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The oyster enigma variations: a hypothesis of microbial calcification

Geerat J. Vermeij

Abstract.—Oysters, whose inner shell layer contains chambers, vesicles, and sometimes chalky deposits, often have extraordinarily thick shells of large size, prompting the idea that there is something unusual about the process of shell formation in these and similarly structured bivalves with the oyster syndrome. I propose the hypothesis that calcifying microbes, especially sulfate-reducing bacteria growing on organic substrates in fluid-filled shell-wall chambers, are responsible for shell calcification away from the shell-secreting mantle of the host bivalve. Other phenomena, including the formation of cameral deposits in fossil cephalopods, the cementation of molluscs and barnacles to hard substrata, the formation of a calcified intritrix on the shell's exterior, and cementation of objects by gastropods on the shell for camouflage, may also involve calcifying bacteria. Several lines of inquiry are suggested to test these hypotheses.

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Introduction

The British composer Edward Elgar (1857–1934) could have been thinking about the many bizarre, unexplained phenomena that confront scientists when he wrote his *Enigma Variations*. In the realm of evolutionary biology, these phenomena often represent extreme variations on familiar themes that we claim to understand. Extremes can be thought of either as the inevitable endpoints of a statistical distribution or as the outcomes of unusual circumstances or processes. Our interpretation of extremes represents a tension between description and explanation, between what makes something possible and what propels it into existence.

Among shell-bearing animals, one of those enigmatic extremes is the vast size and thickness of the shell of bivalves exhibiting what I call the oyster syndrome, the condition in which the inner layer of the shell contains chambers, vesicles, and secondary mineral precipitates referred to as chalky deposits or mocret (Malchus 1990). Oysters exceeding a shell height of 130 cm and a valve thickness of up to 10 cm are known from shallow-water marine settings in many locations from the Late Cretaceous (Cenomanian) onward (Stephenson 1952; Sohl and Kauffman 1964;

Chinzei 1986, 2013; Kirby 2001; Titschack et al. 2010).

The only bivalves rivaling oyster-like species in valve thickness are some taxa known or inferred to harbor photosymbionts (fossil megalodontids, alatoconchids, some Jurassic pinnids, an Eocene cardiid, and living tridacnine giant clams) as well as cool-temperate Permian bivalves of the Australian genera *Eurydesma* and *Myonia* (Runnegar 1979; Vermeij 2013). Very large bivalves (length 200 mm or more) with chemosymbionts (some solemyids, bathymodioline mytilids, vesicomysids, Cretaceous myoconchids, and fossil Cenozoic lucinids) have thin to moderately thick shells (maximum thickness 28 mm in a Late Cretaceous species of the myoconchid *Capsiconcha* [see Kelly et al. 2000]). The same applies to very large bivalves that are known or presumed to lack symbionts, including some living mytilids, pectinids, deep-sea limids, pteriid pearl oysters, fossil Bakevelliidae and Isognomonidae, living pinnids, placunids, and deep-burrowing mactrids, hiattellids, and pholadomyids. In photosymbiotic bivalves, great valve thickness may be enabled by a positive feedback between calcification in the host and photosynthesis by the guests. An explanation for exceptional thickness in bivalves with the oyster syndrome must therefore focus on shell

calcification rather than on the production of nonskeletal biomass.

Given that thick-shelled oysters are known from open marine environments (Kirby 2001) as well as from dark unproductive caves and deep-water rock walls (Hayami and Kase 1992; Wisshak et al. 2009), the oyster syndrome requires an explanation that does not depend on the presence of photosymbionts. Moreover, as I shall show below, the oyster enigma and its variations extend to many other calcification-related phenomena as well. An understanding of this enigma is therefore of great interest in view of biomineralization processes in general and of the unparalleled rate of acidification (which interferes with calcification) in today's ocean waters in particular (Kump et al. 2009; Zeebe 2012).

An understanding of any evolutionary enigma requires two complementary approaches. One is an investigation of the potential benefits of the phenomenon in question. This approach in turn entails the identification of selective agents or agencies and knowledge of how they work to produce the purported benefits. Complementing this line of inquiry is an explanation of how the selected trait or benefit comes about phylogenetically, developmentally, physiologically, and mechanically. Without ignoring the first of these approaches, I emphasize the second, with the aim of proposing a hypothesis about how the unusual thickness and pattern of calcification in bivalves with the oyster syndrome are achieved.

