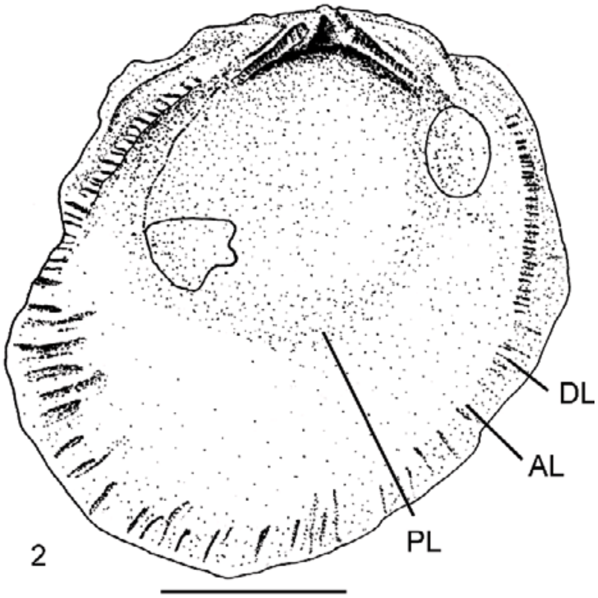

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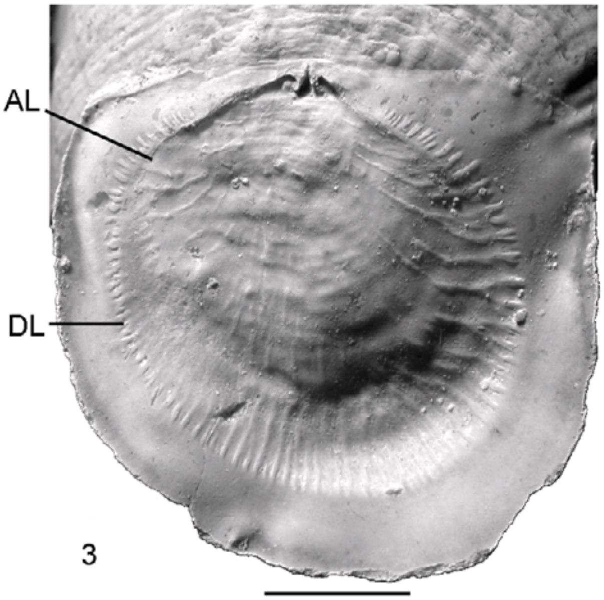

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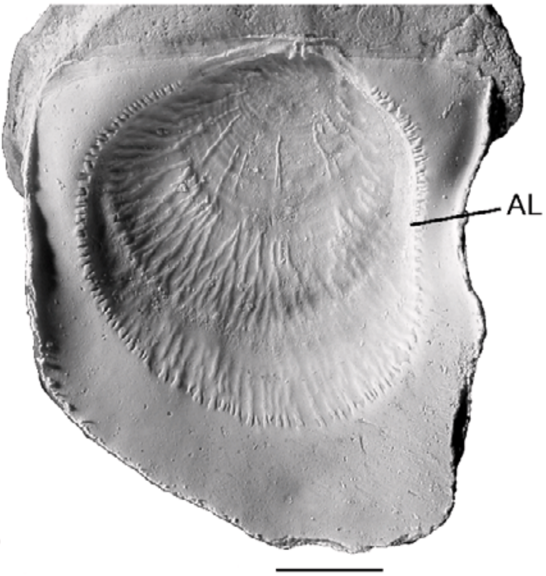

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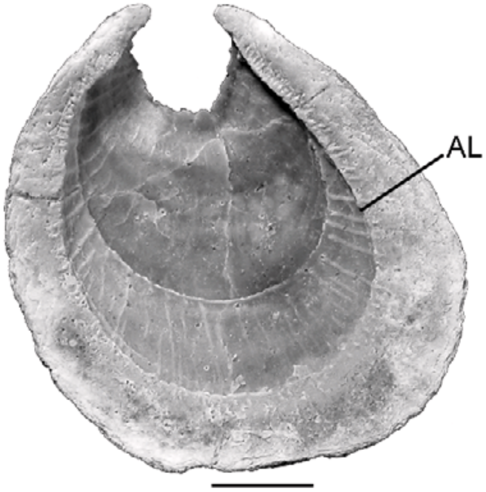

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the scar formed by the attachment of striated muscle tissue) relative to the pallial line. Vokes (1979, p. 34, 35) indicated that the posterior margin of this adductor scar is confluent with the pallial line in *Atreta* (including *Dimyodon* as a junior synonym) but inset from the pallial line in *Dimya*. Although this distinction seems to hold for *Atreta*, the pallial line is also in contact with the margin of the posterior adductor scar in some specimens of Recent *Neoatreta* (Fig. 3.1) and *Dimyella* (Fig. 4.7). *Dimya* is in fact variable in this respect, with the posterior adductor scar well inset from the pallial line in some species, as in *Dimya argentea* (Fig. 5.1), but confluent with the pallial line in others, as in *Dimya grandis* (Fig. 1).

The two adductor scars of dimyids consistently differ from one another in shape and position (Fig. 1). The anterior scar is smaller, more dorsally located, and closer to the shell margin than is the posterior scar. The anterior scar is elliptical in shape, elongated along its dorso-ventral axis, and is never bilobed, because the muscle that forms it is entirely non-striate tissue (Yonge, 1978, p. 360). In contrast, the shape of the posterior adductor scar is variable, depending on the positions of the two components of the scar, a posteroventral component formed by the attachment of non-striate muscle tissue and an anterodorsal component formed by the attachment of striated tissue (Yonge, 1978). Because these two types of adductor muscle do not run parallel to one another from one valve to the other, the posterior adductor scars of the two valves tend to differ in shape. In general, the shape of the scar is difficult to observe on the right valve, and descriptions of the shape of the scar in the present study all refer to the left valve. Although very few adductor scars have been observed in the Mesozoic genus *Atreta* because of the differential solution of aragonite relative to calcite, the posterior adductor scars that have been seen have been described as orbicular (Tashiro, 1978) or subcircular (Fürsich and Werner, 1988, p. 144), i.e., with very little separation of the two components. The genera *Neoatreta* (Fig. 3.1) and *Dimyella* (Fig. 4.6, 4.7) also display this condition. In these genera the posterior component of the posterior adductor scar is shaped like a kidney bean, with its straight or slightly concave anterodorsal margin accommodating the curved posteroventral edge of the anterior component, the overall effect being a nearly orbicular scar. In contrast, in *Dimya* and *Basiliomya* the two components are commonly nearly completely separated (Fig. 5.1) or have a deep reentry between the two components (Fig. 6.1), leading to a bilobed outline of the entire scar. The separation of the two components is greater in very young individuals than in mature ones, a phenomenon also observed in the Pectinidae (Waller, 1969, p. 22).

In addition to the pallial line and adductor scars, some small subsidiary scars are present, but their utility in taxonomy has not yet been explored. Apparently all dimyids have a small muscle scar nearly centrally located near the dorsal limit of the umbonal cavity (Fig. 1, GMS, gill muscle scar). Its position recalls the so-called "Quenstedt's muscle" described for the Ostreoidea by Stenzel (1971) and later found to represent the insertion of an anterior gill elevator or protractor muscle (Boss, 1982, p. 1117; Harry, 1985, p. 123).

Hinge structures of the Dimyidae are of critical importance for distinguishing genera and clades within the family. These structures include: 1) an alivincular resilium inserted in a resilifer on each valve that is variously internalized or submerged below the axis of rotation of the hinge; 2) an arch of shell material over the apex of the resilium (herein referred to as the overarch); 3) a thin, linear secondary periostracal ligament closely aligned or coincident with the axis of rotation of the hinge; and 4) hinge teeth of various shapes and sizes independently developed either from the aragonitic inner layer of the shell below the denticulation line or from the dorsal calcitic rim dorsal to the denticulation line. As in past studies (Waller, 1986, 1991), I refer to dorsal structures that interlock as hinge teeth rather than crura, because the latter term has been used indiscriminately for structures that either interlock or that meet in apposition. For the latter, I use the functionally more explicit term buttress.

The resilifers of the Dimyidae are triangular, narrowly so in *Atreta* and *Diploschiza* (Fig. 2.1, 2.3–2.5) but more broadly triangular in Cenozoic genera (Figs. 5.1–5.4, 7.1). With interumbonal shell growth, the dorsal part of the resilium splits, while the active, ventral part remains as a continuous band between valves, not medially divided along the sagittal plane as in the Plicatulidae (Yonge, 1973; Waller, 1978). Such ligaments were referred to by Hautmann (2004) as "alivincular-fossate". The resilium is mainly fibrous ligament, usually whitish in appearance, consisting of fine, aragonitic fibers in an organic matrix with the fibers oriented perpendicular to the ventral growth surface of the resilium as in other pteriomorphians (Fig. 7.1). The insertions of the resilium on each valve are floored by aragonitic ligostracum, a thin, irregularly prismatic shell layer restricted to ligament insertions (Carriker and Palmer, 1979; Carter, 1990, p. 140). The dorsal parts of the resilium are covered by a tan to dark brown organic layer that is non-fibrous except along its transitional contact with the fibrous layer (Fig. 7.1). Yonge (1978, figs. 7, 8) interpreted this non-fibrous layer as the vestige of original anterior and posterior outer ligaments that during the course of evolution became medially conjoined above and in contact with the fibrous resilium. All dimyids (including *Dimyella*, contrary to Corselli and Bernocchi, 1992, p. 667) have a secondary periostracal outer ligament that extends over the apex of the resilium as it becomes overarched.

In *Atreta*, *Neoatreta*, and *Dimyella*, the hinge teeth develop from the inner aragonitic layer at a level that is inside (i.e, ventral to) the dorsal ends of the denticulation line on the calcitic rim (Figs. 2.1, 3.2, 3.8, 4.2, 4.5). In Neogene and Recent representatives of *Neoatreta* and *Dimyella*, the aragonite line was carefully traced using reflected-light microscopy and found to be dorsal to the hinge teeth, indicating that the teeth are aragonitic, just as in *Atreta*. The hinge teeth of the right valve of *Atreta* (Fig. 2.1) are elongate and strongly denticulate, and fit into corresponding elongate, pitted sockets on the left valve (Fig. 2.2). Cenozoic and Recent *Neoatreta* have almost exactly the same arrangement, the difference being that a prominent overarch of the apical part of the resilium is present in *Neoatreta* (Fig. 3.2) but absent or only minimally developed in *Atreta* (Fig. 2.1). As a result, in *Atreta* the dorsal ends of the hinge teeth of

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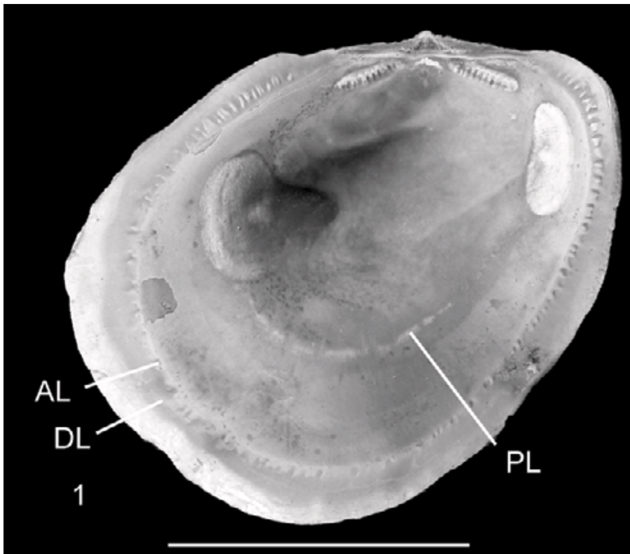
FIGURE 2—Mesozoic Dimyidae. *1*, *Atreta intulaevis* Tashiro, 1978, Upper Cretaceous (lower Santonian), Hinoshima Island, Kumamoto Prefecture, Japan, internal side of right valve and detail of hinge, modified from Tashiro (1978, txt-fig. 9); *2*, *Atreta unguis* (Loriol, 1900), Jurassic (Kimmeridgian), Abadia Beds, north of Arruda dos Vinhos, Portugal, internal side of left valve, modified from Fürsich and Werner (1988, fig. 19); *3–5*, *Diploschiza melleni* Stephenson, 1935, Upper Cretaceous, upper Selma Chalk, near Livingston, Alabama: *3*, *4*, internal side of right valve and detail of hinge, paratype cemented to holotype, USNM(P) 75484; *5*, internal side of another right valve, USNM(P) 75486; *6*, *Diploschiza cretacea striata* Stephenson, 1934, Upper Cretaceous, lower Selma Chalk, near Massillon, Alabama, internal side of right valve, paratype, USNM(P) 75110. Scale=5 mm for *1*; 2 mm for *2–6*. Abbreviations: AL=aragonite line, DL=denticulation line, PL=pallial line.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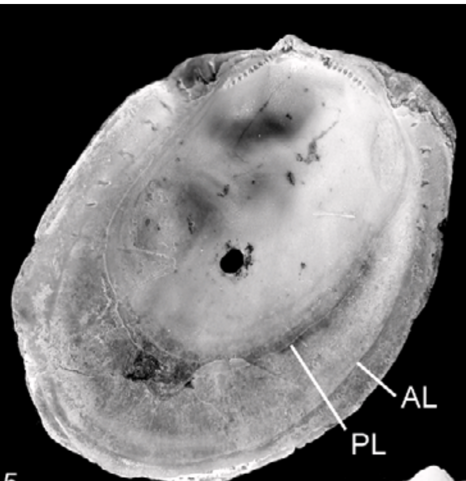
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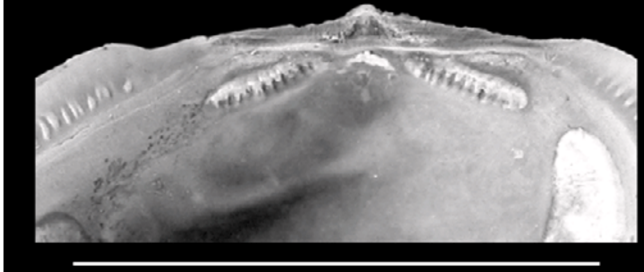
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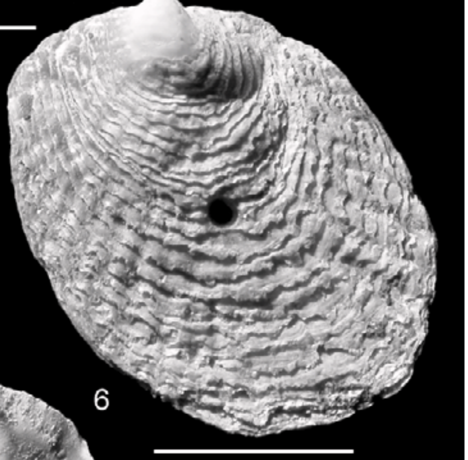
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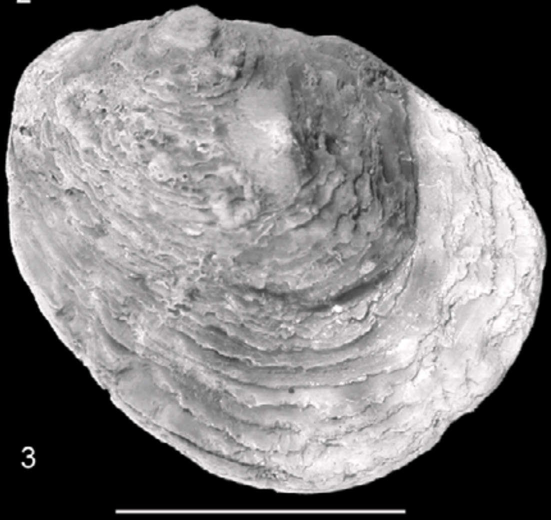
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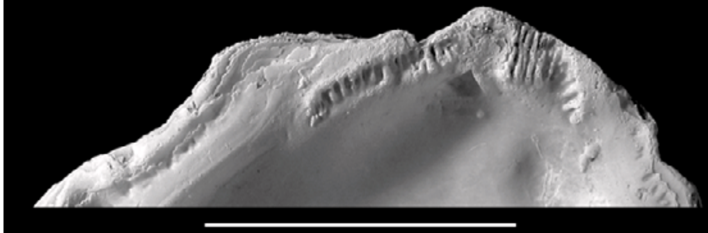
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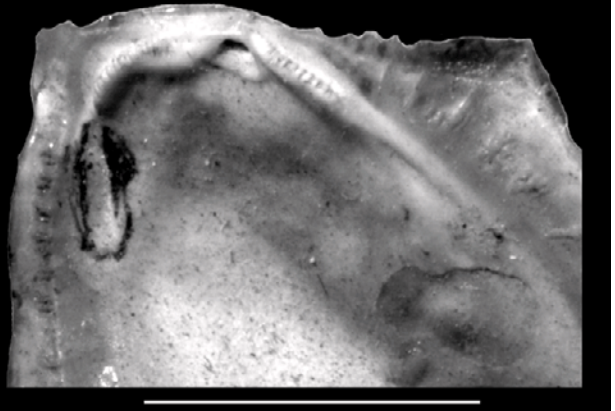
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the right valve nearly contact the apex of the resilifer, whereas in *Neoatreta* the dorsal ends of the hinge teeth are more remote from the apex. The hinge teeth of the right valve of *Dimyella*, rather than being elongate as in *Atreta* and *Neoatreta*, are stubby and hook-shaped but still denticulate (Fig. 4.10), aligning with irregular pitted sockets on the left valve (Fig. 4.2, 4.5, 4.8). In *Atreta*, *Neoatreta*, and *Dimyella*, the denticles present on the hinge teeth of the right valve tend to be on the dorsal side of the teeth, aligning with the ventrally facing pits of the sockets of the left valve.

