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The function and evolution of lateral asymmetry in boring endolithic bivalves

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Abstract. A substantial lateral asymmetry of the shell is observed in the bivalve genera *Claudiconcha* (Petricolidae), *Jouannetia* (Pholadidae), *Clavagella* and *Bryopa* (Clavagellidae) that bore in rock or mineralised biogenic substrates. Two general adaptive patterns emerge from this study. (1) Lateral asymmetry is associated with cementation of one valve to the substrate, or is otherwise functional in preventing one valve from moving within the borehole, and (2) it is associated with determinate shell growth and appears only in the adult stage. The only important exception to the latter pattern is *Bryopa*, which secondarily lost the determinate growth pattern originally present in clavagellids. These features have evolved independently in each family, and differ in several constructional and functional respects among families.

Key words: Mollusca, Bivalvia, endolithic, lateral asymmetry, functional morphology

Introduction

Typical bivalve shells are bilaterally symmetric, with the exception of small-scale characters. The latter include hinge teeth, which must fit within sockets of the opposite valve, and denticulations of the commissural margin, which interlock with corresponding notches on the commissure of the opposite valve. The lateral asymmetry of these characters is justified by simple functional constraints.

Representatives of several bivalve families possess shells that deviate more conspicuously from lateral symmetry. These include tellinids and comparable forms that burrow with the commissure plane horizontal or inclined and as a result have evolved a bent commissure plane, forms cemented to the substrate by one of the valves, like oysters, spondylids and chamids, and byssate or reclining bivalves that likewise always rest with the same valve in contact with the substrate. Cemented rudists, in which one valve often is reduced to an operculum-like plate closing the aperture of a large, conical opposite valve, are extreme examples of this type of asymmetry. Further examples include a few pteriomorph and ostreid mud stickers in which one valve became reduced to an extremely thin, flexible structure (Chinzei, 1982, 1986; Chinzei *et al.*, 1982; Savazzi, 1996), bivalves with twisted commissure planes (McGhee, 1978; Tevesz and Carter, 1979; Savazzi, 1981, 1984a, 1984b, 1989) and the Corbulidae, in which one valve is smaller and its margin closes onto a conchiolin layer sandwiched between two calcareous layers of the opposite valve (Lewy and Samtleben, 1979).

Functional and constructional reasons can be invoked to explain most of these examples of valve asymmetry, although the adaptive significance of a few instances (e.g., the commissural asymmetry and sculpture asymmetry of the arcid *Scapharca*; see Savazzi, 1982c, and references therein) remains unclear. On the other hand, as a general rule-of-thumb, it can be stated that bilateral symmetry of the shell normally is associated with a non-cemented life style and a life orientation in which the commissure plane is approximately perpendicular to the surface of the substrate. The above rule applies also to boring bivalves (i.e., bivalves that actively excavate a permanent cavity in solid substrates).

As discussed below, the large majority of boring bivalves possess bilaterally symmetrical shells, and several adaptive justifications can be formulated for this preference. This is true also of the large majority of taxa within the families Petricolidae and Pholadidae. However, one genus within each of these families has secondarily evolved a substantial amount of bilateral asymmetry. Within the family Clavagellidae, a whole lineage consisting of several genera (see below) displays a lateral asymmetry of the shell and associated structures. This paper studies these instances of bilateral asymmetry in boring bivalves, the adaptive significance of this feature in the context of their life histories, and the possible evolutionary pathways leading to lateral asymmetry in these forms.

General characters of boring bivalves

Two boring mechanisms exist in bivalves. Chemical boring involves the secretion of substances to dissolve the substrate, and is restricted to calcareous substrates, including biogenic and nonbiogenic ones, as well as carbonate-cemented sandstones and siltstones containing non-carbonate grains (Hodgkin, 1962; Kleemann, 1973, 1974, 1980; Carter, 1978; Bolognani Fantin and Bolognani, 1979; Savazzi, 1999; discussions and references therein). Mechanical boring involves abrasion of the substrate by friction of the shell (and/or clasts wedged on the surface of the shell). Mechanical boring takes place in a broad variety of substrates, including calcareous, non-calcareous and metamorphic rocks, wood, bone, concrete, softer metals and plastics (e.g., Boreske *et al.*, 1972; Wilson and Kennedy, 1984; Kelly, 1988; Savazzi, 1999, Jenner *et al.*, 2003, and therein).

In calcareous substrates, both mechanisms are frequently combined, although a few bivalve taxa show a clear predominance of one or the other mechanism (Ansell, 1970; Savazzi, 1999, and therein). Most often, mechanical borers are attached to the substrate by a large and muscular foot or by a strong byssus, which allows the valves to be pressed against the substrate in order to exert friction.

With few exceptions, mostly found in very early or unusual representatives (e.g., Pojeta and Palmer, 1976; Savazzi, 1999), the shells of boring bivalves are elongated in the antero-posterior direction and penetrate the substrate roughly in the anterior direction (Savazzi, 1999, and therein). This minimizes the cross-sectional area of the borehole and maximises its depth (and consequently, the speed with which a suitable depth is reached). Both factors afford a better protection against potential epifaunal predators and other endolithic organisms crowding the substrate. The siphonal opening of the borehole, which is necessary for respiration and filter feeding, constitutes a weak element in this strategy, because it can provide a passage for predators and is vulnerable both to erosion of the substrate and to overgrowth by epifaunal organisms. Most boring bivalves possess adaptations that lessen these risks (e.g., Carter, 1978; Savazzi, 1982a, 1999; Morton, 1993; and therein).

Most boring bivalves, including representatives of either boring mechanism, slowly rotate within their boreholes about the antero-posterior axis of the shell during growth (Savazzi, 1999, and therein). This factor should be expected to favour (1) a bilaterally symmetric shell geometry, (2) a roughly circular cross-section of the shell (allowing for geometric constraints imposed by helical shell growth) and (3) a circular cross-section of the borehole. Point (3) is a simple consequence of rotation of the shell within the substrate. For the same reason, drilled holes, machine parts manufactured on a lathe and pottery turned on a wheel are all round in cross-section. Points (1) and (2) allow shell rotation within the borehole and minimise the ''wasted'' space (i.e., the space not occupied by the organism) within the borehole. It is useful to remember that space within the borehole is expensive to the organism, because it requires a large amount of energy to produce.