In this speculative paper, I briefly review the morphological peculiarities, phylogenetic and geological distribution, and dimensions of bivalves with the oyster syndrome. I then develop the hypothesis, first suggested but not elaborated on by Chinzei and Seilacher (1993), that microbes housed inside the valves enhance calcification and make great size and valve thickness possible. Specifically, I argue that sulfate-reducing bacteria, known to be involved in calcification in other contexts, are the responsible agents. I speculate that microbial assistance in skeleton formation and cementation is widespread among sedentary animals with calcareous hard parts. I propose further work to test these ideas, and highlight

other outstanding issues related to the geological history of calcification. The aim of this unabashedly exploratory exercise is to awaken interest by microbiologists in evolutionary problems of great environmental importance and not to test the hypothesis rigorously.

Materials and Methods

In order to document valve sizes and thicknesses of bivalves with and without the oyster syndrome, I measured valve lengths (longest linear dimensions) and thicknesses of thick-shelled Late Cretaceous to Recent bivalves at the Florida Museum of Natural History (abbreviated UF), and complemented these measurements with data from the taxonomic literature and my own collections. Particular attention was focused on oysters (Ostreoidea), Spondylidae, Malleidae, Arcidae, Chamidae, and Veneridae. For each species and site, I selected the individual with the thickest valve. In addition, I surveyed Miocene to Recent regional bivalve faunas based on the taxonomic literature and my collections in order to ascertain where and when bivalves with the oyster syndrome were the thickest-shelled species in the assemblage. Taxonomic assignments for Cenozoic and living oysters follow Harry (1985) and Bolton and Portell (2013).

The Oyster Syndrome

I define the oyster syndrome as the condition in which the shell is porous and lightweight thanks to the presence of vacuoles, chambers, vesicles, and sometimes chalky deposits (or mocket) in the inner layer of the shell wall. This condition is best exemplified by Late Triassic to Recent oysters (Ostreoidea) (Harry 1985; Chinzei 1986, 1995, 2013; Malchus 1990; Chinzei and Seilacher 1993; Carriker 1996; Hautmann 2001; Kirby 2001).

In oysters that have them, chalky deposits may represent cases of calcification not directly controlled by the inner mantle surface. Chalky deposits in the living oyster *Crassostrea virginica* consist of bladelike structures oriented perpendicular to the inner shell surface, where the blades are separated by spaces. These deposits form in extrapallial fluid, whose composition in the pores between the

blades may differ from that of the extrapallial fluid situated between the mantle surface and the foliated calcite laid down over most of the rest of the inner surface of the valves (Carriker 1996: pp. 137–140). Although their mode of formation remains controversial (Carriker 1996), the contrast between the inner shell layer of foliated calcite and deposits of chalky material may indicate remote calcification of the latter, that is, biomineralization not strongly controlled by either the mantle edge or the inner mantle surface (Chinzei and Seilacher 1993; Chinzei 2013). Cyclical (usually seasonal) fluctuations in stable isotope ratios in the shell indicate that gigantic thick-shelled oysters grow substantially faster in both height and valve thickness than smaller, thinner-shelled oysters with smaller chambers and fewer chalky deposits (Kirby et al. 1998; Kirby 2000, 2001; Kirby and Jackson 2004). The porous condition and remote calcification typical of very large oysters are therefore associated with rapid mineralization, especially in valve thickness.

This shell structure characterizes many oysters of Late Triassic and younger ages. The earliest ostreoids, belonging to the genus *Umbrostreia*, lacked chambers; but by the Late Triassic, *Actinostreon* developed chambers (Hautmann 2001). Members of the ostreid subfamily Lophinae in the broad sense (Late Triassic to Recent), to which *Actinostreon* belongs, are characterized by a chambered shell, as are the Early Jurassic to Late Cretaceous Exogyrinae (Malchus and Aberhan 1998). The Jurassic to Recent Ostreinae and Crassostreinae developed chalky deposits in addition to chambers (Chinzei 1995), whereas the Pycnodontinae (family Gryphaeidae) have a vesicular, honeycombed shell structure (see also Chinzei 1986, 2013; Malchus 1990; Chinzei and Seilacher 1993; Hayami and Kase 1992).