In contrast to the aragonitic hinge teeth of *Atreta*, *Neoatreta*, and *Dimyella*, those of *Dimya* (Fig. 5.1–5.6) and *Basiliomya* (Fig. 6.2) develop from the calcitic rim medial and slightly dorsal to the dorsal ends of the denticulation line, and aragonitic teeth are absent. The aragonite line in the dorsal regions of these genera is at the ventral edge of the hinge plate and passes along the ventral edge of the overarch. The calcitic articulation is highly variable and commonly not distinctly demarcated, particularly in juvenile shells. Dall (1886, p. 228) described the hinge articulation of *Dimya argentea* as "a leaf-shaped wrinkled area on each side of a small impressed triangular area, below and partly under which is a small, deep, subtriangular pit for the brown, horny cartilage." The "impressed triangular area" refers to the calcitic overarch of the resilifer, which in some taxa, particularly in *Dimya*, may become another articulating structure, raised to form a central tooth on the right valve (described by Dall in Guppy and Dall [1896, p. 328] as a "keystone-shaped projection"), and depressed to form a socket on the left valve. Such articulation of the calcitic overarch is highly developed in *Dimya grandis* Dall in Guppy and Dall, 1896, from the Pliocene Gurabo Formation of the Dominican Republic (Fig. 1) and *D. fimbricostata* Vokes, 1979, from the Pleistocene Moín Formation of Costa Rica and the present-day Caribbean (Fig. 5.3, 5.4, 5.8), but only weakly developed or absent in most specimens of *D. lima* and *D. argentea* (Fig. 5.2). The "leaf-shaped wrinkled area" mentioned by Dall is the most highly developed in right valves of the genus *Basiliomya* Bayer, 1971, where it is elevated above the plane of commissure (Bayer, 1971, fig. 71D). In *Basiliomya* a small calcitic tooth is present in the left valve at each end of the hinge (Fig. 6.2, 6.5), fitting into a socket on the right valve at each end of the raised leaf-shaped area. Bittner (1895, p. 220) thought that the leaf-shaped areas on either side of the resilifer of *Dimya* are nothing more than the stunted vestiges of the hinge teeth of *Dimyodon* (=*Atreta*). On the contrary, the articulating structures of *Dimya* and *Basiliomya* are secondary, developed within the *Dimya* lineage from the calcitic rim, and they originated independently of the primary aragonitic teeth of *Atreta*. The Cretaceous genus *Diploschiza*, previously placed in the synonymy of *Atreta*, also has a calcitic hinge and in this respect differs sharply from *Atreta*. Unfortunately none of the specimens of *Diploschiza* available for study has the aragonitic inner layer preserved, and left valves are poorly known. Nevertheless, the calcitic outer layer extends medially to the resilifer, and the resilifer is flanked on each side by a calcitic tooth or buttress (Fig. 2.4; see further description in the systematic section).

In all dimyids, the axis of rotation of the hinge approximately coincides with the secondary periostracal ligament. In *Dimya* and *Basiliomya*, the area just ventral to the periostracal ligament is a zone of apposition along which the valves contact one another when closed, separated only by a thin sheet of mantle epithelium. This apposition zone is invariably minutely crenulated by transverse micro-ridges (Figs. 5.2, 5.4, 6.2). This axis moves slightly ventrally and lengthens laterally during ontogeny, producing a small, broadly triangular ligament area on its dorsal side, particularly on the right valve, where interumbonal growth is greater than on the left valve. The crenulations of the hinge line extend across the articulating appositional surface of the hinge teeth and sockets and are much finer than the denticles and pits on the dorsal ends of the denticulation line on the calcitic rim. Bartsch (1913, p. 306) referred to the crenulated hinge of *Dimya lima* as the "provincular area", but it is unlikely that the crenulations of the hinge line are continuations of the provinculum of the larval shell (prodissoconch). It is more likely, based on observations of other pteriomorphian bivalves, that hinge crenulation is a feature of the dissoconch that develops after metamorphosis (Checa et al., 2011).

The exterior ornament of dimyid shells is both extrinsic, reflecting the topography of the substrate on which the right valve becomes cemented, and intrinsic, determined genetically and largely independent of substrate topography beyond the cementation scar. In the cemented stage, the right valve is very thin and appears to literally flow over even very minor irregularities in the substrate, with calcification capturing these irregularities as the growing edge moves forward. In those specimens having conterminous right and left shell margins, the irregularities that deflect the growing margin of the right valve are passed onto the left valve, a phenomenon termed "xenomorphism" by Stenzel (1971, p. N1034). This process may occur on a very fine scale. For example, a left valve of *Dimya lima* stood out from other specimens in having a microscopic polygonal pattern that first appeared to be the surface expression of a simple columnar prismatic outer shell layer, a type of shell microstructure not known to occur in either valve of dimyids. An articulated specimen was later found attached to the inner surface of an echinoid fragment that has the same microscopic surface pattern. The left valve of the *Dimya* displayed the pattern up to the point of flexure of the right valve, marking the point at which close contact with the echinoid fragment was lost.

Intrinsic sculptural features include antimarginal ribs and commarginal lamellae. The antimarginal ribs are of a type commonly present in oysters and plicatulids and described in detail by Checa and Jiménez-Jiménez (2003). When only weakly developed, antimarginal ribs tend to be expressed mainly on the right valve on the part that is turned up from the substrate, and they may be absent or variably developed within populations. When strongly developed and causing the margin to be fluted, the ribs are also expressed on the left valve. Broad undulatory ribs that corrugate the margin of the right valve are present in some species of *Dimya*, e.g., *D. fimbricostata* Vokes, 1979 (Fig. 5.5, 5.6). The internal

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FIGURE 3—Species of *Neoatreta,* new genus. *1–4*, *Neoatreta filipina* (Bartsch, 1913), Recent, Philippines: *1–3*, Ragay Gulf, off north Burias, 192 m, interior and exterior sides of left valve and detail of hinge, USNM(IZ) 1163779; *4*, southeast of Bantayon Island, 59 m, distorted hinge of left valve, USNM(IZ) 1163789; *5–7, Neoatreta phaidra* (Woodring, 1982), upper Miocene, Gatun Formation, Panama; *5*, *6*, interior and exterior sides of left valve, holotype, USNM(P) 647205; *7*, interior of right valve, paratype, USNM(P) 647206; *8*, *Neoatreta dissimilis* (Tate, 1886), middle Miocene (Balcombian), South Australia, hinge of right valve, syntype, SAM T915B (photo provided by South Australian Museum, Adelaide). Scale=5 mm for *1–6* and *8*; 4 mm for *7*. Abbreviations: AL=aragonite line, DL=denticulation line, PL=pallial line.


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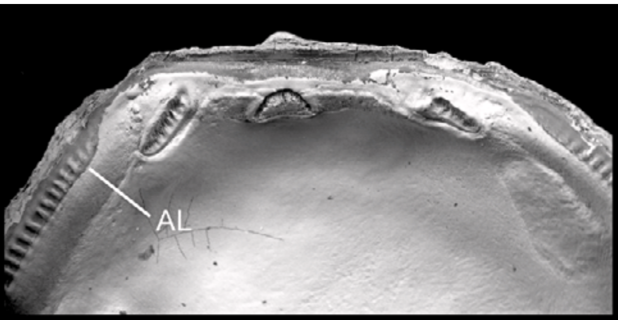

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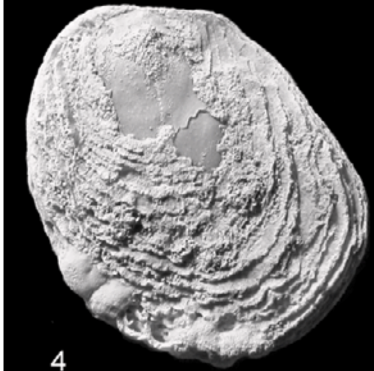
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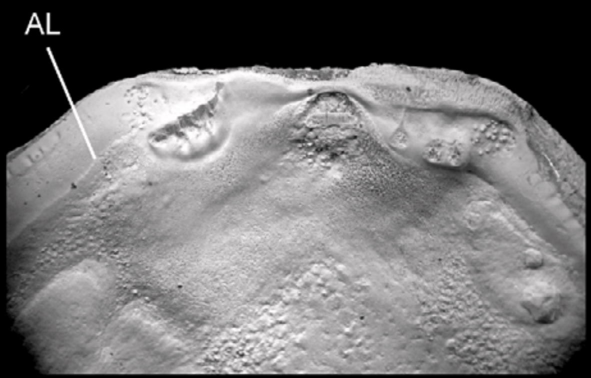

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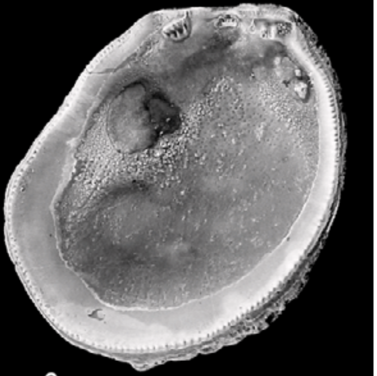
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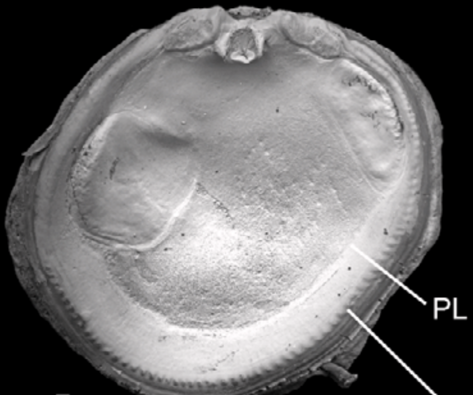

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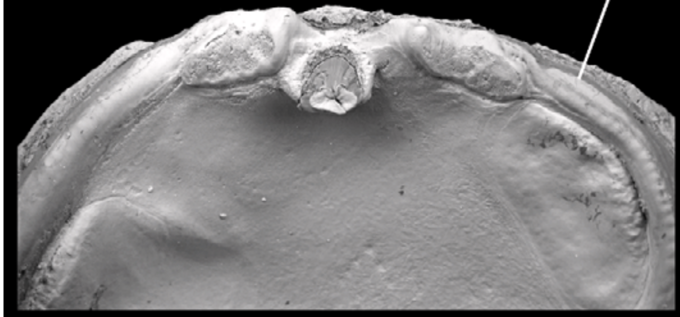
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expression of these ribs on the calcitic rim is unrelated in spacing and amplitude to the finer linear denticles and pits of the denticulation line (Fig. 5.6).