Rotation within the borehole is also advantageous to the organism in that it allows all portions of the anterior region of the borehole to be equally accessible to the boring parts. In this way, the structures involved in both mechanical and chemical boring can be located in a region of the organism where they are optimally placed to perform their function. This is the example, for instance, of the teeth and spines located around the pedal gape in the Pholadidae and Teredinidae (Röder, 1977). In these families, the pedal gape is in an antero-ventral, rather than anterior position, because of biomechanical constraints. Thus, each individual rasping action of these structures erodes the substrate in a corresponding oblique direction, rather than in the anterior direction (i.e., the direction of elongation of the shell). Rotation of the shell within the borehole averages the direction of boring over a period of time, resulting in an overall penetration of the substrate along the antero-posterior axis of the shell. A placement of the pedal gape in an anterior position on the shell is precluded by the fact that the foot would attach to the substrate permanently at the bottom of the borehole, and therefore the foot attachment area would not be accessible to the boring structures (a comparable constraint is posed by the permanent byssal attachment of rock-boring Tridacnidae; see Savazzi, 1999). However, the pholadid *Jouannetia* may have evolved adaptations that lessen these restrictions (see below).

Bivalves that rotate within their boreholes include the Gastrochaenidae, Teredinidae, Hiatellidae and most Pholadidae and Lithophaginae (Purchon, 1955; Carter, 1978; Röder, 1977; Savazzi, 1982a, 1999). Bivalves that do not rotate within their boreholes typically produce boreholes with a non-circular cross-section, and include the Tridacnidae, Clavagellidae, mytilids like *Botula*, *Gregariella* and a few species of *Lithophaga*, and the myid *Platyodon* (see Morton, 1980; Savazzi, 1999, and references therein). Several Petricolidae also display this character (Duval, 1963; Ansell, 1970; see also below).

Non-rotating boring bivalves display variable amounts of ecotypic plasticity in their shell geometries. Virtually all can develop at least a small amount of lateral asymmetry of the shell (or, in the Lithophaginae, of the secondary calcareous deposits that cover the posterior region of the shell; pers. obs.) as a result of crowding of the substrate by nearby borers or of encroaching by epifaunal organisms. In this respect, non-rotating boring bivalves are comparable to nestlers, which display a similar (albeit typically higher) ecotypic plasticity in shell shape (Baluk and Radwanski, 1979; Savazzi, 1999, and therein).

Determinate growth in bivalves

Early in this study, it became apparent that virtually all instances of bilateral asymmetry in boring endolithic bivalves are associated with determinate growth of the shell. This ontogenetic process ends with a non-growing, ''adult'' stage, and lateral asymmetry of the shell develops only at the onset of this stage. The term adult is used here in a morphologic sense and not as an implication of sexual maturity, although the two things are associated in at least one of the bivalve species studied herein (see Morton, 1977). Determinate growth is common in gastropods (Vermeij and Signor, 1992; Savazzi *et al.*, in prep., and references therein) and known in other molluscs (e.g., several of the heteromorphic ectocochleate cephalopods, a few scaphopods) but apparently rare in bivalves. There is a possibility that determinate growth may be more frequent in bivalves than presently recognised. However, this growth pattern is likely to pass unnoticed, unless it is accompanied by modifications of the shell that clearly mark the onset of the non-growing stage.

It must be stressed that determinate growth, albeit not associated with lateral shell asymmetry, occurs in some boring bivalves. Examples are the extension of calcareous lining to the anterior region of the borehole in adult Teredinidae (Savazzi, 1999, and therein), and various types of calluses closing the pedal gape of Pholadidae (see below). Among these instances, only the types that are relevant to the subject of this paper are discussed below.

Materials and methods

Living specimens of *Claudiconcha japonica* (Dunker, 1882) (Petricolidae) were collected from outcrops of soft rock in the middle intertidal area of rocky shores near the Marine Station of Tokyo University at Aburatsubo near Misaki, Miura Peninsula, Japan. The substrate ranges from fine sandstone to coarse rudite with calcareous cement and a variable amount of calcareous clasts, as shown by the occurrence of *Lithophaga* sp. (Mytilidae) in the same substrate (albeit typically not mixed with *C. japonica*). *Lithophaga* is a chemical borer found exclusively in calcareous substrates, including calcite-cemented sandstones (Savazzi, 1999, and therein).

Several tens of dead specimens of *Claudiconcha monstrosa* (Gmelin, 1791) and about 20 dead specimens of *Jouannetia cumingii* Sowerby, 1842 (Pholadidae) were collected from coral rubble used to build dry piers in Tayud, on the eastern coast of Cebu Island, the Philippines. This is the material and locality that provided specimens of the clavagellid *Bryopa lata* (Broderip, 1834) studied by Savazzi (2000), which are also discussed below. A few living specimens of *C. monstrosa* were collected from rubble found on the surrounding tidal flats and from dead coral from the coral reef fringing the outer edge of the tidal flats in the same locality. Additional dead specimens of *J. cumingii* were collected from dead coral boulders on intertidal banks 1–2 km NE of Hilotongan Island, E of Mactan Island, the Philippines.

Abundant living and dead specimens of *Claudiconcha monstrosa* were collected from coral rubble and sandstone at several localities along the northern coast of Iriomote Island, Okinawa, Japan. The substrate ranges from relatively soft biogenic calcarenite and calcirudite to dead coral, but *C. monstrosa* is much more common in the latter, harder substrate. Specimens from this area generally are larger than those collected in the Philippines.

Specimens were extracted from the substrate by manually breaking the latter in the field, or by collecting samples of substrate for further processing in the laboratory.

All the above material is in the possession of the author. Additional material relevant to this study was observed in numerous institutional collections. Repositories of material not in the possession of the author are abbreviated as follows in the figure captions. NHM: Natural History Museum, London, UK. NSM: National Science Museum, Tokyo, Japan. UMUT: University Museum, University of Tokyo, Japan.