Although chambers and chalky deposits are particularly characteristic of oysters, in which these features evolved multiple times, they also occur in other bivalves. These groups include Early Cretaceous (Barremian) to Late Cretaceous (Maastrichtian) rudists (superfamily Radiolitoidea), which are phylogenetically derived from megalodontids (MacGillivray

1937; Skelton 1976; Gili et al. 1995; Seilacher 1998; Skelton and Smith 2000; Fenerci-Masse et al. 2006); some Late Cretaceous to Recent malleids in the clade Pterioidea, including *Euphenax* and large species of *Malleus* (Savazzi 2001); some large species of *Spondylus* in the pectinoidean family Spondylidae (J. G. Carter personal communication by e-mail April 2012); species in the Lithiotidae (cemented pterioideans of the Early Jurassic) (Chinzei 1982); and the large African freshwater cemented oyster-like *Etheria elliptica* (Van Bocxlaer and Van Damme 2009).

With the exception of malleids, which are byssally attached, bivalves with the oyster syndrome have one of the valves cemented with calcium carbonate to a hard object. However, most cemented molluscs do not develop the oyster syndrome. These comprise representatives of at least 20 clades within Bivalvia including gryphaeine oysters, and five clades of Gastropoda (see Burchette and Riding 1977; Savazzi 1996). Among the three clades of cemented brachiopods, only some bioherm-forming productides exhibit the oyster syndrome, possessing tabulae in the pedicle (lower) valve (Rudwick and Cowen 1967).

Chinzei (2013) suggested that the lightweight shells of bivalves with the oyster syndrome are well adapted to life on soft substrates. Although the specific gravity of these shells is indeed less than that of mud (Chinzei 2013), and many oysters and lithiotids live and often aggregate on muddy bottoms, many other taxa with extensive vesicular structure or chalky deposits, such as lightweight pycnodontine gryphaeid oysters, characteristically occupy hard surfaces. The oyster syndrome may predispose many bivalves to live freely as adults on sand or mud, but it is unlikely to be a primary adaptation to that mode of life.

In the modern fauna, the oyster syndrome occurs only in species lacking photosymbionts, but in the geological past several bivalves with chambers in the shell wall may have been photosymbiotic. These include lithiotids, and above all rudists. Vesicular structure of the inner shell layer is particularly characteristic of the rudist family Radiolitidae,

which acquired it in the late Barremian (Cobban et al. 1991; Laviano and Skelton 1992; Seilacher 1998; Fenerci-Masse et al. 2006). As emphasized by Seilacher (1998), the vesicular structure differs from the pore-and-canal system of many other rudists, which likely housed extensions of the mantle, facilitating exchange of nutrients between photosymbionts and the host. Modern photosymbiotic bivalves are not cemented to the substrate and have a compact shell microstructure, but there is no fundamental incompatibility between a porous shell structure and the presence of photosymbionts. In fact, these conditions might well complement one another in large bivalves living in well-lit yet relatively productive waters, environments suggested for many rudists and lithiotids (Gili et al. 1995; Posenato and Masetti 2012; Vermeij 2013). Richthofeniacean brachiopods, which likely were photosymbiotic (Cowen 1970, 1983), also combined this habit with the oyster syndrome.

Chambers, vesicles, and chalky deposits in the inner shell layer are not to be confused with shell pores that extend through the shell and that contain extensions of the mantle, nor with a subdivided or septate inner shell cavity. Pores characterize punctate brachiopods (Cowen 1966; Peck et al. 1986; Peck 1992), many bivalves (the living cardiid *Cardium*, cyrenoideans, arcoideans, and *Archiheterodonta*) (Kennedy et al. 1970; Waller 1980; Morton 1982; Araujo et al. 1994; Isaji 1995; Savazzi and Sälgeback 2004; Malchus 2010). They also occur in some gastropods (Fissurelloidea, Neomphaloidea, and Phenacolepadidae) (Sasaki et al. 2003, 2008; Kiel 2004; Hesz et al. 2008) and, as aesthete canal systems, in the plates of polyplacophorans (Fernandez et al. 2007) and the sclerites of halkieriids (Vinther 2009). A shell cavity secondarily divided by septa or tabulae is known in putatively photosymbiotic Paleozoic productide brachiopods (Rudwick and Cowen 1967, reviewed in Vermeij 2013) as well as in three groups of bivalves (Permian alatoconchids, Late Triassic wallowaconchids, and Late Cretaceous hipuritid rudists) that likely also harbored photosymbionts (reviewed in Vermeij 2013). Septa characterize all shell-bearing cephalo-

pods, and evolved at least seven times in gastropods (Paleozoic euomphalids and macuritids, the Miocene to Recent turritellid *Vermicularia*, late Cretaceous to Recent vermetids, Eocene to Recent dendropomatids, the Miocene hipponicid *Rothpletzia*, and the Miocene Indonesian melongenid *Melongena murifacta*) (Yochelson 1971; Vokes 1982; Savazzi 1996; Wagner 1999; Vermeij and Raven 2009). Among all the groups mentioned here, only rudists and perhaps some productides exhibit the oyster syndrome.

