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PART N, REVISED, VOLUME 1, CHAPTER 21: CEMENTING BIVALVIA

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INTRODUCTION

A number of bivalves have evolved the ability to attach to hard substrates by cementation, a habit that is perhaps best known in the oysters (Fig. 1), but is also widespread in other taxa (Fig. 2). This rigid fixation involves at least part of one valve being constructed directly on to its chosen substrate, forming a permanent bond. Although most cementing bivalves attach in this manner for a substantial part of their lives, in some taxa (e.g., many Gryphaeidae) the attachment area is very small, and confined to the umbonal area, and the animal becomes effectively free-living in adult life. In most cases, this attachment is sufficiently strong to persist long after the animal's death. Cementation is considered a derived life habit, which YONGE (1979, p. 84) regarded as the "culmination of the epifaunistic specialization in the Bivalvia," and it has evolved independently multiple times in marine, estuarine, and freshwater bivalves (YONGE, 1979).

Few cementers live at high latitudes (NICOL, 1964, 1978), and they reach their highest diversity and abundance in the warmer waters of the tropics and subtropics. Marine cementing bivalves are predominantly found in shallow subtidal waters, in particular associated with reefal habitats, but they also occur intertidally (Fig. 1). There are no records of cementing bivalves from the deep sea, although Recent Dimyidae are found in deeper water than most (YONGE, 1978a), with collection at depths in excess of 1000 m (COAN, VALENTICH-SCOTT, & BERNARD, 2000). In freshwater, etheriids appear to favor fast-moving streams and rivers, whereas the cyrenidid *Posostrea anomioidea* BOGAN & BOUCHET, 1998, lives on the undersides of boulders in lakes (BOGAN & BOUCHET, 1998).

Many cementers are highly gregarious, e.g., oysters (GALTISOFF, 1964; SOUTHWORTH & others, 2010), rudists (SKELTON, 1979; GILL, MASSE, & SKELTON, 1995), lithiotids (NAUSS & SMITH, 1988; FRASER, BOTTJER, & FISCHER, 2004), and *Etheria* LAMARCK, 1807 (KAT, 1987), forming bioherms on open surfaces. Such aggregations may considerably influence local sedimentation rates and patterns and form complex habitat systems. Other cementers are more solitary, occupying open surfaces, whereas others may be more cryptic, living on the undersides of boulders or corals.

TAXONOMIC OCCURRENCE

Cementation has been recognized in the Pteriomorphia, Palaeoheterodonta, and Heterodonta, but not in the Protobranchia. Among extant Pteriomorphia, cementation has been recorded in members of Ostreoidea, Plicatuloidea, Dimyoidea, and Pectinoidea (within the Spondylidae and sporadically within the Pectinidae, e.g., *Hinnites* DEFRANCE, 1821; *Eopecten* DOUVILLÉ, 1897; *Prohinnites* GILLET, 1922; *Crassadoma* BERNARD, 1986). Additionally, there are a number of extinct cementing pteriomorph taxa (Terquemiidae, Lithiotidae, Chondrontontidae, a few genera of Pseudomonotidae) (REIS, 1903; FRENEIX & LEFÈVRE, 1967; NEWELL & BOYD, 1970; HAUTMANN, 2001). Most members of the pectinoid superfamily Anomioidea fix themselves permanently to hard substrata by a massive calcified byssus (YONGE, 1977), but this cannot be properly referred to as cementation. It has, however, been suggested that the Jurassic anomiid *Eonomia timida* FÜRSICH & PALMER, 1982, cemented its thin right valve to hard substrates as well as employing a byssus (FÜRSICH & PALMER,



FIG. 1. Living individuals of the oyster *Saccostrea glomerata* (GOULD, 1850) cemented to surfaces of rocks in intertidal zone in Port Jackson, New South Wales (new).

1982). It is notable that within the Pteriomorpha, the cemented habit has never been exploited by members of the Arcoida or Mytiloida.

Within the Palaeoheterodonta, the unionoid superfamily Mullerioidea, the so-called freshwater oysters, comprise three genera on three different continents. *Etheria* LAMARCK, 1807, occurs widely throughout mainland Africa and also in Madagascar; *Acostaea* D'ORBIGNY, 1851, in South America; apparently restricted to the Magdalena Basin in Colombia; and *Pseudomulleria* ANTHONY, 1907, in the Mysore region of India (YONGE, 1962, 1978b).