Observations

Claudiconcha japonica

C. japonica (Fig. 1) is relatively common, albeit patchy in distribution, in the middle intertidal zone.

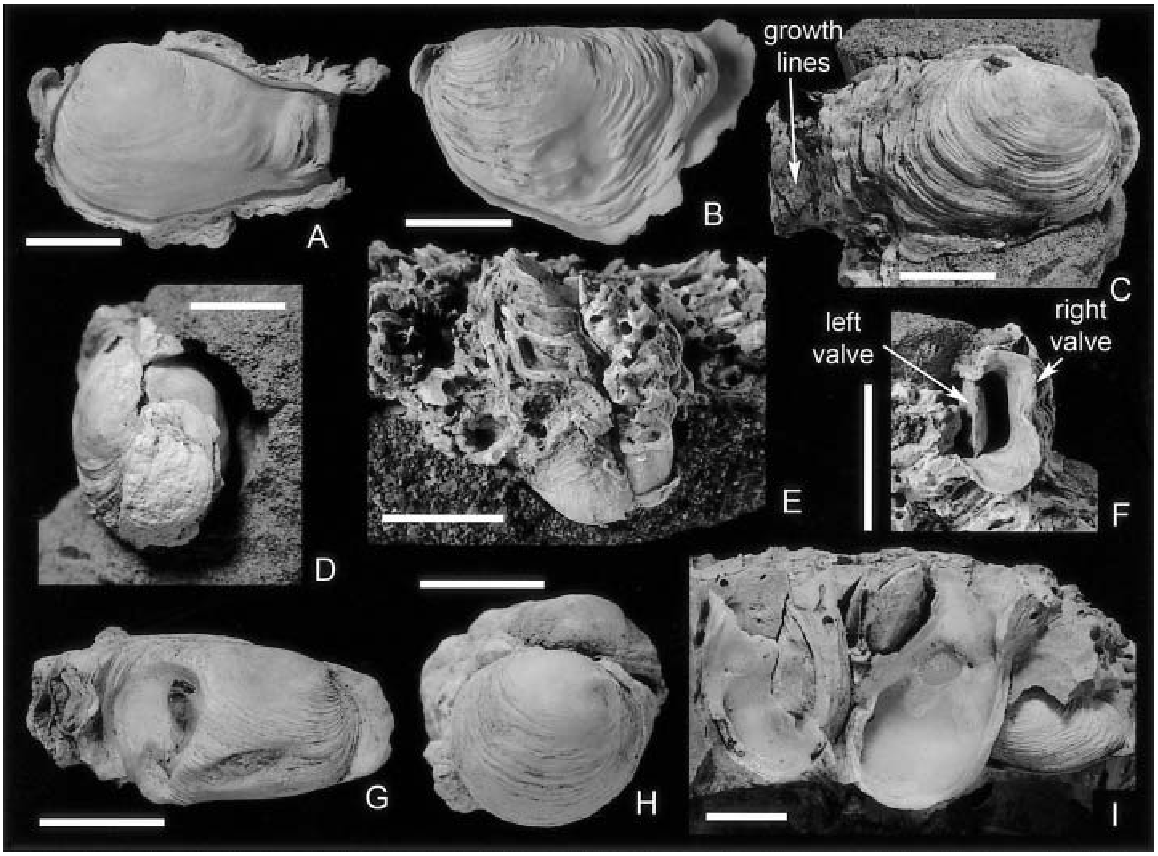

Figure 1. Adult *Claudiconcha japonica* (Dunker, 1882), Recent, from Fukue Island, Nagasaki Prefecture, Japan (A–B, H), Aburatsubo, Misaki, Miura Peninsula, Japan (C–F), Zushi, Kanagawa Prefecture, Japan (G) and unknown locality, Japan (I). **A, B.** Left views (NSM). **C, D.** Right and anterior views of individual collected from complete borehole, with right valve cemented to substrate. **E, F.** Dorsal and posterior views of individual mostly exposed by erosion of the substrate and overgrown by serpulid polychaetes. **G.** Right view of specimen bored-through by other individuals and repaired by secondary shell thickening and conchiolin patches (darker area) (NSM). **H.** Right view of subspherical individual (NSM). **I.** Sample of calcareous rock densely bored by *C. japonica* (UMUT). Scale bars represent 5 mm.

The openings of the boreholes typically are located on rock surfaces not directly exposed to strong waves. This species frequently occurs in clusters of a few individuals, and older individuals or empty shells often are bored by younger and/or smaller specimens. Individuals that became bored while still alive typically are repaired by the secondary deposition of shell material and conchiolin patches on their internal surfaces (Fig. 1G). In crowded conditions, stunted and/or distorted individuals (Fig. 1B, I) often are intermixed with larger and more regular ones.

This species possesses a concentric sculpture pattern especially well developed on the posterior shell slope (Fig. 1A–C, G–H). The adductor muscle scars are well defined, and a relatively deep pallial sinus is present. Total shell length reaches approximately 20–25 mm in the largest individuals.

C. japonica displays a two-stage growth-process. The first stage is characterised by a gradual growth of the shell along its margin and an essentially equivalve condition (with the exception of distortions in shell geometry caused by crowding or irregularities of the substrate). This growth stage is conveniently called subadult. Individuals at this growth stage are byssally attached to the ventral portion of the borehole by weak and thin byssal threads.

Subsequently, the margin of the right valve expands outwards and, along the anterior and ventral portions of the commissure, folds around the edge of the left valve (Fig. 1A–D), leaving sufficient room for the latter to open 2–4 mm in the posterior region (Fig. 1F). The left valve stops growing at the end of the subadult stage and does not display a corresponding expansion. The shape of the expanded portion of the right valve is highly irregular, displays coarse growth lines and conforms closely to the space available within the borehole and/or surrounding substrate (Fig. 1C, F). Shell secretion stops once the edge of the right valve has overlapped the opposite valve to a length of a few mm (Fig. 1A, C–D, F) or, in the posterior region, has curved around the siphons to form a partial chimney of comparable length (Fig. 1A, F–G). The byssus is absent at this stage. Fully grown specimens displaying the above characters herein are called adult.

In the adult stage, the left valve still is free to move within the borehole and the partly enclosing right valve (Fig. 1D). When the valves are adducted, the commissure closes in correspondence of the edge of the subadult, regularly shaped shell edge.

The geometry of the borehole is comparable with that of *C. monstrosa* (see below), but, given the coarse and soft substrate inhabited by *C. japonica*, it is difficult to observe fine detail on its internal surfaces. A weak ridge is frequently present in correspondence of the dorsal commissure posterior to the umbones. The overall shape and size of the cavity conforms closely to the shell shape (allowing for a space of approximately 0.5 to 1 mm between shell and substrate, and for additional space to allow the valves to gape), and in subadult individuals its internal surfaces are devoid of encrustations and epibionts. This is proof that *C. japonica*, as observed by the writer, is an active borer.

Shells of *C. japonica* that were bored by other individuals often show a slight undercutting in correspondence of the contact between different shell layers. The borehole walls do not show a comparable relief. Tool marks (i.e., abrasion marks left by mechanical scraping of the shell sculpture against the substrate) are absent. These observations point to a mostly chemical boring mechanism, although some mechanical activity likely is used by the organism to remove loosened clasts from the matrix.