Commarginal lamellae may be irregular in spacing and flat-lying on either valve, as in species of *Dimya*, or they may be regularly spaced and upturned on the left valve, as in *Neoatreta* (Fig. 3.3, 3.6) and *Dimyella* (Fig. 4.1, 4.4). In both *Neoatreta* and *Dimyella* the upturned lamellae begin on the left umbo and continue throughout ontogeny, closely spaced in *Dimyella*, but more widely spaced in *Neoatreta*. In *Dimya* and *Basiliomya*, commarginal lamellae are commonly not observable in the umbonal region.

LIVING HABITS

Dimyids are pleurothetic bivalves that cement by their right valve to a variety of substrates, including but not limited to fragments of mollusk shells, echinoid tests, corals, bryozoans, sponges, and rocks. Most Recent dimyids live in tropical or subtropical, deep, normal marine waters of the middle and outer continental shelf. Depths of living specimens and dead shells range from 2 to 1,250 m, with the greatest number of species living at depths from about 50 to 300 m (Fig. 8). Some species of the genus *Dimyella*, however, have been reported from the walls and ceilings of submarine caves at depths as shallow as six meters (Moore, 1969, 1978; Hayami and Kase, 1996). Paulay (2003, note 11) reported that "these [*Dimyella*] species are undescribed members of a clade of minute dimyids, with well developed hinge teeth, that occur in reef caves throughout the Indo-West Pacific." *Basiliomya* has been reported as shallow as 23 m (Bayer, 1971, p. 239), and Habe (1971) reported that *Dimya japonica* Habe, 1971, is very common even in the shallow waters of Japan."

Dimyids seem to prefer habitats with very low sedimentation rates. This is indicated by their simple ctenidia with limited sorting ability and the lack of a foot that could be used for clearing the mantle cavity (Dall, 1886; Yonge, 1978). It is also indicated by the occurrence of some species of *Dimyella* deep within submarine caves, commonly on the cave ceilings, where they are the only cementing bivalve present but share attachment space with thecideidine brachiopods (Hayami and Kase, 1996, p. 63). Dimyids are also among the few cementing bivalves present on hard substrates on the deep sea floor. Slow sedimentation rates are evidenced by the gregarious settlement of more than one size class, exemplified by *Dimya lima* in the Philippines living on large dead valves of a deep-sea limid bivalve at a depth of 790 m (Bartsch, 1913) as well as on the exposed surfaces of a 23 cm long bottle dredged from about 400 m (USNM(IZ) 229321).

Although dimyids are suspension feeders, nothing is known about their diet. Their tendency to live in oligotrophic habitats including caves as well as in deep water below the photic zone suggests that they may be generalized feeders ingesting a variety of particle sizes and possibly including zooplankton, the ingestion of which is accommodated by a simple mouth structure and a stomach with limited sorting areas.

All of the Recent dimyids examined have D-shaped, smooth prodissoconchs of about 200 to 210 μm in length. These appear to be entirely in the Prodissoconch-I stage, suggesting lecithotrophic development with limited larval dispersal ability, typical of deep-water bivalves. Only one species, *Dimyella starcki* Moore, 1969, is known to brood its young, as shown by the presence of larval shells in a brood chamber developed from the calcitic rim along the ventral margin of the left valve (Moore, 1969). These larval shells are not distinguishable from those of the other dimyids examined. Preserved prodissoconchs are rare in fossil dimyids, but Malchus (2000) figured a prodissoconch from the Middle Jurassic of Poland that he inferred came from the genus *Atreta*. Its umbonate form with well-developed growth lines in the Prodissoconch-II stage suggesting planktotrophic development is unlike that of any known Recent dimyid.

Most dimyids show evidence of predation in the form of chipped shell margins. Among left valves, beveled circular holes attributed to drilling by predatory gastropods are uncommon in species such as *Dimya argentea* and *D. lima* from depths greater than 200 m but relatively more common in shallower occurring species, such as *Dimya fimbricostata*, *Dimyella* sp., and *Basiliomya goreaui*.

PHYLOGENY

There is as yet no agreement on the closest outgroup for the Dimyidae, although there is general agreement that the family is related to the Prospondylidae Pchelinceva, 1960, Plicatulidae Watson, 1930, and Anomiidae Rafinesque, 1815, families that were placed in a new suborder Prospondyloidina by Waller in Waller and Stanley (2005, p. 47). Hautmann (2001a, 2004) provided evidence, based on the timing of evolutionary trends in alivincular-fossate ligament systems, that the Dimyidae and Plicatulidae probably evolved independently, the Plicatulidae from a prospondylid ancestor and the Dimyidae from a more remote pectinoid ancestry.

In the light of evidence from the fossil record, many of the characters that are said to characterize the Dimyidae are in fact plesiomorphic. These include right-valve cementation, dimyarian (anisomyarian) adductor muscles, an oblique, posteroventrally extended shape, an orbicular rather than bilobed left posterior adductor scar, possibly an alivincular-fossate ligament system, and a bimineralic shell with an outer foliated calcitic layer and an inner aragonitic crossed-lamellar layer. All of these characters are present in *Protostrea* Chen in Gu et al. 1976, from the Middle Triassic (upper Anisian) of China, which Chen et al. (2006) suggested may be the earliest dimyid. Compared to *Atreta*, however, *Protostrea* lacks exterior antimarginal costae and an internal denticulation line, and the ligament system and hinge dentition present in adult specimens do not closely resemble those of *Atreta* (based on illustrations in Chen et al., 2006).

Figure 9 is a phylogenetic hypothesis for the Dimyidae drawn by hand and based on shell characters and perceived synapomorphies of the six genera recognized in the present study (Table 1). The paraphyletic stem genus *Atreta* is characterized by its pair of aragonitic, linear, denticulate hinge teeth diverging ventrally from near the apex of the resilifer of the right valve and fitting corresponding aragonitic, linear, pitted sockets in the left valve. Its ligament system is of the alivincular-fossate type (Hautmann, 2004), with the resilium functional ventral to the axis of rotation of the valves and without significant overarching of the apex of the resilium. Its

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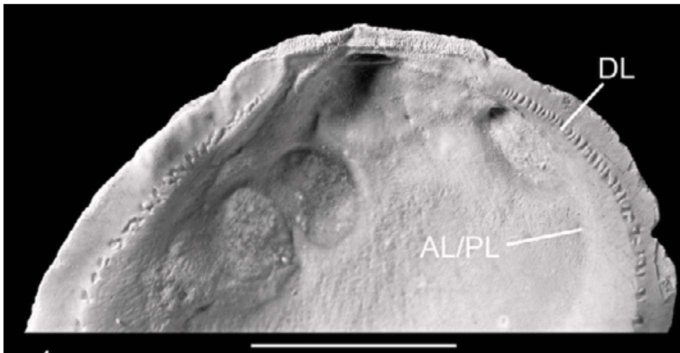
FIGURE 4—*Dimyella* sp, Recent. *1–3*, off western Puerto Rico, 37 to 73 m, exterior, hinge, and interior of left valve, USNM(IZ) 430600; *4–6*, off Si Amil Island, Sibuko Bay, Borneo, 534 m, exterior, hinge, and interior of left valve, USNM(IZ) 1163780; *7–10*, Indian Ocean, off Rodriquez Island, Mauritius, 91 m; *7*, *8*, interior of left valve and detail of hinge, USNM(IZ) 1163781; *9*, *10*, interior of right valve and detail of hinge, USNM(IZ) 1163782. Scale=2 mm for *1* and *3*; 1 mm for *2*, *5*, and *7–10*; and 3 mm for *4* and *6*. Abbreviations: AL=aragonite line, PL=pallial line.



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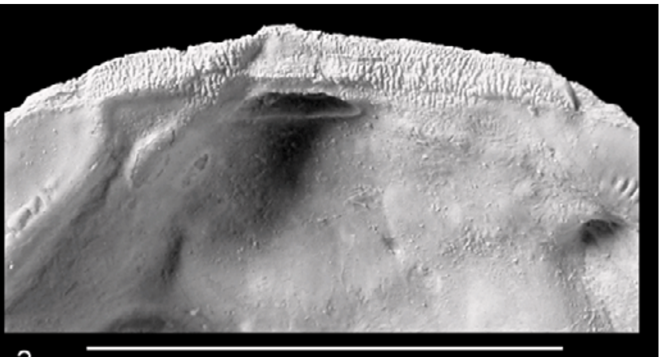

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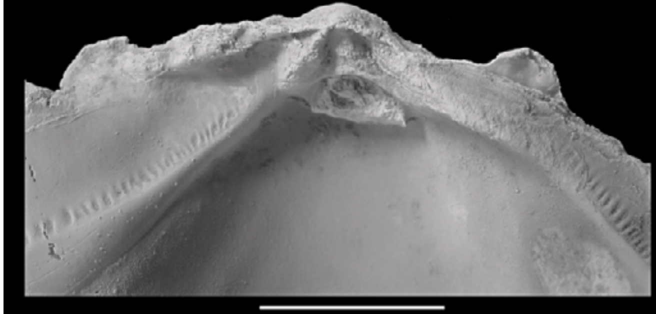

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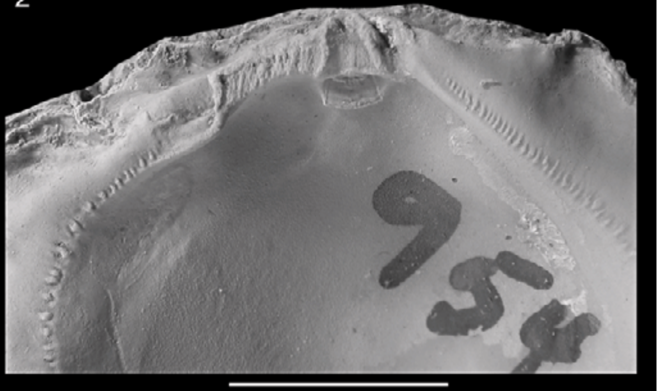

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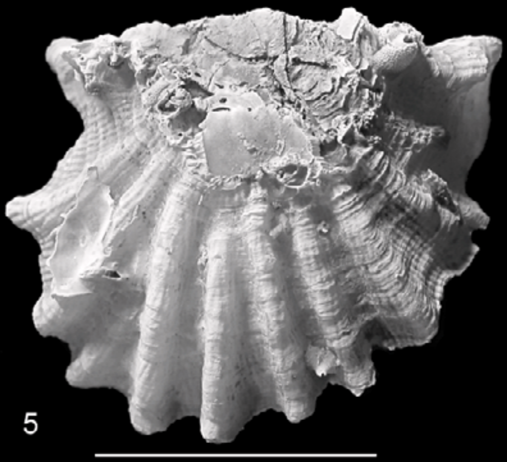

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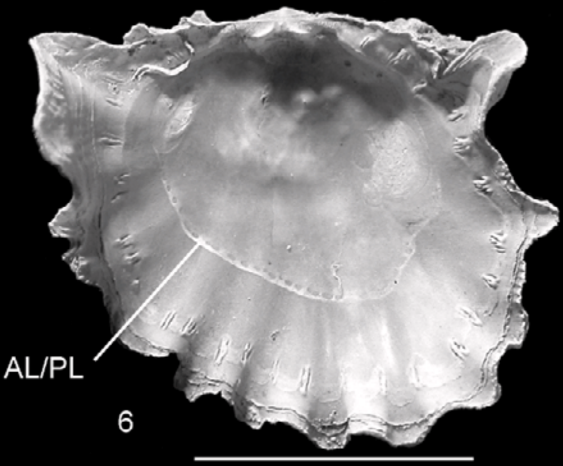

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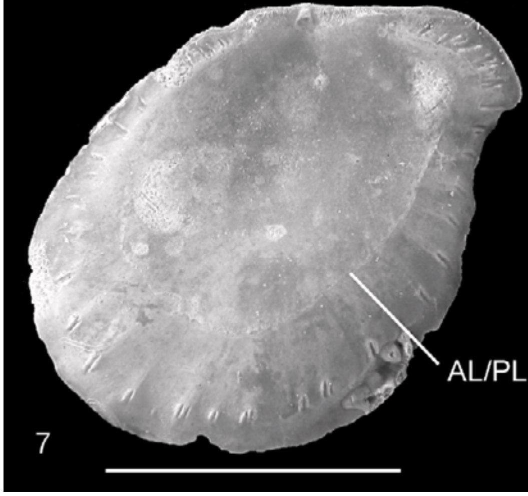

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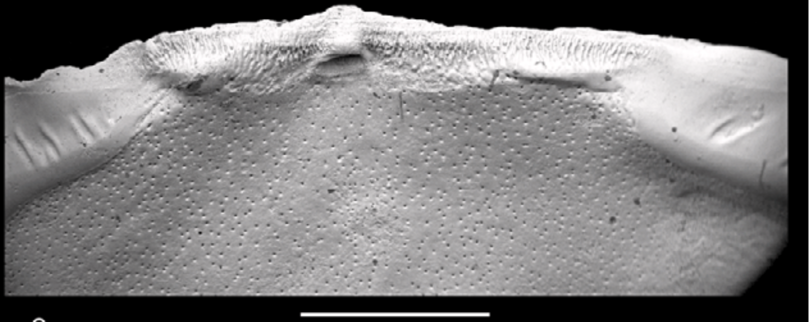