Valve Thickness

Massively thick bivalves, defined here as those in which at least one valve is 5 cm or more thick, are recorded in Table 1. Additional species certainly exist, including the early Miocene to Pliocene *Crassostrea gryphoides* from southern Europe and the Indian Ocean (Kirby 2001), but I was unable to find measurements of valve thickness. Runnegar (1979) reported shell thicknesses of 58 mm in the umbonally weighted epifaunal pteriodean *Eurydesma cordatum* (length up to 16 cm) and 55 mm for the anteriorly thickened infaunal megadesmid anomalodesmatan *Myonia corrugatum* (length about 15 cm), both from the Permian of cool-temperate eastern Australia. Neither of these bivalves is known to have exhibited the oyster syndrome or to have harbored photosymbionts.

Almost all massively thick bivalves exhibit the oyster syndrome. In the Cenozoic, the only exception is the living *Spondylus varius*, although this species may yet prove to possess chambers or chalky deposits in its umbonal area. The thickest non-photosymbiotic bivalves with a compact microstructure I have seen in the tropical Indo-West Pacific, western Atlantic, and eastern Pacific are, respectively, a specimen of *Chama limbula* from Aitutaki, Cook Islands (UF 286503, length 120 mm, thickness 45 mm); the venerid *Mercenaria campechiensis* from the west coast of Florida (UF collection, length 170 mm, thickness 24.6 mm); and the arcid *Grandiarca grandis* from Panama (Vermeij collection, length 113 mm, thickness 19 mm).

As shown in Table 1, exceptionally thick-shelled bivalves with the oyster syndrome

TABLE 1. Cretaceous and Cenozoic bivalves (other than rudists) with valve thicknesses of 5 cm or more.

Age and species	Formation or site	Length (mm)	Thickness (mm)	Source
Campanian				
<i>Crassostrea cusseta</i>	Blufftown Fm., Georgia	42.0	79.0	Sohl and Kauffman 1964
Maastrichtian				
<i>Arctostrea aguilerae</i>	Gulf Coast and Caribbean	352	71	Sohl and Kauffman 1964
Late Eocene				
<i>Hyothisa podagrina</i>	Ocala Limestone, Florida	207	51	UF 17973
<i>Striostrea gigantissima</i>	Shell Bluff, Georgia	400	56	Howe 1937
Late Oligocene				
<i>S. gigantissima</i>	Upper Chickasawhay Fm., Alabama	244	60	UF 127788
<i>Crenostrea segurai</i>	Costa Rica	195	70	Woodring 1976
<i>Flemingostreini</i> sp.	Te Kuiti Group, New Zealand	300	50	Nelson et al. 1983
Early Miocene				
<i>S. gigantissima</i>	Belgrade Fm., North Carolina	500	70	Lawrence 1995
<i>Hyothisa</i> sp.	Bruce Creek Limestone, Florida	144	54.8	UF 112096
<i>Crassostrea hatcheri</i>	Monte León Fm., Argentina	250	60	Parras and Casadío 2006
<i>C. gravitesta</i>	Japan	300	50	Hayasaka 1960
Miocene				
<i>Crassostrea</i> sp.	Calcutta, India	405	60	Newton and Smith 1912
Late Miocene				
<i>Crassostrea titan</i>	Santa Margarita Fm., California	384	87	Kirby 2001
<i>C. cahobasensis</i>	San Gregorio Fm., Venezuela	320	86	UF (uncataloged)
Pliocene				
" <i>Ostrea</i> " <i>turbinata</i>	Zanzibar	150	60	Cox 1927
<i>Crassostrea</i> (or <i>Striostrea</i>) sp.	Caracasbaai, Curaçao	330	58	UF 114700
<i>Hyothisa meridionalis</i>	Pinecrest Bed 10, Sarasota, Florida	194	72	UF 22272
Recent				
<i>Hyothisa hyotis</i>	Moorea	175	56	Vermeij collection
<i>H. hyotis</i>	Red Sea, Egypt	229	100	Zuschin and Baal 2007
<i>H. hyotis</i>	Comoro Islands	240	60	UF 320031
<i>Striostrea iridescens</i>	Mazatlán, Mexico	199	50	UF 343219
<i>Spondylus varius</i>	Papua New Guinea	247	54	UF 424965