The expanded portion of the right valves in live-collected adults always adheres to the substrate. This does not seem to be a true cementation comparable to that of oysters and other bivalves that attach to the substrate by one valve, because the force necessary to detach the shell from the substrate is much lower. At least in part, this is due to the friable nature of the substrate. However, the shell, although conforming closely to the substrate on a macroscopic scale, still shows clear growth lines when detached, and the detachment usually is clean and does not leave shell fragments adhering to the substrate. Therefore, adhesion of *C. japonica* to the substrate may be due principally to a mechanical effect caused by the shell closely replicating the topography of the substrate and ''embracing'' its contours.

Samples of *C. japonica* observed in collections contain individuals boring in hard calcareous rock (e.g., Fig. 1I). These shells strongly adhere to the substrate, to the point that normally they break instead of separating cleanly from the rock.

Adult individuals of *C. japonica* collected by the writer were frequently found with the shell partly exposed by erosion of the substrate. It is common to find shells that are exposed halfway or more, with the posterior region of the shell projecting above the substrate and covered by encrusting serpulid polychaetes and oysters (Fig. 1E). These epibionts cover also the surrounding rock surfaces, and by bridging the space between the right valve and the substrate actually contribute to anchoring it in place. The left valve, although also encrusted, often is still free to close because the epibionts on its surface are not joined mechanically to those on the surrounding substrate. Likely, this is prevented by the left valve periodically closing.

Individuals with the commissure plane roughly parallel to the surface of the substrate and either the right or the left valve exposed are also observed. The former is possible because the right valve adheres to the substrate only by its irregular adult expansion, not by its whole surface, and by curving around the margin of the left valve the expanded portion of the right valve may actually attach to the substrate lying to the left side of the organism. Individuals in this life orientation frequently are roughly spherical (Fig. 1H) and their commissure is thickened and bears growth lines that show a contraction of the soft parts within the shell, rather than an outward expansion, near the end of the growth process. The exposed shell regions sometimes are secondarily thickened, but not to the extent of the following species (see below).

The portions of external shell surfaces exposed by erosion, when not overgrown by epibionts, are smoothened by mechanical abrasion (presumably by wave-carried sediment and/or by grazing organisms). Occasionally, polychaetes or other worm-shaped organisms live in the spaces between the shell and the borehole and etch shallow cavities on the shell surface. However, no wear attributable to friction of the shell against the substrate as part of a mechanical boring process was observed.

The life span of *C. japonica* is not known, but a few individuals show a small number of broadly spaced, particularly marked growth lines on their external surfaces. If these growth lines correspond to winter breaks in shell secretion, it can be estimated that *C.*

japonica attains the adult stage within five to ten years. The extent of time spent after the end of the growth process cannot be determined from shell morphology. However, the occurrence of living adults halfway exposed and adhering to the substrate indicates that erosion of the substrate took place after the attainment of the adult stage, because an unattached shell is most likely to be washed away by strong waves. As noted by Morton (1977), byssal attachment of adult individuals is prevented by the expanded margin of the left valve.

Empty shells of *C. japonica* were observed within their boreholes in sandstone in the field, but not in large numbers. This is in contrast with observations on samples of hard rock inhabited by this species and stored in museum collections (e.g., Fig. 1I), in which individuals that obviously were dead at the time of collection (as shown by their shells being bored through by individuals that settled subsequently in their vicinity) are frequent. This may further indicate that dead *C. japonica*, in the locality and substrate studied herein, tend to be destroyed or freed from the substrate in a relatively short time. A few empty adult shells of *C. japonica*, isolated from the substrate, were recovered from shell rubble accumulated in crevices and at the basis of the rock outcrop, thus proving that erosion does free shell of this species from the substrate.

Claudiconcha monstrosa

This species is locally abundant in coral rubble in the intertidal zone in Iriomote Island, but typically is subtidal in Cebu Island. Other boring bivalves associated with this species are absent or very rare, but nestlers (especially *Barbatia*, *Cardita* and Isognomonidae) are relatively frequent. The volume of substrate occupied by the boreholes of *C. monstrosa* largely exceeds that of other endolithic organisms, thus making this species probably the most important agent of bioerosion in the above environments.

C. monstrosa differs from the preceding species mostly in possessing a reticulate sculpture pattern. Specimens from Iriomote Island are also significantly larger (up to 34 mm in shell length) than those collected in the Philippines (20–25 mm) and than *C. japonica*. The overall shell geometry and growth pattern, instead, are comparable in the two species.

The boreholes are also comparable in the two species, but large individuals of *C. monstrosa* boring in coral rubble often display an elongated siphonal canal (Fig. 2I) that typically is not observed in *C. japonica*. This difference could be at least in part the result of a much faster rate of erosion of the substrate in the latter species. However, samples of *C. japonica* in hard calcareous rocks observed in museum collections also lack a siphonal canal comparable with that of *C. monstrosa*.

Boreholes in dead coral retain a finer detail and are more easily prepared and observed than those in soft rock. The following discussion, therefore, centres on boreholes in the former type of substrate. In subadult individuals, the shape of the borehole conforms roughly, but not exactly, to the geometry of the shell. The borehole is slightly larger than the shell, displays one weak ridge in correspondence with the hinge line of the shell posterior to the umbones and two well-defined grooves in correspondence with the mantle edge projecting from the anterior and ventral portion of the commissure (Fig. 2J–K). The groove on the right side of the organism is visibly larger and deeper than the left one in adults, as well as subadults that have not begun to build the adult expansion of the right valve (Fig. 2J–K).

Along the posterior commissure, the adult expansion of the right valve often forms a ridge or tooth that separates the inhalant and exhalant siphons and restricts the siphonal opening of the borehole (Fig. 2D, F). This character is developed to a lesser extent in *C. japonica* (Fig. 1F).

Like in the preceding species, a weak byssus is sometimes present in subadult *C. monstrosa*, but always absent in adults.

In living individuals at all growth stages, the external shell surface and the walls of the borehole typically are covered by a layer of loose mud (Fig. 2I). No mechanical wear of the external sculpture was observed in individuals extracted from their boreholes.