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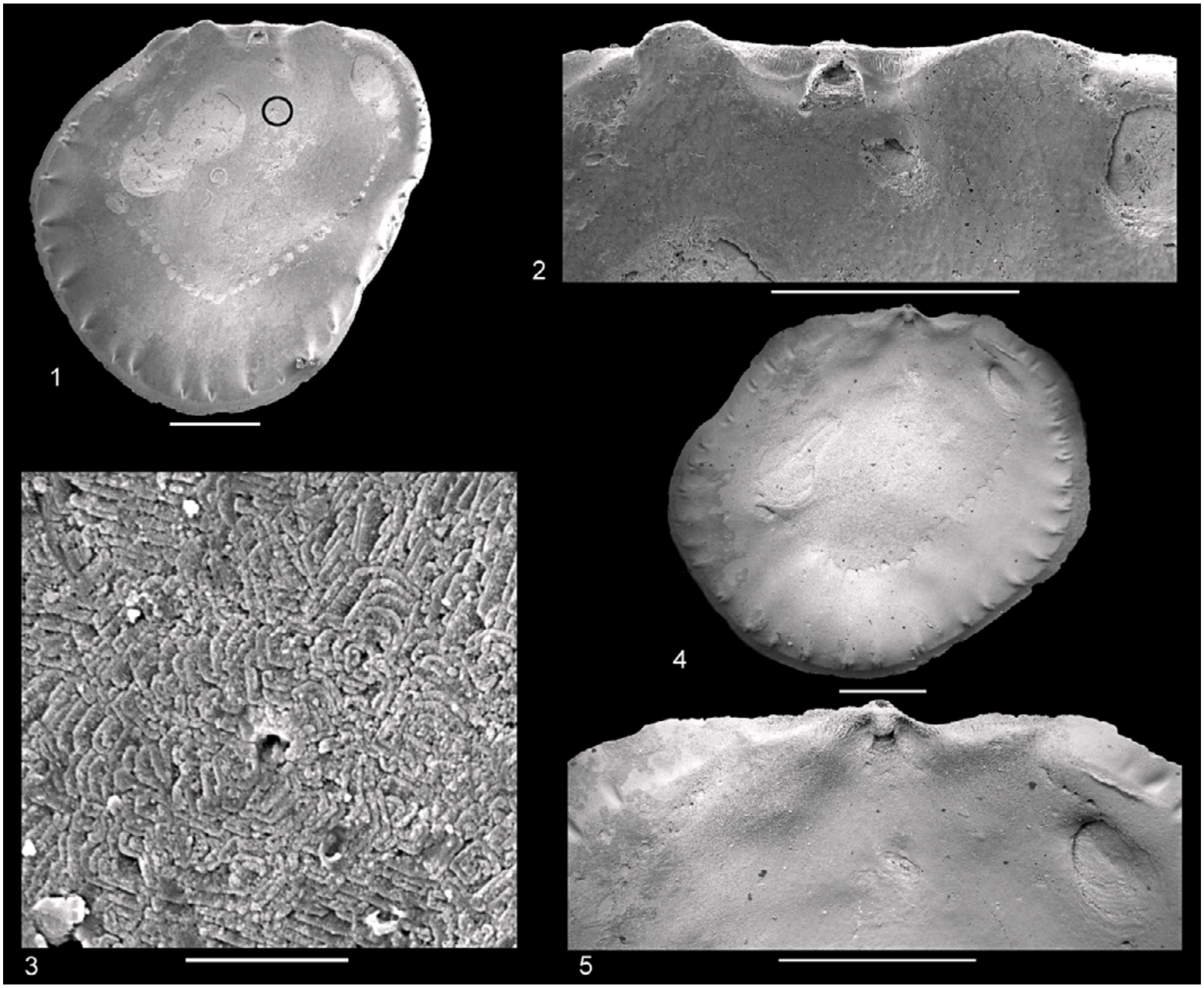

FIGURE 6—*Basiliomya goreaui* Bayer, 1971. *1–3*, Recent, off Telegraph Island, Barbados, 73–137 m: *1*, interior of left valve, detail of hinge, and depositional surface of complex foliated calcite in umbonal region at site indicated by circle in *1*, USNM(IZ) 1163784; *4*, *5*, middle Pliocene Mao Formation, northern end of Río Cana gorge, 40 m below top of "Mao Adentro limestone", northern Dominican Republic (Locality NMB 17023 of Saunders et al., 1986), interior side of left valve and detail of hinge, NMB G1782. Scale=1 mm for *1*, *2*, *4*, and *5*, 5 µm for *3*.

denticulation line on a broad calcitic rim is well within the ventral shell margin and consists of rather closely spaced denticles or ridges that are more closely spaced dorsally than ventrally. These denticles or ridges leave branching or intercalated costellae, commonly in a dendritic pattern, on the inner surface of the outer shell layer as they track outward, antimarginally, during ontogeny. So far as can be determined, the aragonite line of *Atreta* is well outside the pallial line and nearly coincident with the denticulation line. The left posterior adductor scar is orbicular, commonly without significant separation of the striate and non-striate components and with the posterior margin of the scar in contact with the pallial line. The exterior of both valves distal to the area of cementation commonly possess coarse, antimarginal costae.

The two clades that branch from *Atreta* are regarded as independent and monophyletic, because there are no convincing synapomorphies that unite them as sister groups and because their origins appear to be at different times. The *Diploschiza*-*Dimya*-*Basiliomya* clade appears to be the older, with the first appearance of the paraphyletic genus *Diploschiza* being in the Cretaceous (Albian to Maastrichtian). These three genera are tied together (Fig. 9, point 1; Table 1) by their apomorphic

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FIGURE 5—*Dimya* Rouault, 1850, species. *1*, *2, Dimya argentea* Dall, 1886, Recent, Monterserrat and St. Vincent to Barbados, 161–382 m, interior of left valve and detail of hinge, syntype, USNM(IZ) 610141; *3–6*, *Dimya fimbricostata* Vokes, 1979; *3*, *4*, Pleistocene, Moin Formation, west of Puerto Limón, Costa Rica; *3*, left hinge, USNM(P) 263983; *4*, right hinge, USNM(P) 263977; *5*, *6*, Recent, off northern Puerto Rico, N 18°30′20″, W 66°22′05″ to N 18°30′30″, W 66°23′05, 60–73 m, exterior and interior of right valve, USNM(IZ) 430241; *7, 8, Dimya* sp. aff. *japonica* Habe, 1971, Recent, off Tactuc Point, east Leyte, Philippines, 104 m, interior of left valve and detail of hinge, USNM(IZ) 1163783. Scale=5 mm for *1–7*, 1 mm for *8*. Abbreviations: AL/PL, coincident aragonite line and pallial line.

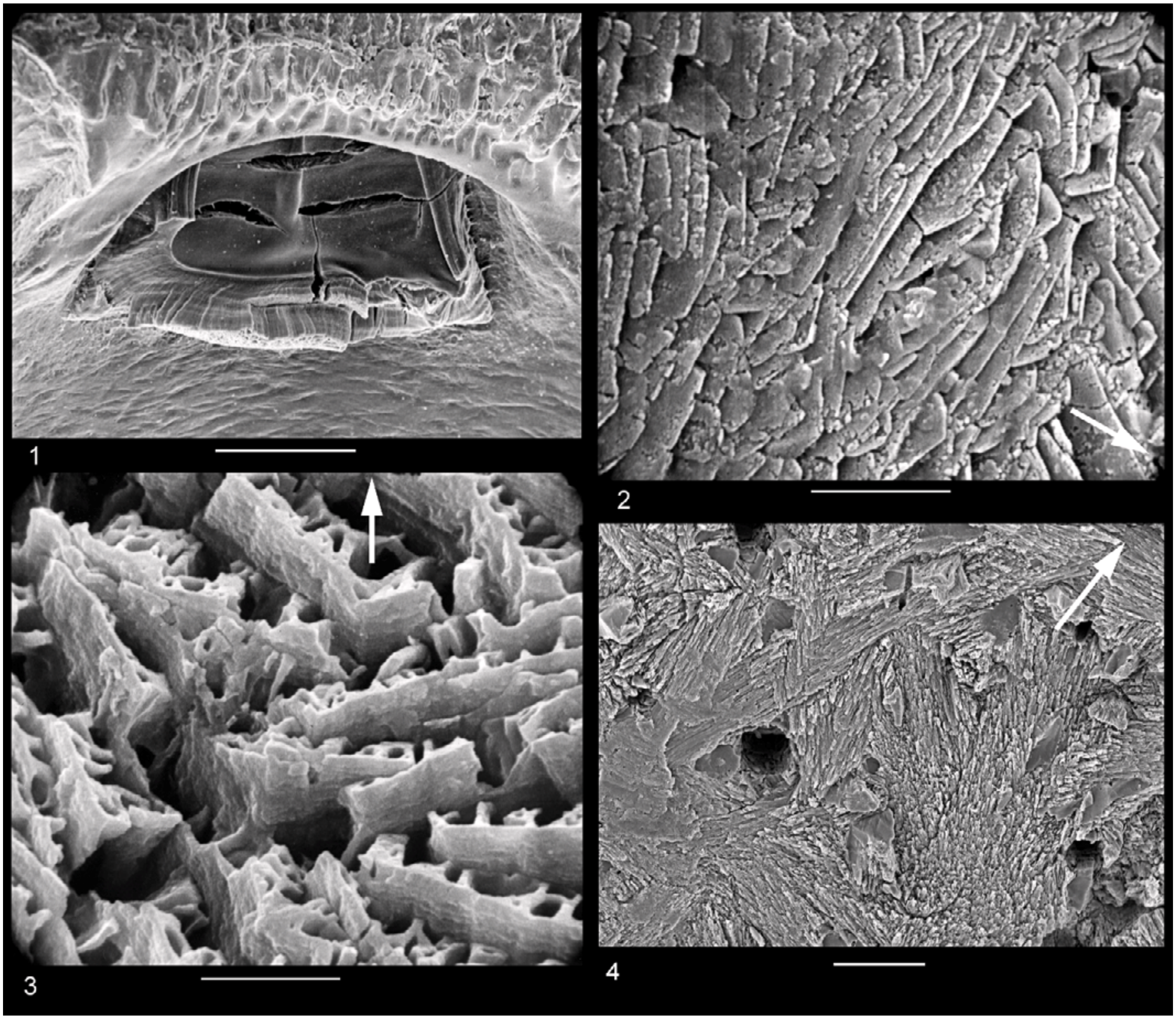

FIGURE 7—Scanning electron micrographs. *1–3*, *Dimya lima* Bartsch, 1913: *1*, resilium of left valve, Recent, 97 km northeast of Cap St. Andre, Madagascar, 47–49 m, USNM(IZ) 1163785; *2*, depositional surface of foliated calcite between denticulation line and midventral margin, Recent, Pujada Bay, east Mindanao, Philippines, 313 m, USNM(IZ) 1163786; *3*, depositional surface of chalky calcite layer of right valve between denticulation line and midventral margin, same locality as proceeding, USNM(IZ) 1163787; *4*, *Dimya* sp. aff. *japonica* Habe, 1971, weathered depositional surface of inner shell layer of complex crossed lamellar aragonite dorsal to midventral pallial line, Recent, off Tacbuc Point, E. Leyte, Philippines, 104 m, USNM(IZ) 1163788. Scale =200 μm for *1*, 5 μm for *2* and *3*, and 20 μm for *4*. Arrows point in direction of shell margin.

calcitic dorsal margin that impinges on the sides of the resilifer, forming calcitic buttresses or hinge teeth and by the loss of aragonitic denticulate teeth and pitted sockets. (Because no aragonite is preserved among specimens of *Diploschiza* examined, the absence of aragonitic teeth and sockets is inferred on the basis of its calcitic dorsal margin and possible weak calcitic dentition that is unlike the more ventrally located aragonitic dentition of *Atreta*.)

In the monophyletic *Dimya*-*Basiliomya* clade, the close relationship of these genera is indicated by a number of synapomorphic morphological characters (Fig. 9, point 2; Table 1): 1) hinge articulation developed from the calcitic rim medial and dorsal to the dorsal ends of the denticulation line (weakly developed in *Dimya* but strongly developed in *Basiliomya*); 2) a broad calcitic rim that extends from the pallial line to the shell margin, owing to the near coincidence of the aragonite line and pallial line in *Dimya* and by an intrapallial calcitic region in *Basiliomya* that is also delimited by the pallial line; 3) the two components of the left posterior adductor scar separated or nearly so, giving the scar a distinctly bilobed or bipartite appearance; 4) a pallial line that commonly does not contact the posterior margin of the posterior adductor scar, which is inset from this line; and 5) a left-valve exterior that has irregularly spaced, flat-lying lamellae, antimarginal costae, or broadly rounded plicae that scallop the right-valve margin or the margins of both valves. *Basiliomya* (Fig. 9, point 3; Table 1) is the more derived genus (rendering *Dimya* paraphyletic), as indicated by its more strongly developed calcitic articulation consisting of a blunt tooth at each end of the hinge line of the left valve and a cross-striated leaf-shaped tooth on each side of

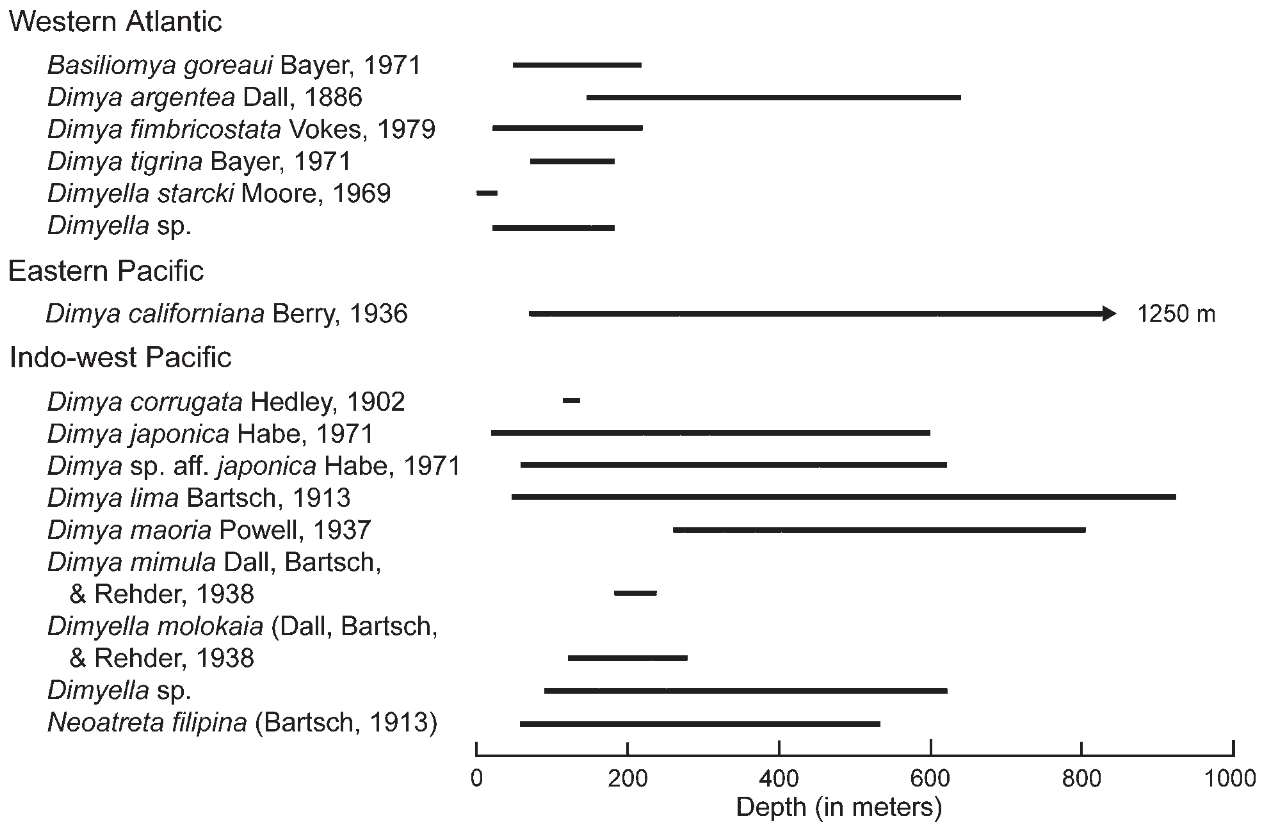

FIGURE 8—Depth ranges of extant species in Dimyidae based on data in USNM collections and in original descriptions of species.

the right resilifer, its lack of umbonal shoulders, its coarsely disjunct pallial line, and, unique in the Dimyidae, a calcitic rather than aragonitic layer inside the pallial line.