Cementation occurs sporadically among the Heterodonta, but is most spectacularly developed in the extinct Hippuritida (the rudistids), whose often massive, coiled shells formed large bioherms in Tethyan carbonate sequences (e.g., SKELTON, 1978; GILI, MASSE, & SKELTON, 1995). Among anomalodesmatan bivalves, two small families, the Cleidothaeridae and Myochamidae, both centered around Australasia, have cemented taxa. In the case of the Cleidothaeridae, all members of the single

described genus, *Cleidothaerus* STUTCHBURY, 1830, cement by the right valve, usually to open rock surfaces, intertidally, or in shallow water (MORTON, 1974; MORTON & HARPER, 2001). In the second family, Myochamidae, most members (e.g., *Myadora* GRAY, 1840) are active shallow burrowers (MORTON, 1977), but one genus, *Myochama* STUTCHBURY, 1830, cements by the right valve, most frequently to shells of large, shallow-burrowing bivalves (e.g., *Neotrigonia* COSSMAN, 1912; *Eucrassatella* STEWART, 1930; *Glycymeris* DA COSTA, 1778) (YONGE & MORTON, 1980; HARPER & MORTON, 2000). In the order Venerida, cementation occurs in two living clades. The best known of these is the marine superfamily Chamioidea, in which the family Chamidae is common in tropical and subtropical regions (YONGE, 1967). Most chamids cement by the anterior portion of their left valve, although a few do so using the right valve, and others (*Arcinella* SCHUMACHER, 1817) are secondarily free-living (NICOL, 1952). The taxonomic significance of which valve is used for attachment, and whether those that cement by the right valve should be



FIG. 2. Cementing pectinid *Crassadoma pusio* (LINNAEUS, 1758) attached by its right valve to inside of an oyster; scale bar, 10 mm (new).

assigned to the genus *Pseudochama* ODHNER, 1917, has been much debated (ODHNER, 1919; YONGE, 1967; MATSUKUMA, 1996; CAMPBELL & others, 2004). The second veneroid (=cardioid *sensu* CARTER & others, 2011) clade within the freshwater family Cyrenidae is much smaller, being restricted to the species *Posostrea anomioioides* BOGAN & BOUCHET, 1998, endemic to Lake Poso in Indonesia (BOGAN & BOUCHET, 1998).

CHARACTERISTICS OF CEMENTING BIVALVES

Despite belonging to disparate taxa, many cementing bivalves share a number of conchological and anatomical characters. Indeed, the resulting convergent anatomical and conchological characters have hindered attempts to recognize evolutionary relationships between cementing taxa.

Cementers have highly irregular and plastic morphologies, because the attached valve has to conform so precisely to their attachment site, producing an irregular

attachment scar. For those taxa that cement relatively later in ontogeny, e.g., *Crassadoma* BERNARD, 1986, there is a marked boundary where regular idiomorphic shell growth ceases and the irregular attachment scar begins. It should be noted that the extent of the attachment scar is different between different taxa. Many cementers attach to hard substrates for much of their lives and, as a result, have large areas of attachment scars, although many, for example spondylids and pectinids, lift their ventral valve margins away from the substrate and regular shell accretion and ornamentation resumes. Other taxa, for example gryphaeids, cement only for very short periods of their life and therefore have only minute attachment scars.

The intricacy with which the attached valve tracks the topography of the substrate may allow the exceptional preservation of soft-bodied organisms, such as hydroids and ctenostome bryozoans, through bioimmuration (Fig. 3; TAYLOR, 1990; TODD, 1993). In most cementing taxa, the requirement

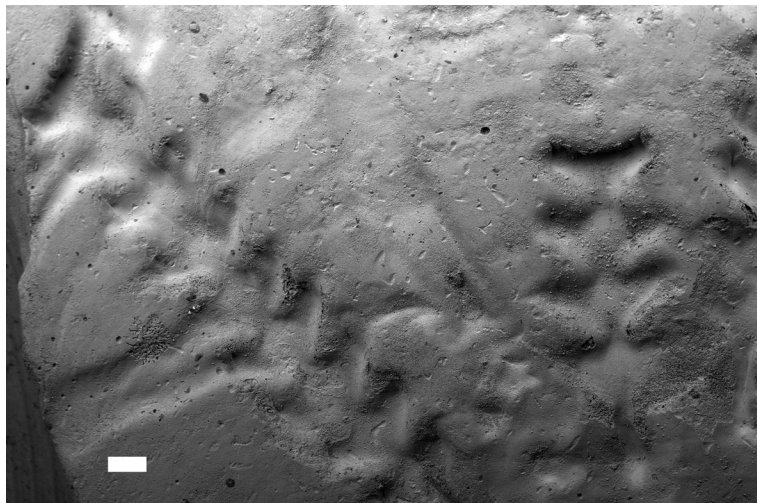


FIG. 3. SEM showing exceptional preservation of a hydroid bioimmured by an oyster, Eocene, Le Goepelle, France; scale bar, 200 μ m (new; courtesy of Paul D. Taylor, NHM London).