occur only in the tropical Indo-West Pacific and Eastern Pacific. During the Miocene and Pliocene, by contrast, they were widespread in the tropical Atlantic as well. Thick-shelled Atlantic species either became extinct or evolved thinner shells (Kirby 2001; Kirby and Jackson 2004). The thickest post-Early Pleistocene oyster I have seen from the Atlantic is a 234-mm-long specimen of *Crassostrea virginica* (UF 15483, thickness 25.2 mm) from a shell mound at Philippi Hammock, Pinellas County, Florida. In the living fauna of Florida, the only species with a thicker shell is *Spondylus americanus* (UF 23890, length 260 mm, thickness 37 mm). I have surveyed Recent and fossil Cenozoic regional faunas based on the taxonomic literature and my own collections in order to assess where bivalves with the oyster syndrome rank in terms of absolute valve thickness. Bivalves with the chambers and chalky deposits diagnostic of

the oyster syndrome are the thickest-shelled species in all 13 late Oligocene to early Pleistocene faunas studied and in 14 of 19 Recent faunas. The exceptions in the Recent are either island faunas (Easter Island) or regions where thick-shelled oysters became extinct during or before the early Pleistocene (California, southern South America, southeastern United States, Caribbean).

Given these unusual attributes and the fact that the chambered, lightweight shell has evolved convergently in at least six bivalve clades collectively ranging from the Late Triassic to the Recent, mechanisms for enhancing normal shell calcification should be considered. Just as photosymbionts are associated in many clades with rapid calcification and thick shells, other agents that do not necessarily require exposure to light may also be involved. This possibility is explored in the next section.

Microbial Calcification

It has long been recognized that most of Earth's carbonate deposits are of biogenic origin (Knoll et al. 1993; McConnaughey 1994; Riding 2000; Wright and Oren 2005; Kahle 2007; Pomar and Hallock 2008).

Photosynthesizing cyanobacteria and partnerships between photosymbionts and sedentary animals such as corals have been considered the primary culprits (McConnaughey 1994; McConnaughey and Whelan 1997). By providing a source of protons (H^+), photosynthesizers lower the activation energy for precipitating calcium carbonate even in waters supersaturated with Ca_{2+} and CO_3^{2-} ions. McConnaughey (2012) has further suggested that toxins released by *Symbiodinium*, the photo symbiont of corals and many other photosymbiotic animals, opens calcium channels in the host and therefore promotes precipitation of $CaCO_3$.

However, much biogenic calcification takes place away from the light in environments where photosynthesis is unlikely (Wright and Oren 2005). Archaea are responsible for the formation of carbonate minerals in methane-seep environments (Peckmann et al. 1999; Peckmann and Goedert 2005; Stadnitskaia et al. 2005). Sulfate-reducing bacteria, comprising a diverse assemblage representing many clades and various biochemical pathways, abet dolomitization under anoxic hypersaline conditions (Vasconcelos and McKenzie 1997). Depending on which organic substrate they use, sulfate-reducers may create alkaline conditions (high concentrations of dissolved inorganic carbon) favorable for the precipitation of calcium carbonate (Gallagher et al. 2012) in a process analogous to diagenetic sulfate reduction in sediments where organic carbonates are precipitated (Schrag et al. 2013; Canfield and Kump 2013). Although Meister (2013) has suggested that the (acidic) hydrogen ions released by sulfate reduction counteract the rise in alkalinity, thus potentially preventing precipitation of carbonate minerals, experiments on and models of microbial mineral formation indicate that sulfate-reducers, perhaps together with bacteria using other biochemical pathways, can precipitate carbon-

ate minerals including calcium carbonate (Visscher et al. 2000; Visscher and Stolz 2005; Bergmann et al. 2013).