The *Dimya-Basiliomya* clade was certainly present by the middle Eocene (e.g., *Dimya deshayesiana*, the type species of *Dimya*) and may have been present in the Paleocene, if the identification by Glibert and Van de Poel (1973, p. 52) of a single valve of "*Dimya* sp." from the Danian of Belgium can be confirmed. I have been unable to confirm any Mesozoic occurrences of *Dimya*, the calcitic hinge structures of which should be detectable even in specimens missing aragonitic inner layers. There is at present no fossil record of *Basiliomya* older than the early Pliocene. However, given the presence in the western Pacific of *Dimya* species that approach *Basiliomya* in some characters, particularly *Dimya* sp. aff. *D. japonica* of the Philippines (Fig. 5.7, 5.8), the genus may have a Tethyan origin and a far longer fossil record than that known at present.

In the *Neoatreta-Dimyella* clade (Fig. 9, point 4; Table 1), both genera retain aragonitic, denticulate teeth and sockets similar to those present in *Atreta*. These genera also retain a plesiomorphic left orbicular posterior adductor scar that is in contact with the pallial line and an aragonite line that is well outside the pallial line and nearly astride the denticulation line. The clade is set off from *Atreta*, however, in having a well-developed aragonitic overarch of the resilifer and a left-valve exterior with distinct thin, commarginal lamellae that are upturned at their margins. In *Neoatreta* n. gen., the hinge teeth are broader and more irregular in shape than in *Atreta*. In *Dimyella* (Fig. 9, point 5) the hinge teeth are further modified in being shortened in an anterior-posterior direction and on the right valve becoming peg-like or hook-shaped, emanating from the floor of a deep umbonal cavity beneath the hinge line and

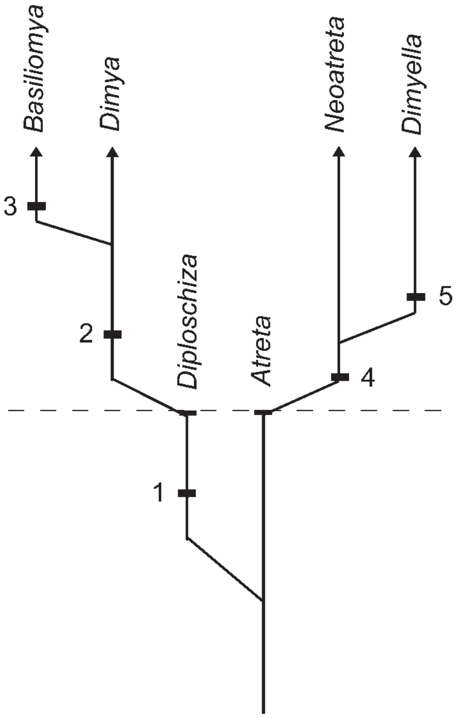

FIGURE 9—Phylogeny of dimyid genera. Synapomorphies for numbered branching points are discussed in the text and listed in Table 1. Lineages ending in arrows are extant; those ending in cross bars are extinct. All genera are paraphyletic except for *Basiliomya* and *Dimyella*. The dotted horizontal line is the Cretaceous–Paleogene boundary.

TABLE *1*—Character states among genera of Dimyidae. Abbreviations: 0=plesiomorphy; 1, 2, 3=succesive apomorphies; na=not applicable; nd=no data.

Characters	*Atreta*	*Diploschiza*	*Dimya*	*Basiliomya*	*Neoatreta*	*Dimyella*
Calcitic rim: (0) not extending medially to sides of resilifer; (1) impinging on sides of resilifer.	0	1	1	1	0	0
Aragonitic denticulate teeth on right valve ventral to dorsal ends of denticulation line: (0) present; (1) absent.	0	1	1	1	0	0
Shape of aragonitic hinge teeth and sockets: (0) linear, denticulate, diverging ventrally; (1) a short, stuppy, strongly elevated tooth on each side of right resilifer, with corresponding socket on left valve.	0	na	na	na	0	1
Calcitic hinge structures on calcitic rim medial and dorsal to ends of denticulation line: (0) absent; (1) buttresses but no definite articulation; (2) transverse articulating ridges; (3) blunt calcitic tooth at each end of right hinge.	0	1	2	3	0	0
Overarching of apex of resilifer by the calcitic rim: (0) absent; (1) present.	0	1	1	1	0	0
Overarching of apex of resilifer by secondary periostracal ligament: (0) absent; (1) present.	0	0	0	0	1	1
Position of aragonite line relative to ventral shell margin: (0) well outside pallial line and nearly coincident with denticulation line; (1) nearly coincident with pallial line and well inside denticulation line.	0	1	1	na	0	0
Position of denticulation line relative to ventral shell margin: (0) inset; (1) nearly coincident.	0	0	0	0	0	1
Spacing of denticles on denticulation line: (0) well spaced ventrally, more closely spaced dorsally; (1) closely spaced along entire denticulation line.	0	0	0	0	0	1
Shape of left posterior adductor scar: (0) orbicular; (1) bilobed.	0	nd	1	1	0	0
Contact of posterior margin of posterior adductor scar with pallial line: (0) in contact; (1) not in contact.	0	nd	1	1	0	0
Upturned, more or less regularly spaced commarginal lamellae on exterior of left valve: (0) absent; (1) present.	0	0	0	0	1	1
Umbonal shoulders: (0) present; (1) absent.	0	0	0	1	0	0
Disjunction of pallial line: (0) weak or absent; (1) strongly disjunct.	0	0	0	1	0	0
Mineralogy of shell layer inside pallial line: (0) aragonite; (1) calcite.	0	0	0	1	0	0

bending dorsally to penetrate corresponding sockets in the left valve. In *Atreta*, the denticles of the denticulation line are numerous and leave dendritically branching or intercalating costellae on the inner surface of the calcitic outer shell layer. These extend well inward toward the umbo in shells from which the aragonite has been dissolved. In *Neoatreta*, the denticles do not appear to leave elongate traces. In *Dimyella*, the denticulation line is very near the shell margin, and the denticles are closely spaced all around the extent of this line in a pattern not present in either *Atreta* or *Neoatreta*. Overarching of the apex of the resilifer is, so far as known, absent or minimal in *Atreta*, but present and commonly well developed in both *Neoatreta* and *Dimyella*. The earliest occurrence of the *Neoatreta*-*Dimyella* clade is possibly Paleocene (see *Neoatreta* in the Systematics section).

Given the absence of a more complete fossil record, it is difficult to understand what has driven the evolution of the Dimyidae. A significant clue, however, is provided by the phylogeny (Fig. 9). The stem genus *Atreta* had strong hinge articulation and tended to live on the exposed upper surfaces of hardgrounds over a considerable range of water depths. From this generalized beginning, evolutionary trends seem to be along two trajectories. One led toward restriction to deeper water and involved the evolution of thinner shells with weaker dentition, exemplified by extant *Dimya*. The other trajectory was toward cryptic habitats over a range of depths and involved decreasing shell size and stronger hinge dentition, as represented by the independent evolution of *Basiliomya* and *Dimyella*. This pattern is possibly the result of the increasing pressure exerted by duraphagous predators during the Mesozoic, driving evolution either toward deeper-water or into cryptic habitats over a range of depths (Vermeij, 1987, p. 102).

SYSTEMATIC PALEONTOLOGY

Class BIVALVIA Linnaeus, 1758
Subclass AUTOBRANCHIATA Grobben, 1894
Superorder PTERIOMORPHIA Beurlen, 1944
Order PECTINOIDA H. Adams and A. Adams, 1858
Suborder PROSPONDYLOIDINA Waller in Waller and Stanley, 2005
Superfamily DIMYOIDEA P. Fischer, 1886
Family DIMYIDAE P. Fischer, 1886

Genus ATRETA Étallon, 1862
Figure 2.1, 2.2

1868 *Cyclostreon* Eichwald, p. 406.
1886 *Dimyodon* Munier-Chalmas in Fischer, p. 937.
1895 *Dimyopsis* Bittner, p. 219

Type species.—*Ostrea blandina* d'Orbigny, 1850, p. 375, by subsequent designation by Cox (1964, p. 45), Upper Jurassic (Oxfordian) of Europe.

Diagnosis.—Dimyidae with pair of narrow, elongate, coarsely denticulate, aragonitic hinge teeth on right valve diverging ventrally from near apex of resilifer and interlocking with corresponding pitted aragonitic sockets on left valve; aragonite line nearly coincident with denticulation line; denticulation line consisting of short ridges or pits that produce elongate dendritically branching or intercalated costellae on inner surface of outer calcitic layer; resilifer narrowly triangular with apex exposed or rarely covered by very small overarch; posterior adductor scar of left valve tending to be orbicular rather than strongly bilobed or bipartite and in contact with pallial line; shell shape varying from shallowly biconvex to deeply cup-shaped, with upper (left) valve flat or concave; external ornament variable, commonly with antimarginal costae distal to cemented area and/or irregular, flat-lying commarginal lamellae.

Comments on species.—Because the common dissolution of the aragonitic inner shell layer of *Atreta* removes taxonomically important characters, namely aragonitic hinge teeth and muscle scars, and because cementation on irregular substrates deforms the shell, it is not possible to determine how many valid species of the genus are present based on literature searches. Vokes (1979, p. 51) listed 12 species and one subspecies under *Dimyodon*, but as noted by Fürsich and Werner (1988, p. 144), species have been overnamed "based on criteria that are not diagnostic."

The following discussions refer to five species: *Atreta richthofeni* (Bittner, 1895); *Atreta intulaevis* Tashiro, 1978; *Atreta schlumbergeri* (Munier-Chalmas in Fischer, 1886); *Atreta subrichthofeni* (Krumbeck, 1924); and *Atreta redunca* Kendrick and Vartak, 2007.

Occurrence.—Upper Triassic (Carnian) to Upper Cretaceous (Maastrichtian) in Eurasia, Africa, North America, Australia, and New Zealand. The oldest known species of *Atreta*, *A. richthofeni*, occurs in the Upper Triassic (Carnian) of the Alpine region (Hautmann, 2001a, p. 358). The extinction of *Atreta* appears to have been at the very end of the Cretaceous (Heinberg, 1999, table 2, on the extinction of *Atreta* at the Maastrichtian-Danian boundary in Denmark; Stilwell, 1998, p. 47, regarding "*Dimyodon* sp." from the latest Cretaceous of the Chatham Islands, New Zealand). The claim by Vokes (1979, p. 35) that the genus (cited as *Dimyodon*) extends into the Paleogene in Europe is based on *Dimyodon similis* von Koenen, 1893, including specimens from the upper Eocene (Lattorfian) of Germany and the Ukraine. Although von Koenen (1893) placed his species in *Dimyodon* on the basis of its hinge teeth, his illustrations suggest rather that this species belongs in the genus *Dimyella*. The illustrated left valve shows deeply pitted sockets that appear to be ventral to the calcitic rim and hence composed of aragonite as in *Atreta*. The posterior socket, however, is very short, containing only two or three pits and with an arcuate dorsal rim, a common socket configuration in *Dimyella*. Also as in *Dimyella*, the shell is thick relative to its size, and the denticulation line is close to the shell margin and consists of very closely spaced, small denticles, even in the ventral region.

Atreta inhabited a broad range of environments, commonly associated with brachiopods or crinoids in regions of normal marine salinity and slow sediment input, but with sufficient hard surfaces or skeletal fragments on which to attach. Tomasovych (2004) documented the presence of abundant *Atreta* in shallow intra-platform carbonate basins in the Upper Triassic of Slovakia. Fürsich (1979) discussed occurrences on Jurassic hardgrounds in Europe, particularly on exposed upper surfaces. Much deeper, outer-shelf environments are implied by the common occurrence of *Atreta* in Cretaceous chalks nearly free of terrigenous sediments.

Generic comparisons.—*Atreta* closely resembles the Cretaceous genus *Diploschiza* Conrad, 1866a, in shell shape, position of the aragonite line adjacent to the denticulation line, broad calcitic rim, and dentritically branching internal costellae extending inward from the denticulation line on the inner surface of the outer calcitic layer. The two genera differ, however, in the mineralogy and structure of the hinge. In *Atreta* the central part of the hinge is mainly aragonitic, and hinge articulation is by means of strong teeth and sockets developed from the aragonitic inner shell layer. In *Diploschiza*, the entire dorsal margin on either side of the resilifer is calcitic in composition, and hinge articulation is, so far as known, relatively weak, consisting of tiny calcitic teeth or buttresses that border the sides of the resilifer.

Atreta differs from *Neoatreta* n. gen. in having little or no overarching of the resilifers, resilifers that are commonly very narrowly triangular, and internal costellae that are more complexly branching and more elongate on the inner surface of the outer calcitic layer. The aragonitic hinge teeth and sockets of the two genera are remarkably similar, but in *Neoatreta*, these structures are broader and more irregular, with the proximal ends of the hinge teeth and sockets abutting a well-developed overarch of the resilifer. *Atreta*, so far as known, lacks an overarch or has only a very tiny one at the start of dissoconch ontogeny.