for the two valves to meet perfectly results in the upper valve showing a positive of the overgrown surface, a characteristic known as xenomorphism (STENZEL, KRAUSE, & TWINING, 1957). The replication of xenomorphic ornament is of particularly high fidelity in oysters and myochamids (Fig. 4) and has provided paleontological evidence for biogenic substrates that have otherwise low preservation potentials (e.g., LEWY, 1972; ROHR & BOUCOT, 1988). Cementing bivalves are often highly inequivalved, usually, but not invariably, with the lower attached valve being more inflated [although it should be noted that inequivalvy is a common morphological response to a pleurothetic life habit, as shown by the free-living *Pecten maximus* (LINNAEUS, 1758)]. This condition was taken to extreme in some rudistids, where the unattached upper valve may be little more than a lid. Many cementers lay down particularly massive, thick shells, which in some oysters, spondylids, and etheriids is further accentuated by incorporating chambers within them. Additionally, numerous cementing bivalves (e.g., *Chama* LINNAEUS, 1958; *Spondylus* LINNAEUS, 1758) have developed elaborate ornamentation consisting of spines, flanges,

and/or frills. These may have a variety of functions: on the attached valve, flanges may provide buttresses or additional sites of cementation (LOGAN, 1974; FEIFAREK, 1987), whereas on the unattached valves they may be directly defensive (STONE, 1998) or provide attachment sites for epibionts that provide camouflage (VANCE, 1978; FEIFAREK, 1987).

Most clades of cementing bivalves show constancy in terms of which valve is attached to the substrate. This reflects the fact that most appear to have evolved from taxa that were already pleurothetic. In these taxa, the vast majority attach by the right valve, although oysters are a notable exception, cementing only by the left. In other clades, e.g., Chamidae, Hippuritoidea, Lithiotidae, Etheriidae, and *Posostrea*, however, cementation may occur by either valve, although it may be fixed at lower taxonomic levels.

In most cases, it is apparent that the cementing habit evolved from byssate stocks, and, indeed, most cementers pass through a byssate phase early in ontogeny. This is most marked in the pectinoids (i.e., Spondylidae and various pectinid clades; e.g., *Crassadoma* BERNARD, 1986), where the juveniles have a clear byssal notch, which is occluded

once cementation begins, and idiomorphic growth patterns. YONGE (1951) suspected that the onset of sexual maturity is the trigger for cementation by *Hinnites multirugosus* (= *Crassadoma gigantea*). By contrast, the oyster *Ostrea edulis* LINNAEUS, 1758, initiates cementation as it settles from the plankton, 10–15 days after fertilization, initially using a glue produced by the foot (CRANFIELD, 1973a, 1973b, 1973c, 1975; WALLER, 1981).

A common anatomical feature of cementing bivalves is the loss, or marked reduction, of the foot, often initiated at the time of cementation. For example, in *Ostrea edulis*, the foot atrophies immediately following settlement (HICKMAN & GRUFFYDD, 1971; CRANFIELD, 1973a), whereas, in mature cementing *Etheria*, and *Spondylus*, the foot is reduced to a cleansing role only (YONGE, 1979). Many cementers are monomyarian, with the posterior adductor muscle conserved. However, these anatomical features are neither universal among cementing clades, nor are they necessarily a consequence of the cementing habit, as they may be shared by closely related, bysally attached taxa (YONGE, 1953; YONGE & CAMPBELL, 1968).