Living adult individuals are always attached to the substrate by the expansion of the right valve (Fig. 2D, F–G). Attachment seems to take place by a modification of the process used by the juvenile to build commarginal lamellae projecting from the shell surface. In the adult, one or more lamellae are strongly developed, and are secreted with their external (i.e., adapical) side in contact with the substrate (Fig. 2E). However, this does not seem to be a true cementation, since there seems to be a thin layer of periostracum between the shell and the substrate, and not an intimate contact between the two materials.

In sandstone, adhesion of the shell to the substrate typically is stronger than the cohesion of the substrate, and pieces of the latter often remain attached to the right valve of *C. monstrosa* when this is extracted from the rock (Fig. 2G). In coral, instead, the shells of *C. monstrosa* detach more easily, and empty shells often are found already detached from the substrate, with

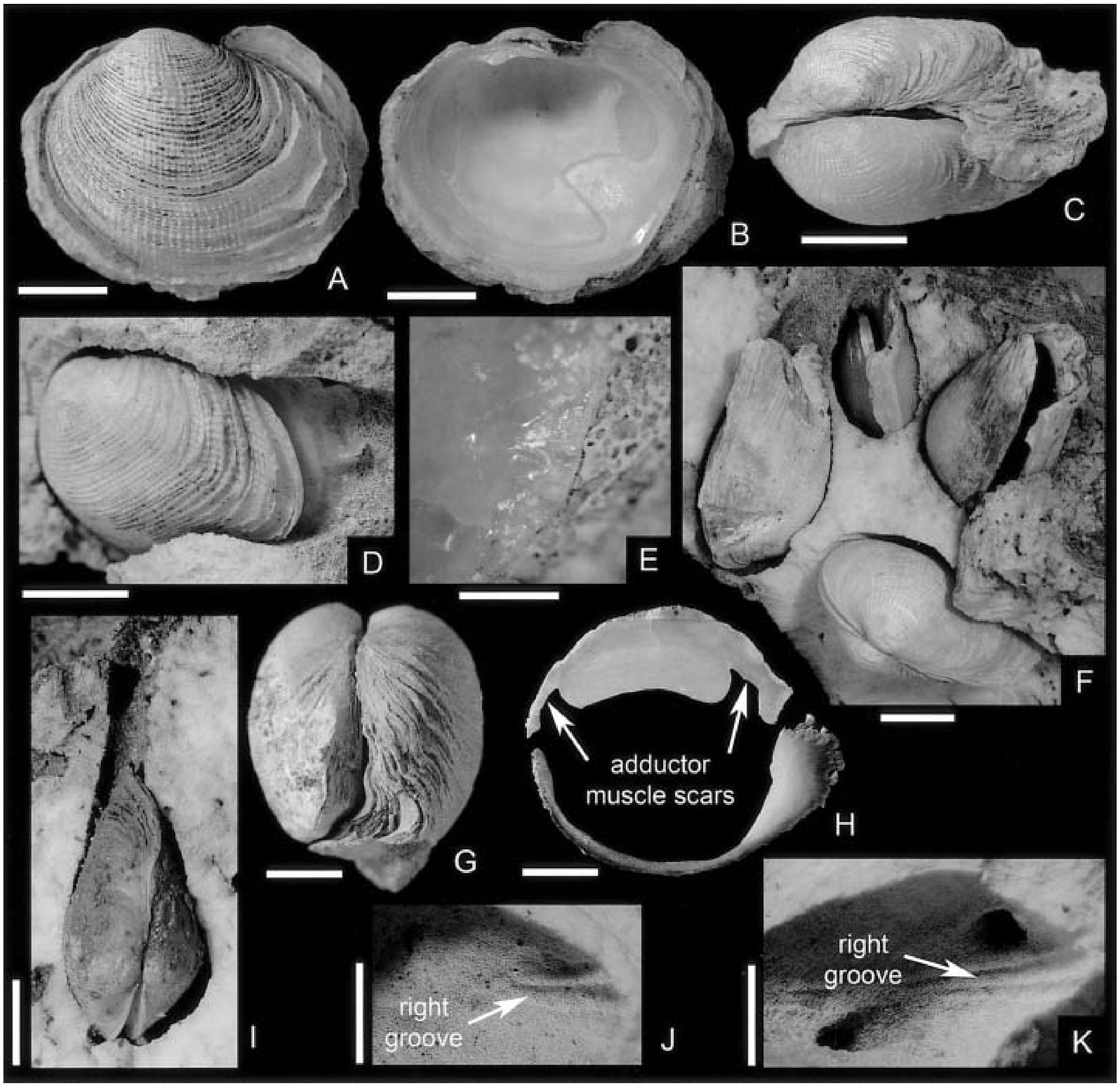

Figure 2. *Claudiconcha monstrosa* (Gmelin, 1791), Recent, Iriomote Island, Japan. **A–B.** Left views of external and internal shell surfaces of regularly-shaped adult. **C.** Dorsal view of a somewhat more irregular adult. **D.** Oblique posterior view of adult in artificially opened borehole, showing cementation of the posterior commissure to the substrate. **E.** Detail of contact between posterior region of expanded margin of right valve (roughly occupying the left half of the picture) and substrate (right half) of individual shown in D. **F.** Dead coral boulder crowded with boreholes of *C. monstrosa*, with subadult and adult individuals exposed by artificially breaking the substrate. The individual at the top right was already partly exposed by erosion of the substrate. The one at the left shows repaired shell damage after boring by smaller individuals (not shown) in crossing boreholes. **I.** Living subadult in artificially opened borehole in dead coral, with mud covering the shell and borehole surfaces. **G.** Posterior view of subspherical adult collected alive and with more than half of the shell (including the whole left valve) exposed by erosion. A fragment of sandstone substrate (lowermost and out of focus) is still attached to the ventral margin of the right valve. **H.** Section of the same individual of the preceding figure along an antero-posterior plane perpendicular to the commissure. The exposed and secondarily thickened left valve is at the top. The posterior region of the right valve (lowermost and to the right) was exposed and also secondarily thickened. **J–K.** Details of the borehole of the subadult specimen shown in I, illuminated to show the grooves etched by the mantle folds onto the borehole walls (antero-dorsal in J, antero-ventral in K). The groove left by the right edge of the mantle is broader and deeper than that of the left edge. Scale bars represent 10 mm (A–D, F, I–K), 2 mm (E) and 5 mm (G–H).

the external surface of the expanded portion of right valves and the corresponding region of the borehole walls covered by mud and/or algae. The dead shells of this species recovered from dry piers in the Philippines are always detached, possibly as a result of weathering of the coral blocks artificially exposed to the subaerial environment. Living specimens from the Philippines presumably were only weakly attached to the coral substrate, but always came free when the latter was broken by hammering.