Sulfate-reducing bacteria may be responsible for 50% to as much as 80% of the carbon oxidized in marine sediments, and up to half of this can precipitate as calcium carbonate even under oxygenated conditions (Visscher et al. 2000; Pomar and Hallock 2008; Halevy et al. 2012). This implies that sulfate is abundant in seawater and that sulfate-reducing bacteria are ubiquitous in marine environments (Bernier and Raiswell 1983). Although the concentration of sulfate in seawater has varied over geological time, being especially low in the Aptian (Early Cretaceous) and the Mesozoic generally, the combination of extensive weathering of evaporites on land and climatic cooling ensures that sulfate concentrations have been high in the Cenozoic since at least the early Eocene (Halevy et al. 2012; Wortmann and Paytan 2012). Given that calcification has been under the control of living organisms throughout the Phanerozoic (Knoll et al. 1993), a dominant role for microbes in calcification in situations beyond the direct influence of calcifying multicellular life is far more likely than precipitation by purely inorganic processes even under conditions of supersaturation of calcium carbonate. The minerals in the microbial-mat communities represented by stromatolites in oligotrophic waters of the Bahamas precipitate by complex interactions involving many bacterial agents (Visscher et al. 2000; Paerl et al. 2001; Visscher and Stolz 2005). The microbial calcification that has characterized reef construction throughout the Phanerozoic (Webb 1996; Pomar and Hallock 2008) is due to many players (Visscher and Stolz 2005). All these cases of microbially induced calcification occur in sediments, on and in microbial mats, and in other situations that are not intimately associated with multicellular organisms.

An association between skeleton-bearing animals and calcifying microbes without the aid of photosynthesis was first suggested for oysters by Chinzei and Seilacher (1993), and was later proposed for bryozoans (Morris and Soule 2004), sponges (Jackson et al. 2010), and somewhat obliquely for a Paleozoic tabulate

coral (Seilacher 2005). In the shallow-burrowing venerid bivalves *Granicorium* and *Samarangia*, a thick layer of sand that is cemented into a “concrete overcoat” with calcium carbonate forms on the outer surface of the shell, where copious mucus secreted by the middle mantle lobe harbors a microbial biofilm community that creates nucleation sites for crystal formation and growth (Taylor et al. 1999; Braithwaite et al. 2000). The calcifying culprits were not identified in any of these cases. The most compelling example described to date is that between sponges of the genus *Hemimycale* and calcibacteria (cocoid alpha-proteobacteria) that live within specialized sponge cells (calcibacteriocytes) near the surface of the host and that contribute up to 60% of the dry weight of some individual sponges (Uriz et al. 2012). This is clearly a mutualistic association, which appears to be more specialized than the cases of remote calcification that are the subject of this paper.

The Shell As Microbial Incubator

The hypothesis I propose here is that calcification in parts of the inner layer of some molluscan shells occurs in the absence or reduced control of the mantle’s epithelial cells that are involved in normal shell deposition. I suggest further that this remote calcification is enhanced by carbonate-precipitating microbes, especially sulfate-reducing bacteria, which colonize and occupy spaces filled with a mixture of extrapallial fluid and seawater, both of which are rich in sulfate. This complementary mineralization benefits the shell-secreting host in competition or defense. If microbial calcification occurs and if it is adaptive to the host, the bacteria must be incubated or housed in specific parts of the shell where carbonate precipitation by them would be most effective and least intrusive in enlarging or thickening the skeleton. The porous structure of bivalves exhibiting the oyster syndrome would therefore seem ideal to house microbes engaged in remote calcification that benefits the host.

Bacteria that reduce sulfate and oxidize carbon are the most likely agents of remote

calcification in molluscs, although those using other pathways may also contribute. As noted in the preceding section, sulfate is abundant in seawater and sediments, and sulfate-reducing bacteria likewise are ubiquitous. Along with seawater, these bacteria would almost inevitably enter extrapallial fluid and potentially colonize fluid-filled spaces within the shell or between the shell and the mantle. The effect of these microbes as remote calcifiers would be greatest when bacterial metabolism causes fluids trapped in enclosed spaces to become more alkaline and when organic substrates such as mucus or the conchiolin sheets produced by the host’s mantle are abundant and accessible. Shells with a high organic content would be the best candidates for housing microbes engaged in remote calcification.

Previous work on calcification in oysters (reviewed by Carriker [1996]) has not considered the possibility of microbial participation, but does not rule it out either. For example, of 259 proteins recovered from oyster shells, at least 61 are associated with exosomes containing extrapallial calcite crystals (Zhang et al., 2012). Although exosomes are vesicles that originate in cells of the oyster, the possibility that they are colonized by calcifying bacteria should be investigated.

The proposed association between mineralizing bacteria and bivalves with the oyster syndrome or with burrowing venerids exhibiting “concrete overcoats” would be much less intimate than that between calcibacteria and sponges, because the bivalves’ bacteria are housed in fluid-filled cavities within the exoskeleton outside the hosts’ tissues, whereas the calcibacteria reside within specialized host cells. Nevertheless, the phylogenetically derived shell microstructure that appears to enable remote calcification in vesicular bivalves, perhaps together with particularly favorable organic substrates, implies some degree of adaptive accommodation by both hosts and guests, as well as a substantial advantage to the hosts in attracting and housing calcifying microbes.