Compared to *Dimya* and *Basiliomya*, *Atreta* has hinge teeth developed from the aragonitic inner shell layer rather than from the calcitic rim and an orbicular posterior adductor scar that is not distinctly bilobed and not separated along its posterior margin from the pallial line.

Remarks.—Although the hinge teeth of *Atreta* are seldom preserved because of their aragonitic composition, adequate illustrations exist that show the configuration of these teeth and their spatial relationship to the resilifer and to the dorsal ends of the denticulation line. For example, on the right valve of *Atreta intulaevis*, from the Upper Cretaceous (Santonian) of Japan, a single elongate, denticulate tooth occurs on each side of a narrow resilifer. These teeth originate near the apex of the resilifer and diverge ventrally below the dorsal ends of the denticulation line (Tashiro, 1978, text-fig. 3, pl. 44, fig. 1c, 1d), clearly indicating that they are within the area of aragonite secretion. The apex of the resilifer is open, not closed by overarching in early ontogeny. Tashiro noted the resemblance of the hinge teeth of his Cretaceous species to those of the European Middle Jurassic type species of *Dimyodon*, *Dimyodon schlumbergeri*, which is now regarded as a junior generic synonym of *Atreta* (Fürsich and Werner, 1988). This species also has a single, elongate tooth diverging from each side of the resilifer, and the figures in Fischer (1886), repeated by Cox and Hertlein (1969, fig. C101), show clearly that these teeth also lie below the dorsal ends of the denticulation line. A nearly identical configuration of aragonitic hinge teeth, again with little or no overarching of the apex of the resilifer, was shown by Hautmann (2001a, pl. 6, figs. 7–9; 2001b, pl. 21, figs. 1–5) for *Atreta subrichthofeni* from the Upper Triassic (Norian-Rhaetian) of Iran and by Kendrick and Vartak (2007, fig. 9A-E, 10A-E) for *Atreta redunca*, from the Cretaceous (Cenomanian) of southeastern India. Although the position of the aragonite line in these taxa still remains to be determined, the exposure of extensive internal riblets, extending inward from the denticulation line in many specimens of *Atreta*, suggests that these riblets were exposed after the dissolution of an aragonitic inner layer that extended nearly to the denticulation line, i.e., to the distal termini of the internal riblets.

Genus DIPLOSCHIZA Conrad, 1866a
Figure 2.3–2.6

Type species.—*Diploschiza cretacea* Conrad, 1866a, p. 71, by monotypy, Upper Cretaceous of Alabama, first figured by Conrad, 1866b, pl. 9, figs. 2, 3. Stephenson (1934) reported the loss of the original type material and selected seven neotypes (actually neosyntypes, USNM(P) 75105 and 75106) from the Selma Chalk at Demopolis, Alabama. He also reproduced Conrad's original figures (Stephenson, 1934, pl. 38, figs. 1–3).

Diagnosis.—Elongate oval Dimyidae with right valve cup-shaped, accommodating flat to slightly convex left valve within its margin; external ornament of right valve mainly with irregular commarginal rugae, that of left valve dominated by thin, upturned, and commonly corrugated lamellae; aragonite line well outside pallial line and nearly coincident with denticulation line; calcitic rim broad ventrally, extending dorsally and medially to sides of resilifer, forming narrow tooth or buttress along each side of resilifer of right valve; transverse microcrenulations or articulating structures present on calcitic rim along dorsal margin; resilifers narrow, without significant overarching of apex; inner surface of outer calcitic layer bearing elongate fine, branching and intercalated costellae emanating from denticulation line. Configuration of adductor scars unknown.

Comments on species.—In addition to redescribing the type species of *Diploschiza*, Stephenson (1934) described two new varieties, *D. cretacea minor* from the Pecan Gap Chalk member of the Taylor Marl of Texas, and *D. cretacea striata* from the Selma Chalk of Alabama, both Late Cretaceous (Campanian) in age. Stephenson later described another species, *D. melleni* Stephenson, 1935, from the upper Selma Chalk in Alabama and Mississippi. *Plicatula nilssoni* Hagenow, 1842 (=*Plicatula sigillina* Woodward, 1864), from the Cretaceous (Albian through Maastrichtian) of Europe (Darragh and Kendrick, 1991, p. 44) is possibly a *Diploschiza*, as suspected by Stephenson (1934, p. 277), and so also is *Plicatula glauerti* Feldtmann, 1963, from the Upper Cretaceous (Santonian) Gingin Chalk of Western Australia (see following discussion). Rao (1964) claimed that four species of *Diploschiza* are present in the Cretaceous (Cenomanian) of Madras, southern India, but their generic assignment is based only on shape and ornament and needs confirmation based on better material.

Occurrence.—Cretaceous (Albian through Maastrichtian) in

Eurasia, southeastern North America, Australia, and possibly southern India.

Generic comparisons.—See preceding generic comparisons under *Atreta*.

Remarks.—*Diploschiza* Conrad, 1866a, previously placed in the synonymy of *Atreta* by Cox (1964, p. 46), has had a long history with some authors doubting that it is a dimyid. Conrad (1866a) introduced the genus with only rudimentary descriptions of the genus and its type species, *Diploschiza cretacea* Conrad, 1866a, from the Cretaceous of Alabama. He placed *Diploschiza* in the Anomiidae, apparently because he mistook the missing umbonal region of the shell to be the foramen in the byssally attached lower valve of *Anomia*. Stephenson (1934) revived the genus in a thorough study of its distribution in the Upper Cretaceous of Alabama and Texas. Determining that Conrad's type material of *D. cretacea* is lost, Stephenson selected neotypes (actually neosyntypes, USNM(P) 75105 and 75106) from the Selma Chalk at Demopolis, Alabama. Although he noted a resemblance of *Diploschiza* to *Plicatula*, he tentatively placed *Diploschiza* in the Dimyidae rather than the Plicatulidae because of the obscurity of its "crural ridges" and small size. Stephenson (1935) later extended the geographic range of *Diploschiza* to Mississippi and described a new species of larger size, *Diploschiza melleni*, the type material of which is also in the Smithsonian (USNM) collections. Subsequently, the *Diploschiza cretacea* zone has become a useful stratigraphic marker horizon for the Pecan Gap Chalk and correlative horizons of late Cretaceous (middle Campanian) age in Texas, Alabama, Mississippi, and Arkansas (Stephenson, 1937; Elder, 1996).

Stephenson (1935, p. 590) suggested that *Diploschiza* may prove to be a senior synonym of *Dimyodon* (=*Atreta*) on the basis that several English species that resemble *Diploschiza* in shape and ornament had been removed from their original position in *Plicatula* and placed in *Dimyodon*. Feldtmann (1963, p. 113), however, asserted that "a pair of small short crural ridges diverging inwardly" present in some right valves of the type species of *Diploschiza* are "*Plicatula* teeth." On this basis he concluded, "Without doubt the shells of Conrad's species are really *Plicatula* from which the teeth and innermost layers of the shell have been eroded. Therefore, as a generic name *Diploschiza* is invalid." Feldtmann (1963), however, was clearly influenced by the new species from the Cretaceous Gingin Chalk of Western Australia that he described as *Plicatula glauerti*. But this species, as figured by Feldtmann (1963, pl. 2, figs. 4a, 5) has a narrow tooth on each side of the right resilifer similar to the teeth present on the right valve of *Diploschiza melleni* and unlike the strong denticulate teeth of *Plicatula*. Furthermore, because the aragonitic layers are not preserved in the Gingin chalk material (Feldtmann, 1963, p. 115), nor in the type material of *Diploschiza cretacea* and *D. melleni*, these teeth were likely originally calcitic, not aragonitic as in *Plicatula*.

Rao (1963), accepting the validity of *Diploschiza,* reported four possibly new but unnamed species of the genus from the Upper Cretaceous (Cenomanian) of southeastern India, based on shell shape and external ornament. Subsequently, however, Kendrick and Vartak (2007) described a new species, *Atreta redunca*, from the Cenomanian of SE India that they thought may be synomymous with the undescribed "*Diploschiza*" species of Rao (1963). *Atreta redunca*, however, has preserved aragonite and has all of the features diagnostic of *Atreta*, including an orbicular posterior adductor scar in contact with the pallial line, strongly cross-ridged hinge teeth and sockets developed from the aragonitic inner layer, an aragonite line that is well outside of the pallial line and nearly coincident with the denticulation line, and a resilifer that appears to lack overarching.

In view of the controversy over the taxonomic status of *Diploschiza*, the type material of Stephenson (1934, 1935) was reexamined. All of this material is missing the aragonitic inner shell layer and therefore lacks any trace of aragonitic hinge teeth and muscle scars. The best preserved specimen is the right valve of *Diploschiza melleni* that was illustrated by Stephenson (1935, pl. 70, fig. 11, USNM(P) 75486) and is refigured herein (Fig. 2.3, 2.4). Its pattern of branching costellae on the inner surface of the outer calcitic layer is like that in *Atreta*, these costellae representing the growth tracks of the denticles or short ridges along the denticulation line. The resilifer is bordered on each side by a small, narrow, non-denticulate raised ridge (the "crural ridges" described by Stephenson, 1935, p. 591). These ridges are continuous with the calcitic rim that occupies the entire dorsal margin and abuts the sides of the resilifer, possibly forming a tiny calcitic overarch of the resilifer apex. Because there are no left valves in this collection, it is uncertain whether these are true teeth, in the sense that they articulated with grooves along the edges of the resilifer of the opposite valve, or are buttresses, matched by corresponding ridges on the left valve. Two right-valve paratypes of *Diploschiza melleni* display comparable calcitic resilial ridges (e.g., Fig. 2.5). *Diploschiza cretacea*, the type species of the genus, is smaller in size than *D. melleni*, and only one right valve in the USNM collection has calcitic resilial ridges preserved, with a tiny calcitic overarch across the apex of its narrow resilifer. Stephenson (1935, p. 591) commented that "imperfect shells [of left valves] appear to show that it possesses a pair of small crura, inclosing the resilifer as on the right valve," thereby suggesting that the ridges may be buttresses rather than hinge teeth. In any case, these ridges are not comparable to "*Plicatula* teeth", contrary to Feldtmann (1963, p. 113).

In the present study *Diploschiza* is removed from the synonymy of *Atreta*, because the hinge plate of the former is calcitic rather than aragonitic and has distinctive resilial calcitic buttresses or teeth. Because of its calcitic hinge plate, *Diploschiza* may be the earliest member of a clade that includes the Cenozoic genera *Dimya* and *Basiliomya*, both of which have calcitic hinge plates and lack denticulate aragonitic hinge teeth.

Genus NEOATRETA new genus
Figure 3

Type species.—*Dimya filipina* Bartsch, 1913, p. 305, pl. 28, figs. 1-4. Type locality: Recent, Anima Sola Island, Philippine Islands, N 13° 20′, E 123° 14′ 15″, depth 192 m, collected by the United States Fisheries steamer *Albatross*, Station 5217.

Diagnosis.—Dimyidae with orbicular, biconvex shell posteroventrally elongated, with pair of elongate, transversely ridged, aragonitic hinge teeth on right valve interlocking with pair of transversely grooved sockets with raised dorsal edges on left valve, diverging ventrally from hinge line near ventral edge of resilifer; teeth and sockets of equal length or with anterior longer; aragonite line nearly coincident with denticulation line; denticulation line consisting of short unbranched costae weakly developed mid-ventrally, not prolonged as internal costellae extending into umbonal region; resilifer broadly triangular, with overarch extending from its apex to at least one-third its height in mature specimens; posterior adductor scar of left valve tending to be orbicular rather than strongly bilobed or bipartite and in contact with pallial line along its posteroventral margin; external ornament of left valve lamellose, with thin upturned lamellae numerous and beginning in early ontogeny of dissoconch; external radial costae weak or absent, restricted to surfaces of lamellae in late ontogeny.

Etymology.—The genus name means "new *Atreta*", with reference to the strong similarity of the aragonitic hinge teeth of the new genus to those of the extinct Mesozoic genus *Atreta*.

Comments on species.—The only known extant species of *Neoatreta* is the type species, *N. filipina*, broadly distributed from southern Japan to Indonesia in the western Pacific (Habe, 1971). Habe (1971, p. 331) determined that *Dimya radiata* Kuroda, 1928, and *D. radiata takii* Kuroda, 1932, are junior synonyms. *Dimya plana* (Martin, 1885) from the Miocene of Java, well-figured by Martin (1909, pl. 49, figs. 37–39) under the combination *Deuteromya plana*, also belongs in *Neoatreta* and may prove to be a senior synonym of *N. filipina*. Other fossil species newly assigned to *Neoatreta* are *Dimya phaidra* Woodring, 1982, from the upper Miocene upper Gatun Formation of Panama, *D. dissimilis* Tate, 1886, from the middle Miocene (Balcombian) of South Australia, and *D. kaiparaensis* Laws, 1944, from the lower Miocene of New Zealand (Otaian to Altonian according to Maxwell, 1978, p. 16). The age of *Neoatreta dissimilis* is based on that given by Beu and Darragh (2001, p. 151) for the associated pectinid, *Annachlamys murrayana* (Tate, 1886), which was described by Tate from the same localities that yielded *N. dissimilis*. The bases for these new generic assignments are as follows: *Neoatreta phaidra*, based on examination of the holotype and paratype (Fig. 3.5–3.7); *N. dissimilis*, based on the figures of Tate (1886, pl. 3, fig. 9a–c) and Bittner (1895, pl. 23, figs. 33–37) as well as photographs of type material received from the South Australian Museum in Adelaide (Fig. 3.8); and *N. kaiparaensis*, based on Laws (1944, fig. 26). The "*Dimya* sp." of Darragh and Kendrick (1991, p. 44, fig. 11F), from the Paleocene Cardabia Group in the Giralia Range of northwestern Australia, is possibly also a *Neoatreta* based on the exterior ornament of its left valve. This ornament, consisting of regularly spaced, upturned, crenulated commarginal lamellae, closely resembles that on left valves of *N. dissimilis, N. kaiparaensis*, and *N. phaidra*.