While living individuals partly exposed by erosion are uncommon in coral rubble, they are frequent in sandstone. Some of these individuals display a subspherical shell and a secondary contraction of the mantle toward the interior of the shell, resulting in the shell margin tapering inwards in adults (Fig. 2G). The exposed portion of the shell is secondarily thickened, sometimes to a very high extent (Fig. 2H). In the illustrated specimen, the central portion of the exposed left valve is roughly six times thicker than the opposite valve. However, the secondary thickening was much more limited in correspondence to the muscles, resulting in deep depressions at the adductor muscle scars (Fig. 2H) and pallial line (not visible in the figure).

A ground and etched section of the specimen of Fig. 2G–H was observed with a SEM to check for the presence of microtubules or comparable structures within the shell, since microtubules might be used to sense whether part of the shell is exposed. However, no such structures were observed. The outermost shell layer of the exposed left valve was found to contain algal microborings, and the non-thickened portion of the right valve cemented to the substrate contains smaller, perhaps fungal microborings. None of these extended to the inner shell layers, and therefore the secondary shell thickening of the left valve cannot be interpreted as a reaction to microborings. Thus, secondary thickening could be triggered by a number of other factors, including sensing by the mantle edges projecting along the edges of the expanded portion of the right valve, sunlight filtering through the exposed shell portion, and/or mechanical stimulation of the soft parts caused by waves and currents imparting movements and mechanical stresses on the exposed valve.

Jouannetia cumingii

This species is a borer in dead coral in the shallow subtidal zone. The portion of the borehole occupied by the shell is spherical, grading into a short conical "neck" and a narrow cylindrical, often irregularly bent siphonal tube in the posterior region. There is no calcareous lining on the borehole walls. As a whole, the boreholes observed for this study are slightly pear-shaped, rather than spherical like those illustrated by Morton (1986).

The juvenile shell is higher than long, circular in outline when seen from the anterior or posterior directions, and reminds one of the shell geometry of the Teredinidae (e.g., see Turner, 1966). Shell articulation takes place about an axis that passes through a well developed dorsal condyle (roughly corresponding to the position of the umbones) on either valve and a less developed ventral condyle. This axis is roughly dorsoventral in orientation. Thus, the pedal gape opens while the posterior commissure closes, and vice versa. The pedal gape is extremely large, and the shell occupies only the posteriormost half of the spherical portion of the borehole. In fact, when the valves are adducted posteriorly, the pedal gape corresponds to the shell outline when viewed from the anterior or posterior directions (Fig. 3A).

The shell is approximately equivalve at this stage, except for a minor asymmetry of the dorsal condyle and attachment area of the ligament, which are slightly larger in the left valve, and of the postero-ventral commissure, where the margin of the right valve slightly overlaps that of the left valve. This overlap continues in the ventral direction, where the edge of the right valve slightly encases and protects the ventral condyle.

The posterior adductor muscle is inserted onto the surface of a myophore, or buttress, which in turn is attached almost perpendicularly to the internal shell surface (Fig. 3C). The anterior adductor is inserted onto an anterior extension of the dorsal condyle (Fig. 3C). The planes of the attachment surfaces of the anterior and posterior adductor lie at an angle of 40–50° to each other. This suggests that the valves can rotate with respect to each other by a large amount when the muscles are alternately contracted, albeit not enough to close the pedal gape (because this would require an unrealistic amount of stretching of the posterior adductors, besides being prevented by the attachment of the foot to the substrate and by friction of the projecting posterior commissure against the walls of the borehole). Although Morton (1986) suggested a chemical boring mechanism in *J. cumingii*, the capability for such broad movements is compatible with a boring process at least in part mechanical. This also would be consistent with the strong commarginal ridges and, in the dorsal region, rows of denticles that flank the sides of the pedal gape (Fig. 3B, D–E, G). In other pholadids, comparable sculptures flanking the pedal gape are used for mechanically abrading the substrate (e.g., Fig. 4F, and Röder, 1977).