TEMPORAL OCCURRENCE

Although a small number of Late Paleozoic pseudomonotids are known to have been able to cement (NEWELL & BOYD, 1970), the habit is predominantly a post-Paleozoic adaptation. It is notable that the majority of cementing taxa, and in particular the larger, more important marine clades (i.e., oysters, rudists) first appeared during the Mesozoic. Cementation evolved a number of times in small clades (consisting of only a few genera and, generally, of restricted geographic distribution) during the Cenozoic. For example, both clades of anomalodesmatan cementers evolved in a similar geographic area during the Neogene. The impoverished and incomplete nature of the freshwater fossil record makes the history of cementation in these environments difficult to establish. In the case of disparate

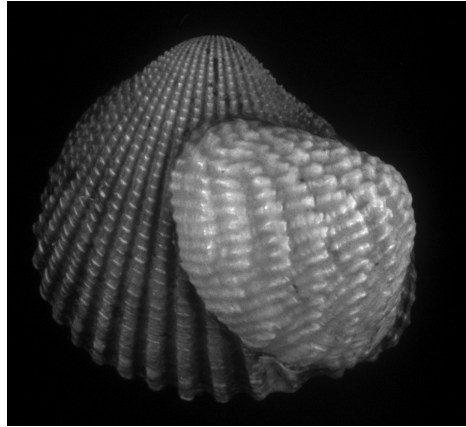


FIG. 4. *Myochama anomioides* STUTCHBURY, 1830, attached to *Neotrignonia margaritacea* (LAMARCK, 1804), Moreton Bay, Australia; note intricate ornament of trigoniid reflected in left valve of myochamid by xenomorphism (new).

unionoid genera, the oldest recorded fossil is Miocene (KAT, 1987), although the suggested monophyly of these taxa suggests common ancestry in the Mesozoic, in order to predate Gondwanan breakup (GRAF & CUMMINGS, 2009). There are no fossils of cementing cyrenidids yet reported, and the only known living example, a monotypic genus, is endemic to Lake Poso, which occupies a tectonic suture of mid-Miocene age (HAASE & BOUCHET, 2006), implying a geologically recent origin.

HOW MANY TIMES HAS THE CEMENTED HABIT EVOLVED?

YONGE (1979, p. 84) suggested that cementation was acquired independently in every superfamily in which it occurs, and HARPER (1991) suggested that there were at least 20 clades that evolved this adaptation. However, a high degree of morphological plasticity, which results in highly variable forms within taxa strongly influenced by substrate morphology, in addition to common anatomical features and the fact that many clades are closely related, has made it rather difficult to pinpoint the ancestry of some groups, and hence, to accurately differentiate clades. These

problems are further exacerbated as the fossil record includes a number of extinct clades. A particular problem has been to establish the origin of oysters and their relationships to some of the rather problematic extinct early Mesozoic cementers, such as terquemiids. This topic has provoked a rather lively debate (e.g., NEWELL & BOYD, 1970; CARTER, 1990, p. 220, 250; HAUTMANN, 2001, 2006; MÁRQUEZ-ALIAGA & others, 2005; CHECA & others, 2006; MALCHUS, 2008), although the paleontological, anatomical, and molecular data now clearly indicates that oysters were derived from pterioids, rather than from pectinoids (CARTER, 1990, p. 220, 250; CAMPBELL, 2000; STEINER & HAMMER, 2000; GIRIBET & WHEELER, 2002; GIRIBET & DISTEL, 2003).

It has also been debated whether the extant chamids were descended from the extinct rudists (ODHNER, 1919; YONGE, 1967). Although seemingly resolved when KENNEDY, MORRIS, and TAYLOR (1970) suggested, largely on the basis of shell microstructure, that the sister group of the chamids might be the Carditidae, this view has not been supported by molecular evidence, which instead places chamids closer to cardiids and other veneroids (=cardioids *sensu* CARTER & others, 2011) (TAYLOR & others, 2007). However tantalizing the similarities between the chamids and rudists, any hypotheses linking the two are currently untestable (TAYLOR & others, 2007).

The number of times cementation has evolved among unionoid freshwater oysters has also proved controversial. The seemingly very disjunct geographic distribution of the three genera (*Etheria*; *Acostaea* D'ORBIGNY, 1851; *Pseudomulleria* ANTHONY, 1907) on different continents led some authors (e.g., ANTHONY, 1907; PRASHAD, 1931), to hypothesize that the similarities between the three taxa were simply convergent, whereas YONGE (1962, 1978b) supported their close common ancestry on the basis of his studies of their anatomy and morphology. Recent molecular analyses have failed to reach

consensus, with some analyses and interpretations recovering polyphyletic origins (BOGAN & HOEH, 2000; HOEH & others, 2009), and those by GRAF and CUMMINGS (2006, 2009, 2010) suggesting monophyly.