These advantages include a demonstrated protection against shell-drilling predatory gastropods (Kirby 2001; Chattopadhyay and

Dutta 2013) and bioeroders (Fenerci-Masse et al. 2006) as well as faster growth (Kirby 2000, 2001; Kirby and Jackson 2004, Chinzei 2013) and a strong tendency for the bivalves to grow upward into the waters above. In the case of predation, half the drill holes in the Miocene *Crassostrea titan* from California (Kirby 2001) and "*C. gigensis*" (*C. gingensis*, a synonym of *C. gryphoides*) from India (Chattopadhyay and Dutta 2013) are incomplete, indicating that the very thick shell afforded effective protection against drilling gastropods. Kirby (2001) inferred the culprits to be muricids, likely members of the genus *Forreria*, whereas Chattopadhyay and Dutta (2013) suggested naticids as predators on the basis of the characteristically parabolic shape of the drill holes. I suspect muricids were involved in this case as well. Many bivalves with the oyster syndrome, including various living and fossil oysters as well as lithiotids, rudists, and *Malleus*, show rapid upward growth above muddy sediments. This mode of growth enables the bivalves to feed well above the boundary layer near the surface of the sediment, and could provide a competitive advantage over organisms functioning at a lower tier. The low-density microstructure characteristic of the oyster syndrome (Chinzei 2013) makes this mode of life possible, although it must be noted that similarly rapid upward growth away from the boundary layer at the seafloor characterizes pinnids (pen shells) and some modioline mytilid mussels, which do not exhibit the oyster syndrome. As pointed out in the introduction, these potential benefits refer to the function rather than to the mechanism of formation of structures associated with oyster-like bivalves. They provide a complementary, not an alternative, explanation for the lightweight, thick-shelled construction of these peculiar clams.

Tests

Experimental approaches and the genomic identification of microbes will be necessary to test the hypothesis that shell calcification is enhanced by in-house sulfate-reducing bacteria. The first step would be to sample the chambers, extrapallial fluids, and chalky

deposits of bivalves with the oyster syndrome for the presence of these bacteria and to assess whether the chemical microenvironment—alkalinity and the presence of organic substrates—is especially conducive to calcification by these microbes. Manipulative experiments in which ambient fluid in the chambers is replaced with sterilized seawater of the same pH are needed to establish that calcifying agents indeed contribute to crystal formation and growth. Artificial chambers can be created in shells with a compact microstructure, some with and others without an inoculation of sulfate-reducing bacteria. If these preliminary tests confirm the hypothesis, additional work should probe the nature of the association between bacteria and their bivalve hosts, especially whether particular bacterial strains are specialized to specific host species. The relation between calcification orchestrated at the mantle margin by the host bivalve and that due to microbes also needs to be clarified. For example, if mucus produced at the mantle edge indeed promotes the growth of biofilms associated with calcification on the shell exterior of some venerids (Taylor et al. 1999; Braithwaite et al. 2000), mucus can be added to the shell margins of some bivalves and removed from others. A microbial examination of fresh and aged mantle-derived mucus would provide further clues about the presence of calcifying bacteria.

It would also be useful to examine the stable isotope composition of carbon and sulfur in shells. Carbonate of bacterial origin should be relatively enriched in the light isotope of carbon.

Broader Implications

Given the ubiquity of sulfate and of sulfate-reducing bacteria in seawater, the question arises why remote calcification is not more widespread. The answer could be, of course, that bacterially mediated calcification in meta-zoan mineralization is far more common than is currently recognized, especially in enclosed spaces filled with organically enriched fluid. In order to investigate these important matters, broad surveys of the distribution and activity of calcifying bacteria in and around

metazoans should be carried out, and the sensitivity of these bacteria to changes in ocean chemistry deserves urgent attention. In particular, it would be important to know whether calcification that is under effective control by metazoans is affected differently by decreasing ocean-water pH than is calcification due to sulfate-reducing and other non-photosynthesizing microbes.

I suspect that microbes will prove to be important in many contexts in addition to those already discussed. Here I briefly highlight five such potential situations.