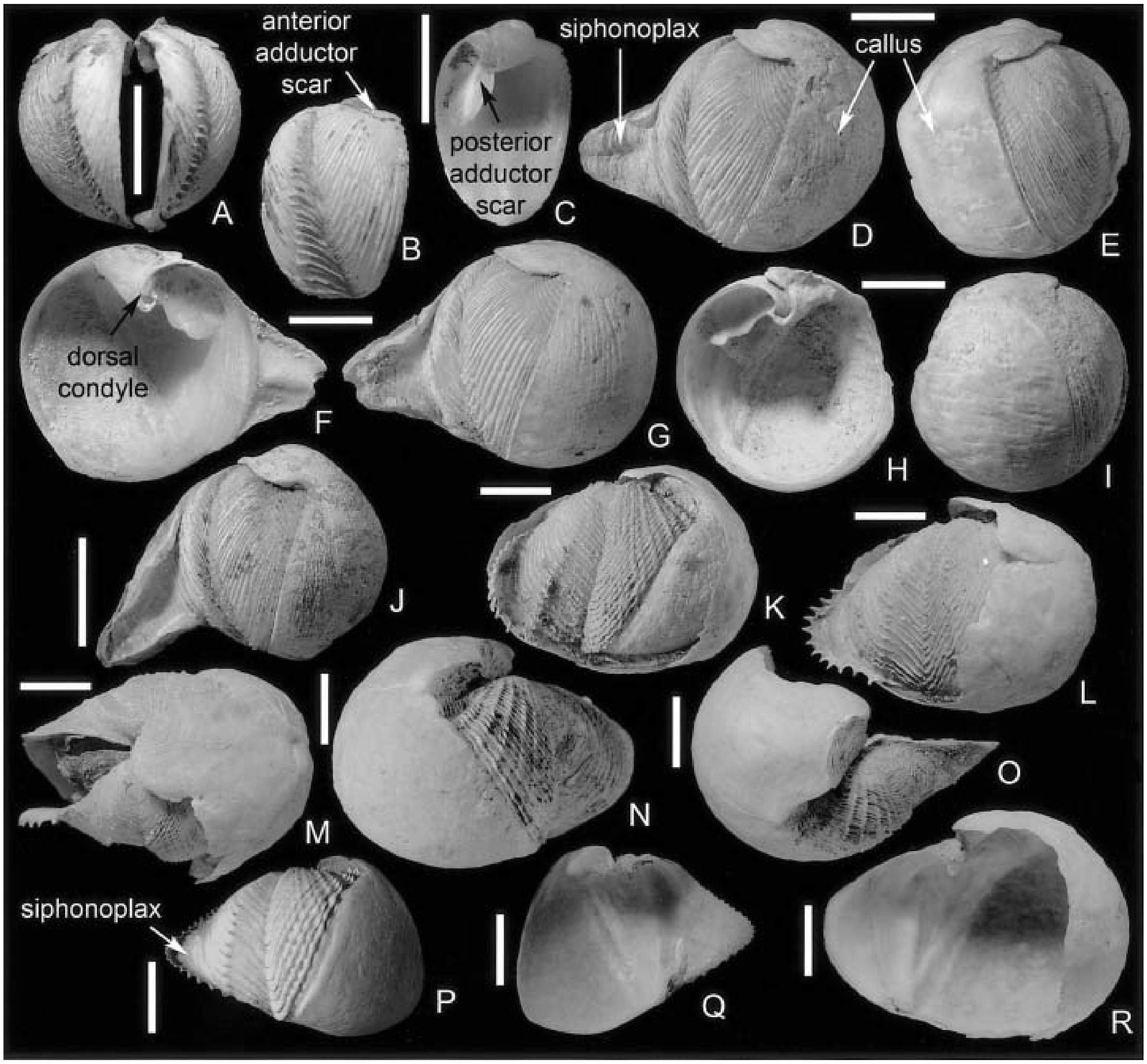

Figure 3. *Jouannetia cumingii* Sowerby, 1842, Recent, Tayud, Cebu Island, the Philippines (A–J) and *Jouannetia* (*Pholadopsis*) *globulosa* (Quoy and Gaymard, 1835), Recent, Setochi, Amami, Ohshima, Japan (K–R) (NSM). **A–C.** Posterior view, exterior of right valve and interior of left valve of juvenile shell. **D–E.** Exterior of right and left valves of adult. **F–I.** Exterior and interior of right (F–G) and left valves (H–I, with edge of the callus partly fractured) of adult. **J.** Exterior of right valve of adult with deformed siphonoplax. **K.** Right lateral view of almost adult individual, with callus of left valve (enclosing the one of the right valve) not fully grown. **L–M.** Right lateral and dorsal views of adult. The right valve may be slightly misplaced and protruding in the posterior direction to a higher extent than during life. **N–R.** Individual with disarticulated valves, showing the exterior (N–O) and interior (R) of the left valve and the exterior (P) and interior (Q) of the right valve. Scale bars represent 5 mm.

It is not documented in the literature whether the shell of *J. cumingii* rotates about its antero-posterior axis within the borehole during growth, but such rotation is almost certain, in view of the circular cross-section of the borehole and almost circular cross-section of the shell. Such a rotation is commonly employed by mechanically boring Pholadidae (e.g., Röder, 1977). Because of the almost spherical geometry of the shell and soft parts, a reduced amount of shell rotation about other axes within the borehole is also possible, although restricted by the need to extend the siphons through the siphonal canal of the borehole. In this context, it can be noted that the conical "neck" of the borehole at its junction with the siphonal canal (see above) allows such a rotation without impeding the passage of the siphons.

Morton (1986) stated that mechanical boring in *J. cumingii* would require a rotation of the shell within

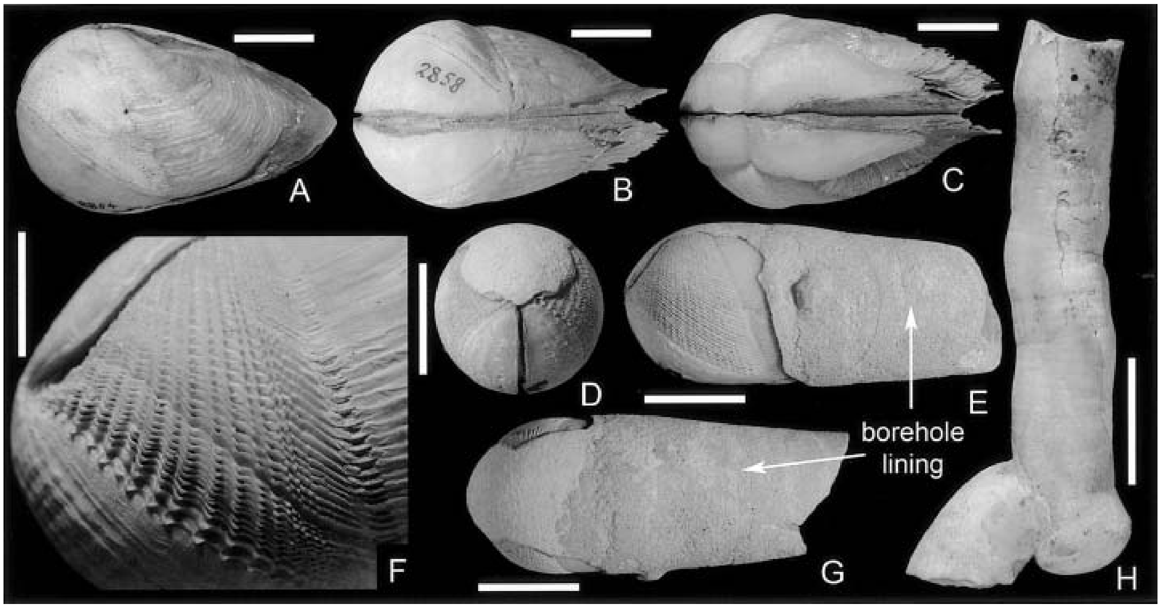

Figure 4. **A–C.** Adult *Parapholas quadrizonata* (Spengler, 1792), Recent, Hakone, Kanagawa Prefecture, Japan (NSM). Left (A), ventral (B) and dorsal (C) views. **D–E, G.** Adult shell and incomplete borehole lining of *Aspidopholas yoshimurai* Kuroda & Teramachi, 1930, Recent, Nanao, Ishikawa Prefecture, Japan (NSM). Anterior (D), left-lateral (E) and dorsal (G) views. **F.** Detail of anterior portion of left valve of adult *Penitella kamakurensis* Yokoyama, 1922, Recent, Sagami Bay, Japan (UMUT). **H.** Calcareous lining of borehole (originally in wood) of undetermined teredinid, Quaternary, Byculla Flat, Bombay, India (NHM). The direction of boring is from top to bottom. Scale bars represent 10 mm (A–E, G–H) and 5 mm (F).

the borehole by almost 360º and expressed doubts as to its feasibility. It is not clear whether he was referring to rotation about the antero-posterior axis (which appears to be unrestricted), or about other axes (which is restricted to perhaps 15–20° in either direction). These feasible rotations, combined together and with a broad range of gaping of the anterior commissure, appear sufficient to bring all portions of the anterior hemisphere of the borehole within reach of the anterior shell margin, thus making mechanical boring possible.