Given these uncertainties, it is difficult to be confident about the number of times the cementing habit evolved. However, a conservative estimate would allow for at least 16 clades. It is to be anticipated that the employment of increasingly sophisticated techniques in molecular phylogenetic reconstruction, in tandem with a greater understanding of the fossil record, will improve our understanding. Nevertheless, there are two interesting implications of the repeated ability to evolve cementation: (1) that cementation is relatively easy to acquire, and (2) that there must be selective advantage(s) of the habit, in particular over byssate attachment.

MECHANISM OF CEMENTATION

Although early cementation in larval oysters may be effected by a cement derived from the byssal glands (CRANFIELD, 1973a, 1973b, 1973c), that of larger individuals can only be achieved by the mantle lobes, and therefore, by modification of the normal shell-secretion mechanisms (CRANFIELD, 1974; YONGE, 1979; HARPER, 1992). A key adaptation in this respect is that the shell must be applied directly to the substrate. YONGE (1979) suggested that attachment is achieved by the periostracum being extruded as a fluid onto the substrate surface, thereby acting as a glue. Although this may be true of some clades, in taxa that have been studied in detail, the periostracum appears as a sheet of uniform thickness, and there is no accumulation of periostracal material in hollows below the valve (HARPER, 1992). In most cementing taxa, the periostracum is extremely thin (in pteriomorphs less than 1 μm thick; HARPER, 1997a), and during the cementing phase of the anomalodesmatans *Myochama* STUTCHBURY, 1830, and *Cleidothaerus* STUTCHBURY,

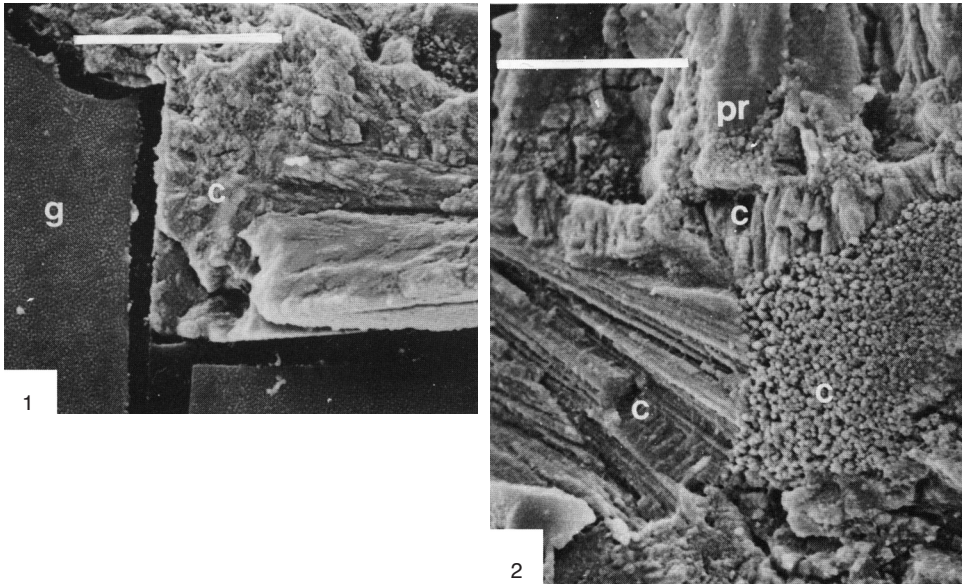


FIG. 5. Scanning electron micrographs of the crystalline cement between left valves of spat of *Crassostrea gigas* (GMELIN, 1791) attached to glass plates (six weeks after settlement). The cement grows in a manner highly reminiscent of diagenetic fabrics, with spherulites nucleating on the bounding surfaces of voids between substratum and outer surface of shells. As a result, any fracture through the cement shows bundles of crystals cut at different orientations; *pr*, calcite prisms of outer shell layer; *g*, glass substratum; *c*, cement; 1, scale bar, 3 μ m; 2, scale bar, 6 μ m (Harper, 1992, fig. 4, reproduced by kind permission of Oxford University Press).