Occurrence.—Extant in western Pacific, fossil records questionable in the Paleocene (*Dimya* sp. of Darragh and Kendrick, 1991) but definite in the Miocene of New Zealand, Australia, Java, and Panama, as detailed above. Based on USNM collections consisting entirely of dead shells, the extant species, *Neoatreta filipina,* ranges from the Philippines and Borneo at depths from 59 to 534 m, with bottom temperatures ranging from 7° to 17.5°C. Japanese records for the species were given by Habe (1971, p. 331) from Amakusa, Kyushu, Kii Channel, and Sagami Bay, Honshu, at depths from 20 to 60 m.

Generic comparisons.—*Neoatreta* shares characters with *Atreta* and *Dimyella* that are not present in *Dimya* and *Basiliomya*: aragonitic denticulate teeth and pitted sockets, aragonite line nearly coincident with denticulation line and well outside the pallial line, and an orbicular posterior adductor scar that is not distinctly bilobed or bipartite and is in contact with the pallial line. Unlike *Atreta*, however, *Neoatreta* has a distinct, well-developed overarch, and the proximal ends of its hinge teeth and sockets are separated from the apex of the resilifer by this overarch and the ligament area produced by a ventrally migrating hinge line. Furthermore, in *Neoatreta* the denticles and pits of the denticulation line do not produce long branching costellae stemming from the umbonal region as in *Atreta*. Lastly, both *Neoatreta* and *Dimyella* differ from *Atreta* in having left valve exteriors that are consistently lamellose throughout dissoconch ontogeny, whereas in *Atreta* such ornament is only part of a range of variation that includes strong antimarginal costae. *Neoatreta* differs from *Dimyella* in the configuration of hinge teeth. The teeth of the right valve of *Dimyella* project from the floor of the umbonal cavity and are hook-like with only a few denticles. They interlock with short but deep sockets on the left valve that may have only two or three pits. Unlike the teeth of *Neoatreta* that diverge ventrally from the resilifer, those of *Dimyella* are well separated from the resilifer and are stubby rather than linear and divergent.

Remarks.—Bartsch (1913, p. 306), in his original description of *Dimya filipina*, referred to the hinge teeth as "the provincular area" and did not distinguish these teeth from those of the two extant species of *Dimya* that were then known, *D. argentea* Dall, 1886, and *D. corrugata* Hedley, 1902. Woodring (1982, p. 602), in his description of *Dimya phaidra*, did not mention its prominent hinge teeth at all. Clearly, however, there is a fundamental difference not only in the form of the teeth of *Neoatreta* compared to those of species of *Dimya*, but also in their mineralogy. In both *Neoatreta filipina* and *N. phaidra*, the aragonite line can be traced around the dorsal sides of the hinge teeth, demonstrating that these teeth are aragonitic in composition. Contrary to Bartsch (1913, p. 306), they are not continuations of the provinculum of the prodissoconch but rather are structures that develop after metamorphosis.

Another character of interest described by Bartsch (1913, p. 305) is a "chestnut colored basal layer" in the left valve of *Neoatreta filipina*. This layer separates the inner crossed-lamellar aragonitic shell layer from the outer foliated calcitic layer and, as noted by Bartsch, is commonly exposed when the inner layer flakes off from it. Fractures across the brown layer examined by SEM indicate that it is completely organic. It is secreted just outside the aragonite line and just inside the denticulation line along a very narrow band that narrows dorsally to only a thin line. In a left valve 7.6 mm in height, the maximum thickness of the organic layer is about 20 μm. Along the hinge line, this organic layer merges with the secondary periostracal ligament and contributes to the brown color of the ligament area and overarch of this species.

A similar organic layer appears also to have been present in the left-valve holotype of *Neoatreta phaidra* from the Miocene of Panama. Its former presence is indicated by the fact that the inner aragonitic shell layer has flaked off between the pallial line and the denticulation line, exposing the inner surface of foliated calcite across this region. Based on the figure of *Neoatrena kaiparaensis* in Laws (1944, fig. 26), an organic basal layer may also be present in that species. A comparable organic layer appears to be absent in *Dimyella*, where no flaking of the aragonitic inner shell layer occurs. Whether such a layer was present in *Atreta* is unknown.

Genus DIMYELLA Moore, 1969
Figure 4

1992 *Emiliomya* Corselli and Bernocchi, p. 671.

Type species.—*Dimyella starcki* Moore, 1969, p. 138, by original designation. Type locality: Recent, Cozumel Island, Mexico, from a depth of 6 m in the dark part of a submarine cave about five miles (=8 km) southwest of the town of San Miguel, attached to colonial corals on the roof of the cave.

Diagnosis.—Small Dimyidae not known to exceed about 8 mm in maximum dimension, commonly oval, acline in shape with short hinge line; right valve turned sharply away from substrate, becoming cup-shaped with deep umbonal cavity; left valve shallowly convex, fitting within margin of right valve, upturned along commarginal flexure that forms internal commarginal ridge along denticulation line. Interior of right valve with pair of short but strongly projecting, denticulate, aragonitic hinge teeth arising from umbonal cavity and well separated from resilifer, inserting into irregular pitted sockets on left valve; aragonite line nearly coincident with denticulation line; denticulation line consisting of short, closely spaced denticles that do not leave elongate traces on inner surface of outer calcitic layer and are commonly evenly spaced even in midventral region; exposed parts of resilifer broad, covered dorsally by extensive overarch on ventrally migrating ligament area; posterior adductor scar of left valve tending to be orbicular rather than strongly bilobed or bipartite and in contact with pallial line; exterior of left valve covered by thin, projecting commarginal lamellae beginning in early dissoconch ontogeny.

Comments on species.—In addition to the Caribbean type species, *Dimyella starcki*, *Dimyella* is represented in the present-day tropical western Atlantic, Caribbean Sea, western Pacific, and southwestern Indian Ocean. Previous published reports of *Dimyella* in the western Indo-Pacific are by Hayami and Kase (1996, p. 61), who reported *Dimyella* species A from Okinawa (Japan) and Bohol (Philippines) and *Dimyella* species B from Guam and Palau, and by Paulay (2003), who listed *Dimyella* species 1 and 2 from Guam. These species have not yet been illustrated or described. Paulay (2003, p. 242) referred to them as "undescribed members of a clade of minute dimyids, with well developed hinge teeth, that occur in reef caves throughout the Indo-West Pacific." *Dimya molokaia* Dall, Bartsch, and Rehder, 1938, from the Hawaiian Islands is also a *Dimyella*. In the Smithsonian collections, many specimens of *Dimyella* were found in unsorted collections or in lots that had been incorrectly identified as species of *Dimya*. These are from the tropical western Atlantic (Fig. 4.1–4.3) as well as from the western Pacific (Fig. 4.4–4.6) and western Indian Ocean (Fig. 4.7–4.10). Almost all of these specimens are left valves at least twice the size of the largest known *D. starcki*, and, unlike *D. starcki*, none has a brood pouch. Because I am unable to distinguish the western Atlantic shells from those in the Indo-Pacific based on this material, and because right valves are insufficiently known, I refer to all simply as "*Dimyella* sp."

In the fossil record, *Dimyella* is reported for the first time from the Pleistocene of Panama (USNM(P) 1163779, USGS Loc. 8305, Swan Cay, north of Bocas Island, Panama, probably from the Swan Cay Formation, dated as early Pleistocene by Aubry and Berggren, 1999, p. 39) and from the uppermost Pliocene or early Pleistocene of Costa Rica (USNM(P) 1163780, USGS Loc. 21035, Puerto Limon, Costa Rica, probably from the Moin Formation of latest Pliocene or early Pleistocene age). *Emiliomya malnatrensis* Corselli and Bernocchi, 1992, from the lower Pliocene of northern Italy, is also assigned to *Dimyella* for reasons discussed below. The oldest fossil species assigned herein to *Dimyella* is *Dimyodon similis* von Koenen, 1893, from the upper Eocene (Lattorfian) of Germany. The assignment is based on the excellent figures by Sokolow (1905, fig. 2, pl. 12, figs. 14c, 15c).

Occurrence.—*Dimyella* is extant in the tropical western Atlantic and Caribbean, Hawaiian Islands, and the western Indo-Pacific and apparently has a broad depth range. Extant species that live in the inner parts of submarine caves occur as shallow as 6 m, e.g., the type species as reported by Moore (1969, p. 139); see also Hayami and Kase (1996), regarding *Dimyella* in cave faunas of the northwestern Pacific. In the Smithsonian collections, depth records for *Dimyella* sp. in the western Atlantic range from 2 to 183 m and in the western Indo-Pacific from 90 to 622 m. Abundant records from off Barbados indicate that *Dimyella* sp. is commonly associated with coarse sand or rubble or rocky substrates. Fossils thus far assigned to *Dimyella* are from the upper Eocene of Europe and from the Pliocene and Pleistocene of Panama, Costa Rica, and northern Italy, as discussed above.

Generic comparisons.—The presence of aragonitic hinge teeth and an aragonite line that is well outside the pallial line separates *Dimyella* from *Dimya* and *Basiliomya*. Compared to *Neoatreta*, the hinge teeth of *Dimyella* are stubby or hook-shaped and well separated from the resilifer, with corresponding sockets on the left valve.

Remarks.—In both the Atlantic and Pacific, dredge collections of *Dimyella* sp. consist almost entirely of left valves. This is possibly because the preferred living habit is on hard substrates, possibly deep within crevices but not necessarily in submarine caves. After death, the right valves would remain in their original cemented position, but the left valves, freed by predators or the eventual decay of the shell ligaments, would accumulate in sediment accessible to dredging operations. Another indication that *Dimyella* species may live outside of caves is the high incidence of gastropod boreholes among these left valves (16/70 or 23 percent in the western Atlantic; 10/50=19 percent in the western Indo-Pacific). According to Hayami and Kase (1996, p. 63), boring gastropods such as naticids and muricids are absent from the caves that they studied.

The monotypic genus *Emiliomya* is synonymized with *Dimyella* based on the description and figures in Corselli and Bernocchi (1992). The shape, size, external ornament of the left valve, muscle scar pattern, position of the aragonite line, presence of very fine denticles on the denticulation line, and the morphology of hinge teeth in *Emiliomya* are all comparable with these characters in *Dimyella. Emiliomya* lacks a brood pouch, but so also does *Dimyella* with the sole exception of its type species. The habitat of *Emiliomya*, inferred by Corselli and Bernocchi (1992) to be on "the deeper part of the continental shelf and the upper continental slope", is within the range of habitats of *Dimyella*.

Genus DIMYA Rouault, 1850
Figures 1, 5, 7

1903 *Deuteromya* Cossmann, p. 68; new name for *Dimya* Rouault, 1850; *non* Menke, 1830, p. 101, subordinal name.

1936 *Dimyarina* Iredale, p. 269.

Type species.—*Dimya deshayesiana* Rouault, 1850, by original designation, p. 471, pl. 15, fig. 3, 3a, 3b, middle Eocene, Bos d'Arros, near Pau, southwestern France.

Diagnosis.—Dimyidae commonly of low biconvexity; hinge articulation entirely calcitic, either weak and irregular with transverse striae and nearly flat overarch of resilifer in each valve, or with slightly raised leaf-shaped tooth on either side of resilifer of right valve interlocking with shallow depression on each side of resilifer of left valve, or moderately strong calcitic articulation consisting of raised calcitic overarch of right resilifer bordered on each side by narrow socket, interlocking with depressed calcitic overarch of left resilifer, bordered on each side by narrow tooth; lateral teeth absent to weakly developed; aragonite line nearly coincident with pallial line and well inset from denticulation line; umbonal shoulders present and commonly well developed; denticles of denticulation line commonly more broadly spaced in midventral region than dorsally and commonly weak or absent midventrally; posterior adductor scar of left valve distinctly bilobed, with deep reentry between striate and non-striate parts, or bipartite, with scars for attachment of striate and non-striate adductor muscles separated; pallial line commonly not in contact with posterior margin of adductor scar of left valve. Exterior surface of left valve foliaceous and irregular, commonly silvery, with commarginal lamellae commonly flat-lying and irregular in spacing, less commonly projecting and coarsely frilled; antimarginal costae common, especially on right valve distal to cementation area.

Comments on species.—Until 1969, when Moore (1969) described the genus *Dimyella*, *Dimya* had long been the only broadly accepted genus name applied to Cenozoic Dimyidae. Now, with the recognition in the present study that the dimyid genera *Basiliomya*, *Dimyella*, and *Neoatreta* n. gen. have broad geographic and stratigraphic distributions, many of the old generic assignments have to be reexamined. Among the species that I have been able to assign to genera, either by examining specimens or adequate illustrations, 25 are confirmed as being in the genus *Dimya* (Table 2). Ten of these are extant; the remaining 15 collectively range from the middle Eocene to the Pleistocene. Undoubtedly some of these species will prove to be synonymous with further study, but on the other hand new species will likely be discovered with further collecting of fossils and extant specimens.

TABLE 2—Cenozoic Dimyid species in revised genera. Senior synonyms are in boldface; asterisk indicates a new combination.