Many gastropods and bivalves possess an outer calcareous shell layer (intritralx), which forms in association with the organic periostracum (D'Attilio and Radwin 1971), implying at least some control by the shell-secreting mantle (Glover and Taylor 2010). Often white, this layer in many gastropods and in mytilid bivalves may have a sculpture different from that of the underlying calcified layers of the shell. Intritralx has evolved multiple times. Among gastropods it has been reported in some muricids, bursids, epitoniids, liotiids, and liotipomatine colloiids (D'Attilio and Radwin 1971; Kilburn 1985; McLean 2012). In bivalves, continuous calcareous deposits occur on endolithic mytilids (Yonge 1955; Barthel 1982; Owada 2007; Valentich Scott and Tongcherd 2008). Cemented calcareous needles, granules, and spines originating in a thick layer of mucus in or on the periostracum are known in venerids (Taylor et al. 1999; Braithwaite et al. 2000; Glover and Taylor 2010), the lucinid *Lucina* (Taylor et al. 2004), some astartids (Salas et al. 2012), cardiids (Schneider and Carter 2001), anomalodesmatans (Checa and Harper 2010), and palaeoheterodonts including the freshwater Unionoida (Zieritz et al. 2011). Insofar as the formation of these features involves extrapallial calcification, the role of calcifying bacteria should be considered.

Other cases of remote calcification in bivalves may also be influenced by microbes. Checa (2000) has described aragonitic prisms laid down on divaricate ribs in spaces between the periostracum and the underlying

calcareous shell where extrapallial fluid still remains.

Remote calcification with its implied microbial component may account for the formation of cameral and siphuncular deposits in straight-shelled Paleozoic nautiloid cephalopods. As described by Fischer and Teichert (1969), these structures likely precipitate from cameral fluid in parts of the shell set off by septa from the body chamber.

The same potential exists for cementation of the shell to the substrate. Cementation, which effectively protects individuals from many kinds of predators (Harper 1991), is known in craniiform, productide, and thecidiine brachiopods, as well as in gastropods and bivalves (see above). Among barnacles (Cirripedia), the primitive means of attachment by an organic membrane is replaced in more derived balanomorphs by cementation (Newman 1987; Pitombo 2004). Harper (1997) found that cementation of oysters occurs between the lower valve and the substrate, and suspected that it involves crystallization of cement from trapped fluid saturated with calcium carbonate. The process is aided by the secretion of organic compounds that act as nucleating surfaces on which crystals with random orientation can form (MacDonald et al. 2010). The remote calcification implied by these findings may well be made possible or be enhanced by calcifying bacteria.

A category of special interest is the agglutination of foreign objects—shells, pieces of coral rubble, and sand grains—to the shell exterior of relatively immobile gastropods. This habit, known from the Ordovician onward (in the euomphaloidean genus *Lytospira*), is thought to camouflage individuals, and has evolved independently in Silurian and Devonian euomphaloideans (*Straparollus*, *Serpulospira*, *Devonicornu*, pseudophorids), Late Cretaceous to Recent Xenophoridae (carrier shells), early Oligocene to Recent scaliolids, the Miocene modolid *Psammmodulus*, and the late Miocene to Pliocene turritellid *Springvaleia* (Woodring 1958; Linsley and Yochelson 1973; El-Nakhal and Bandel 1991; Frýda 1998; Feinstein and Cairns 1998; Wagner 2002). Linsley and Yochelson (1973) observed that *Xenophora neozelanica* brings bivalve shells and

pieces of rubble to the surface of its shell with the foot, and then begins the process of cementation by involving the mantle. It is possible that, just as in the cementation of bivalves and other shell-bearing animals to the substrate, remote calcification not involving the mantle complements the cementation of the camouflaging objects to the host shell.

Conclusions

In this paper I propose the hypothesis that microbes, especially sulfate-reducing bacteria, enhance calcification within the shells of oyster-like bivalves, whose chambered shell walls appear specialized to house the bacteria in fluid-filled spaces. Although obviously speculative, this hypothesis draws attention to other manifestations of remote calcification that may likewise involve microbes. It also focuses attention on some key intervals of Earth history when exceptional calcification seems to have been particularly common and widespread, including (but not limited to) the Late Cretaceous, late Eocene, late Oligocene to Miocene, and early Pliocene. Some of these intervals coincide with times of moderate to high levels of carbon dioxide in the atmosphere and ocean. Unexplained phenomena such as great shell thickness in oyster-like bivalves deserve scrutiny if we are to improve our understanding of calcification, a process that has profoundly influenced evolution and the chemistry of the biosphere.

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