1830, the periostracum of the attached valve is considerably thinner than that of the unattached valve (HARPER & MORTON, 2000; MORTON & HARPER, 2001). Since the periostracum is the template on which the calcareous part of the shell is formed (TAYLOR & KENNEDY, 1969), possession of a thin periostracal sheet allows the valve to be constructed in very close proximity to substratal irregularities. By contrast, it is not possible for a thick periostracal sheet to be folded with sufficient intricacy to allow the outer shell surface to follow the microtopography of the substratum with enough fidelity to allow adhesion (HARPER, 1997a).

Detailed scanning electron microscopic examination of oysters has shown the growth of crystalline cement between the periostracum and substratum (Fig. 5) (HARPER, 1992, 1997b). This cement is highly reminiscent of inorganic cavity-fill cements observed in sedimentary rocks, so

HARPER suggested that extra-pallial fluid leaks through the periostracum and then crystallizes between it and the substratum. However, subsequent analyses of these oyster cements by MACDONALD, FREER, and CUSACK (2010), using more sophisticated techniques such as electron backscatter diffraction and Raman spectroscopy, have revealed that the cements are high magnesium calcite, which they suggest is biologically induced to grow directly from the sea water by an organic glue. These observations are similar to those made for *Myocahama anomioides* STUTCHBURY, 1830, and *Cleidothaerus albidus* (LAMARCK, 1819), in which the cement appears to be largely organic but with patchy development of spherulites of mineralized cement (HARPER & MORTON, 2000; MORTON & HARPER, 2001). Although the source of the mineral-inducing glue is unclear for oysters, MORTON and HARPER (2001) recognized development of glands in the anterior portion of the right mantle

lobe (no longer present once cementation had ceased), which they suggested supplied the organic glue.

SELECTION PRESSURES

Although NICOL (1978, p. 41) stated that “there is no compelling necessity to become shell cemented,” the frequency with which epifaunal taxa have acquired the habit, and the relative success of some of those groups, argue that there are selective advantages over primitive byssate attachment in certain situations. KAUFFMAN (1969) suggested that the habit was important in establishing a stable life orientation in high-energy wave and current conditions. However, byssate fixation, for example in the Mytilidae, which dominate high-energy rocky shores worldwide (BAYNE, 1976), appears to have a number of advantages in such turbulent conditions in offering a strong, flexible attachment that is readily renewed if severed and allows voluntary movement. By contrast, having selected their attachment site, cementing bivalves must remain immobile throughout life and, if accidentally dislodged, have no capacity to reattach. Perhaps an alternative hypothesis to explain the selective advantage of the cemented habit is required.

As noted earlier, most clades of cementing bivalves originated during the Mesozoic. An attractive alternative hypothesis to explain their evolution may be that it is linked with the increased predation pressure associated with the Mesozoic Marine Revolution (MMR) (VERMEIJ, 1977, 1987). The increased diversity and sophistication of predators during the MMR has been linked to many different responses by bivalves (VERMEIJ, 1987; SKELTON & others, 1990; HARPER & SKELTON, 1993; HARPER & KELLEY, 2012). Of particular interest here is the concomitant decline in byssate taxa and the rise of major cementing groups (SKELTON & others, 1990) at a time when major durophagous groups, such as crustaceans and extra-oral feeding asteroids, were diversifying. Aquarium-based experiments,

which offer the choice of byssally attached and cemented *Mytilus edulis* LINNAEUS, 1758, to extra-oral feeding asteroids and crabs, have shown that these durophagous predators are more successful at preying on the former (HARPER, 1991). Similar experiments using drilling muricid gastropods as the predators showed no such preference (HARPER & SKELTON, 1993). These results suggest that predators that actively manipulate their prey are less successful at tackling those that are firmly attached to a substrate, but that cementation does not hinder those that do not actively manipulate their prey. In this respect, cementation may be seen as part of the extensive repertoire of defensive adaptations shown by bivalves (VERMEIJ, 1978, 1987; HARPER & SKELTON, 1993; HARPER & KELLEY, 2012).

It is likely that the trigger for cementation in the anomalodesmatan *Myochama* STUTCHBURY, 1830, is rather different. This taxon, which apparently evolved from active shallow burrowers, has a preference for cementing to the valves of other live bivalves, most often large, shallow-burrowing taxa, such as *Neotrigonia* COSSMAN, 1912; *Eucrassatella* STEWART, 1930; and *Glycymeris* DA COSTA, 1778. Although the relationship between the *Myochama* and its host is not obligate, HARPER and MORTON (2000) have shown that individuals that attach instead to rock do so at a larger size, perhaps indicating failure to locate a suitable bivalve host.

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