Species	Geographic region	Stratigraphic range	Source for synonymy
***Basiliomya goreaui* Bayer, 1971**	western Atlantic	Pliocene–Recent	
***Dimya akasakiensis* Tashiro and Otsuka, 1980**	western Indo-Pacific	middle Eocene	
***Dimya alleni* Vokes, 1979**	SE USA	middle Eocene	
Dimya argentea Dall, 1886	western Atlantic	Recent	
***Dimya californiana* Berry, 1936**	eastern Pacific	Recent	
=*Dimya coralliotis* Berry, 1944	eastern Pacific	Recent	Coan et al. (2000)
***Dimya corrugata* Hedley, 1902**	western Indo-Pacific	Recent	
***Dimya crearoi* Oppenheim, 1900**	Italy	upper Eocene	
***Dimya deshayesiana* Rouault, 1850**	France	middle Eocene	
=*Anomia intusstriata* D'Archiac , 1850	France	middle Eocene	Dall (1886, p. 228)
=Anomia obliqua Schafhäutl, 1863	Germany	Eocene	Zellinskaya et al. (1968, p. 53)
Dimya fimbricostata Vokes, 1979	western Atlantic	Pleistocene–Recent	
=Dimya acuminata Forti Esteves, 1984	western Atlantic	Recent	Waller; see *Dimya* discussion
***Dimya fragilis* v. Koenen, 1893**	Germany	upper Eocene	
***Dimya grandis* Dall, in Guppy and Dall, 1896**	western Atlantic	Pliocene	
=Dimya grandis divaricata Dall, in Guppy and Dall, 1896	western Atlantic	Pliocene	Waller, present study
***Dimya hohndorfi* Welle, 1998**	Germany	lower Oligocene	
***Dimya japonica* Habe, 1971**	western Indo-Pacific	Recent	
***Dimya* sp. aff. *japonica* Habe, 1971**	western Indo-Pacific	Recent	
Dimya lima Bartsch, 1913	western Indo-Pacific	Recent	
***Dimya maoria* Powell, 1937**	western Indo-Pacific	Recent	
***Dimya mimula* Dall, Bartsch, and Rehder, 1938**	Hawaiian Islands	Recent	
***Dimya pamplonensis* (Carez, 1881)**	Spain	upper Eocene	
=Dimya richei Doncieux 1911	France	Eocene	Calzada and Astibia (1996)
***Dimya rahkiensis* Eames, 1951**	Pakistan	middle Eocene	
***Dimya raulini* Cossmann and Peyrot, 1914**	SW Europe	Miocene?	
***Dimya rufaripa* Vokes, 1979**	SW USA	lower Oligocene	
***Dimya sigillata* Tate, 1886**	W Australia	upper Eocene	
***Dimya*? *spondyliformis* Eames, 1951**	Pakistan	middle Eocene	
***Dimya tenuiplicata* (Seguenza, 1879)**	SW Europe	Miocene–Pleistocene	
=Dimya extenuiplicata Sacco, 1897	SW Europe	Miocene–Pliocene	Corselli and Bernocchi (1992)
=Dimya fragilis crassiplicata Sacco 1897	SW Europe	Miocene	Corselli and Bernocchi (1992)
=Dimya fragilis miopliocenica Sacco 1897	SW Europe	Miocene–Pliocene	Corselli and Bernocchi (1992)
***Dimya tigrina* Bayer, 1971**	western Atlantic	Pleistocene–Recent	
***Dimya westonensis* Maxwell, 1978**	New Zealand	upper Eocene	
Dimyella malnatrensis* (Corselli and Bernocchi, 1992)	SW Europe	Pliocene	
Dimyella molokaia* (Dall, Bartsch, and Rehder, 1938)	Hawaiian Islands	Recent	
Dimyella similis* (v. Koenen, 1893)	Germany, Ukraine	upper Eocene	
***Dimyella starcki* Moore, 1969**	western Atlantic	Recent	
Dimyella sp.	western Atlantic; Indo-Pacific	Recent	
Neoatreta dissimilis* (Tate, 1886)	W Australia	middle Miocene	
Neoatreta filipina* (Bartsch, 1913)	western Indo-Pacific	Recent	
=Dimya radiata Kuroda, 1928	western Indo-Pacific	Recent	
=Dimya radiata takii (Kuroda, 1933)	western Indo-Pacific	Recent	
Neoatreta kaiparaensis* (Laws, 1944)	western Indo-Pacific	Miocene	
Neoatreta phaidra* (Woodring, 1982)	Panamic	Miocene	
Neoatreta plana (Martin, 1885)*	Java	Miocene	
***Neoatreta*? sp. (*Dimya* sp. of Darragh and Kendrick, 1991)**	Paleocene	NW Australia	

Occurrence.—Extant in the western Atlantic, eastern Pacific, and Indo-west Pacific; fossil occurrences worldwide, stratigraphic range Paleocene or Eocene to Recent. Although the oldest fossil occurrences of *Dimya* shown in Table 2 are middle Eocene, it is likely that the genus originated in the Paleocene from a Cretaceous ancestor. A possible but unconfirmed Paleocene occurrence is the *Dimya*? sp. of Vincent (1930, pl. 4, fig. 6, showing only the exterior of a right valve) from the early Paleocene of Belgium.

Generic comparisons.—The principal differences between *Dimya* and *Basiliomya* are the presence in the latter of stronger hinge denticulation (particularly the presence of strongly projecting stubby lateral teeth in the left valve), lack of umbonal shoulders, denticles that are widely spaced even at the dorsal ends of the denticulation line, and a shell layer inside the pallial line that is calcitic rather than aragonitic. Compared to *Atreta*, *Diploschiza*, *Neoatreta*, and *Dimyella, Dimya* differs in having its aragonite line nearly coincident with the pallial line rather than extending to the denticulation line. In *Dimya* the hinge articulation is calcitic, whereas in *Atreta*, *Neoatreta* and *Dimyella*, strong denticulate hinge teeth and sockets develop from the aragonitic inner shell layer. *Dimya* shares with *Basiliomya* a left posterior adductor scar that is commonly bilobed or with nearly or actually separated striate and non-striate component scars that are inset from the pallial line. This is in contrast to *Atreta*, *Neoatreta*, and *Dimyella*, wherein the left posterior adductor scar is more orbicular and commonly in contact with the pallial line.

Remarks.—Three intergradational types of hinge articulation are present in *Dimya*: 1) a simple cross-striated hinge with only very weak development of larger interlocking structures, as in extant *D. argentea* and *D. lima* (Fig. 5.2); 2) a hinge in which articulation is primarily by means of a raised overarch and bordering sockets in the right valve that articulate in keystone fashion with a depressed overarch and bordering teeth on the left valve, e.g., *D. grandis* and *D. fimbricostata* (Figs. 1, 5.3, 5.4, 5.6); and 3) dentition approaching that of *Basiliomya*, in which teeth adjacent to the resilifer of the right valve are bordered laterally by weak sockets, corresponding to sockets adjacent to the resilifer of the left valve bordered laterally by weakly projecting lateral teeth, e.g., *Dimya* sp. aff. *D. japonica* from the western Pacific (Fig. 5.8). These types of hinge articulation seem to be intergradational among species and therefore not suitable for subdividing *Dimya* into additional genera or subgenera.

Dimya acuminata Forti Esteves, 1984, is listed in Table 2 as a junior synonym of *Dimya fimbricostata* Vokes, 1979. This is based on comparison of Forti Esteves's figure of the holotype, a left valve 21.3 mm high, with a paratype of *D. fimbricostata*

(USNM(P) 264979) of about the same size from the Moin Formation of Costa Rica. The USNM specimen has its calcitic overarch broken off except for its anterior edge. When viewed under a light directed from the anterodorsal side, as is the case in Forti Esteves's figure, the comparison is close indeed. This synonymy stands in contrast to that given by Ríos (2009, p. 502), who regarded *D. acuminata* as a junior synonym of *D. argentea*.

Genus BASILIOMYA Bayer, 1971
Figure 6

Type species.—*Basiliomya goreaui* Bayer, 1971, by original designation, p. 227, figs. 70, 71C-E. Type locality: Recent, "Discovery Bay, Jamaica, depth 170 feet (=52 m); attached to dead branch of scleractinian coral (*Madracis*). Collected by Thomas F. Goreau, December 25, 1964." (Bayer, 1971, p. 229)

Diagnosis.—Original, Bayer (1971, p. 225): "Shell subcircular in outline, translucent, with negligible iridescence; left valve smooth externally, but sometimes reproducing irregularities of the substrate; radial ornament on outer surface of free margin of right valve; edge of right valve more or less widely extended as a thin, lobate marginal frill. Hinge of right valve with a blunt, triangular tooth on each side of the internal ligament and a shallow socket at each end of the hinge line; left valve with a shallow groove on each side of the internal ligament and a blunt tooth at each end of the hinge line; a series of interlocking small teeth and pits around the perimeter of both valves. Anterior adductor near end of hinge line; posterior adductor remote from hinge, conspicuously bilobed; pallial impression marked by a row of shallow pits."

Emended diagnosis: small Dimyidae commonly less than 10 mm in maximum shell dimension, with cup-shaped lower valve having one or more flaring frills scalloped by broad radial plicae near margin; left valve fitting inside margins of right valve, with exterior lacking plicae or costae. Hinge articulation entirely calcitic; resilium on each valve small and narrow; resilifer of right valve small, with convex overarch bordered on each side by a cross-striated tooth and then a socket, corresponding on left valve to sockets adjacent to resilifer and stubby teeth at ends of hinge. Inner shell composed of irregularly foliated calcite, with micropitted or pustulose surface, its distal boundary approximately coincident with pallial line. Denticles on denticulation line of right valve weakly developed, at ends of low, narrow, widely spaced internal riblets on calcitic rim, corresponding to pits with raised edges on left valve at ends of widely spaced, finely paired internal riblets; left posterior adductor scar distinctly bilobed or bipartite, inset from pallial line; pallial line commonly coarsely disjunct, consisted of well-separated small muscle scars; umbonal shoulders absent or only weakly developed.

Comments on species.—*Basiliomya* is monotypic, represented only by its extant type species, *Basiliomya goreaui*, reported by Bayer (1971, p. 229) from Jamaica (see above) and from a reef off Goat Bay, Fresh Creek, Andros Island, Bahamas, depth 23 to 30 m, attached to bottom of a large coral (*Agaricia*). Further study of unidentified Recent samples in the USNM collections has established that this species has a much broader geographic range than that given by Bayer (1971). Sixteen lots newly identified as this species are from off Barbados (14 lots) and Antigua (two lots), with a depth range from 46 to 219 m, these being mainly disarticulated left valves associated with coarse sandy and rubbly rough bottoms with dead coral.

Basiliomya has not previously been reported from the fossil record, but based on extensive collections from the northern Dominican Republic reposited in the Natural History Museum of Basel (NMB), Switzerland (see Saunders et al., 1986; Waller, 2011), *B. goreaui* can now be reported from the Pliocene of the northern Dominican Republic (Fig. 6.4, 6.5). The specimens occur in the Mao Formation on the Río Gurabo (NMB Localities 15823 and 15829) and Río Cana (NMB Localities 16884 and 17023). These localities are in deep-water facies that are dated on the basis of planktic foraminifera and nannofossils as early and middle Pliocene (Saunders et al., 1986, p. 19, 23). At these localities, *Basiliomya* is associated with other macro- and microfossils that indicate a deep-water environment, perhaps greater than 200 m in depth (Saunders et al., 1986; Cairns and Wells, 1987; Waller, 2011).

Occurrence.—Extant in the tropical western Atlantic (Bahamas, Jamaica, Antigua, and Barbados) at depths from 23 to 219 m; fossils in lower and middle Pliocene Mao Formation, northern Dominican Republic.

Generic comparison.—The characters that separate *Dimya* and *Basiliomya* from *Neoatreta* and *Dimyella* have been discussed above. Compared to *Dimya*, *Basiliomya* differs in having a more differentiated calcitic hinge dentition, the most prominent features of which are a single blunt tooth at each end of the hinge of the left valve and a cross-striated tooth on each side of the resilifer of the right valve. *Basiliomya* also differs from *Dimya* in having a strongly disjunct pallial line and marginal denticles that are widely spaced all around the denticulation line rather than becoming closely spaced dorsally. *Basiliomya* is the only dimyid genus in which the inner shell layer inside the pallial line is calcitic rather than aragonitic. At macroscopic levels this is indicated by the uniformity in color of inner shell surfaces on either side of the pallial line. This is particularly evident in weathered specimens of Pliocene age from the Mao Formation of the Dominican Republic. Fossils of *Dimya fimbricostata* from the same localities in the Mao Formation (NMB 15823 and 15829) have aragonitic microstructure inside the pallial line clearly distinguishable by its chalkiness from the calcitic rim.

Although *Basiliomya* is well-separated morphologically from other dimyids in the western Atlantic region, some species of *Dimya* in the tropical western Pacific possess some of the morphological characters of *Basiliomya. Dimya japonica* has a few out-turned radially plicate lamellae on the exterior of its cup-shaped right valve. Furthermore, its right valve has a limited area of attachment and a straight dorsal margin. Internally, however, it lacks the characteristic dentition, although some specimens possess a shallow ridge-like projection at each end of the hinge of the left valve in a position that appears to be homologous with the more strongly developed teeth in the left valve of *Basiliomya*. These features are also present in *Dimya* sp. aff. *D. japonica*, a probable new species recognized in USNM collections (Fig. 5.7, 5.8) from the Philippines and northeast Borneo but not described due to insufficient material. It resembles *Basiliomya goreaui* even more closely in its small size, D-shaped acline or prosocline shape, and widely spaced denticles, but like *D. japonica*, it lacks fully developed *Basiliomya*-type dentition. Incipient teeth are present at the ends of its left hinge, but the teeth on the right valve and their corresponding sockets along the sides of the resilifer of the left valve are not developed. Furthermore, *Dimya* sp. aff. *D. japonica* has a nearly continuous pallial line and aragonitic shell material inside the pallial line.

Remarks.—Bayer (1971, p. 227), impressed with the unusual dentition of *Basiliomya goreaui*, remarked on the resemblance of his new genus to *Dimyodon*, a Jurassic genus that is now known to be a junior synonym of *Atreta*. Bayer equated the projecting hinge tooth bordering each side of the resilifer on the right valve of *Basiliomya* with what he regarded as similar teeth in *Dimyodon*. As shown in the present study, however, these teeth are not homologous. Those of *Atreta* are developed from the inner aragonitic layer of the shell, whereas those of *Basiliomya* are developed from the calcitic rim that extends medially to the sides of the resilifer. As indicated in the preceding phylogeny section, the likely ancestor of *Basiliomya* is more likely *Dimya*, which developed a calcitic hinge but without the elaborate dentition of *Basiliomya*.

Except for the holotype and paratypes, the USNM collections of *Basiliomya goreaui* consist entirely of left valves. This is clearly the effect of living habit. The holotype and paratypes are right valves or articulated specimens that were collected by SCUBA divers directly from their sites of attachment to corals on a deep reef front (Bayer, 1971, p. 229). The remainder of the collection, obtained by dredging on rubbly or sandy sea bottoms, consists only of disarticulated left valves that were clearly transported away from their original living sites. Death and ensuing disarticulation are in part the result of predation as evidenced by the presence of gastropod boreholes in 15 percent of the valves.

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