A combined rotation about different axes requires a shell geometry that can be enclosed tightly within a sphere. This condition occurs also in the Teredinidae, where it is functional in allowing the borehole to make sharp turns within a wood substrate (Turner, 1966; Röder, 1977) and even to back up within the borehole and resume boring in a different direction (Fig. 4H). A comparable condition also occurs in the wood-boring and tube-dwelling Palaeogene pholadid *Teredina* (see Savazzi, 1982a). However, no other rock-boring Pholadidae (including other species of *Jouannetia*) possess a shell geometry fitting within a sphere and comparable to that of *J. cumingii*. The wood-boring pholadids *Xylophaga* and *Martesia* possesses antero-posteriorly shortened shells with a rapidly narrowing posterior slope (Bartsch and Rehder, 1945; Turner, 1955). This gives the shell a pear shape, which allows a limited amount of rotation about the dorso-ventral and lateral axes within a long subcylindrical borehole in order to change the direction of boring.

The adult growth stage of *J. cumingii* is characterised by a callus growing from the sides of the pedal gape. Instead of meeting or fusing in the centre of the pedal gape like in other pholadids (see below), the callus of the left valve slightly overlaps and encloses that of the right valve. In the material collected for this study, the amount of overlap does not exceed 10–15° sideways (regarding the shell as a sphere and measuring the overlap relative to the centre of the sphere), but in material illustrated by Morton (1986) the overlap is significantly larger. The material available for this study does not allow one to decide whether the callus of both valves grows simultaneously, or first on one valve and subsequently on the other.

In the adult stage, the posterior region of the right valve bears a siphonoplax, i.e., a siphonal extension of the shell margin (Fig. 3D, F–G, J). The siphonoplax typically shows evident growth lines on its external surface (Fig. 3D, G, J) and a central ridge on its internal surface separating the inhalant and exhalant siphons (Fig. 3F). The siphonoplax sometimes is distorted, either to follow an irregular siphonal canal of the borehole or to compensate for a slight misalignment of the shell within the latter (Fig. 3J).

Morton (1986) reported that a few juvenile (i.e., devoid of callus) shells of *J. cumingii* do possess a siphonoplax. Therefore, it is possible that this feature normally precedes shortly the construction of a callus. The material available for this study contains no such individuals. The overlapping callus obviously prevents the attachment of the foot to the substrate, as well as continued boring. At this point, the shell, because of its spherical shape, could accidentally rotate within the borehole, bringing the siphonal region of the shell out of alignment with the siphonal canal of the borehole. This is prevented, however, by the siphonoplax, which extends like a spike into this region of the borehole.

A slight misalignment of the shell to the siphonal canal of the borehole could take place in spite of the presence of the siphonoplax. In particular, the siphonoplax could come to lie with its interior (i.e., left) side against the substrate (instead of its opposite side) when the posterior commissure is open. This would prevent the siphons from being extended into the siphonal canal. However, contraction of the large posterior adductors and/or forcing the siphons to expand into the siphonal neck of the borehole should be sufficient to cause the shell to realign within the borehole.

In time, the left valve and its callus may be prevented from moving within the borehole by the deposition of muddy sediment between the shell and the borehole, with the right valve still free to move in order to open and close the siphonal opening. The siphonoplax may also be functional to prevent access to the soft parts by predators, as suggested by Morton (1986). In this respect, this feature can be compared with the aristae of lithophaginid bivalves, which are built by the secondary cementation of substrate and sediment particles onto the external shell surface and often are comparable in shape (although equally developed on both valves) to the siphonoplax of *J. cumingii* (see Kleemann, 1980; Morton, 1993).

Jouannetia (Pholadopsis) globulosa

This species (Fig. 3K–R) is more elongated than *J. cumingii*. In particular, its posterior slope (as demarcated from the anterior one by a furrow corresponding to the internal ventral condyle) is proportionally longer. The edges of the pedal gape, however, are the region of the shell with the broadest cross-sectional area about the antero-posterior axis, like in *J. cumingii*. Only adult individuals of *J. globulosa* were available in museum collections inspected by the writer.

A posterior myophore is present, but much less developed than in *J. cumingii*. Instead of being attached to the inside of the posterior shell slope, it is built as a secondary thickening of the already thick internal ridge of shell material that runs from the umbo to the ventral condyle.

The outer surface of the anterior shell region bears both commarginal ridges and radial rows of denticles (Fig. 3K, N, P). This sculpture is quite comparable to that of pholadids known to bore by mechanical means (e.g., Fig. 4F, see also Röder, 1977).

The callus is laterally asymmetric like in the preceding species, but the callus of the left valve overlaps the right one to a higher extent (Fig. 3K–O, R) and is separated from the callus of the right valve by a much wider gap (Fig. 3K–M). This is likely a consequence of the fact that the subadult shell in this species conforms less to the shape of a sphere, and thereby to the shape of the anterior region of the borehole, than in *J. cumingii*. The callus of the right valve usually does not extend beyond the vertical mid-plane of the shell.

The posterior region of the left valve is broader than the corresponding region of the opposite valve. The right valve bears a siphonoplax of variable length, the edge of which is reflected outwards and bears numerous sharp denticles. Although the border between valve and siphonoplax is less distinct than in *J. cumingii*, the presence of these denticles allows one to state that this feature is built only at the end of the growth process, since otherwise they would be visible as a sculpture on the external surface of the shell. As a result of this asymmetry of the valves, when the posterior commissure is closed the right valve partly slides within the left one. Judging from adult specimens, it is possible that the posterior commissure of the right valve is broader than the corresponding region of the left valve throughout growth, although juvenile specimens would be needed to be certain of this.

Consequences of this lateral asymmetry are that (1) it allows the pedal gape to open to a larger extent than would be permitted by a laterally symmetrical shell, thus partly compensating for the greater development of the posterior shell slope compared to *J. cumingii*, and (2) by increasing the amount of valve overlap along the posterior commissure, it possibly provides a better protection against predators than a symmetrical commissure, given the low shell thickness in this region.

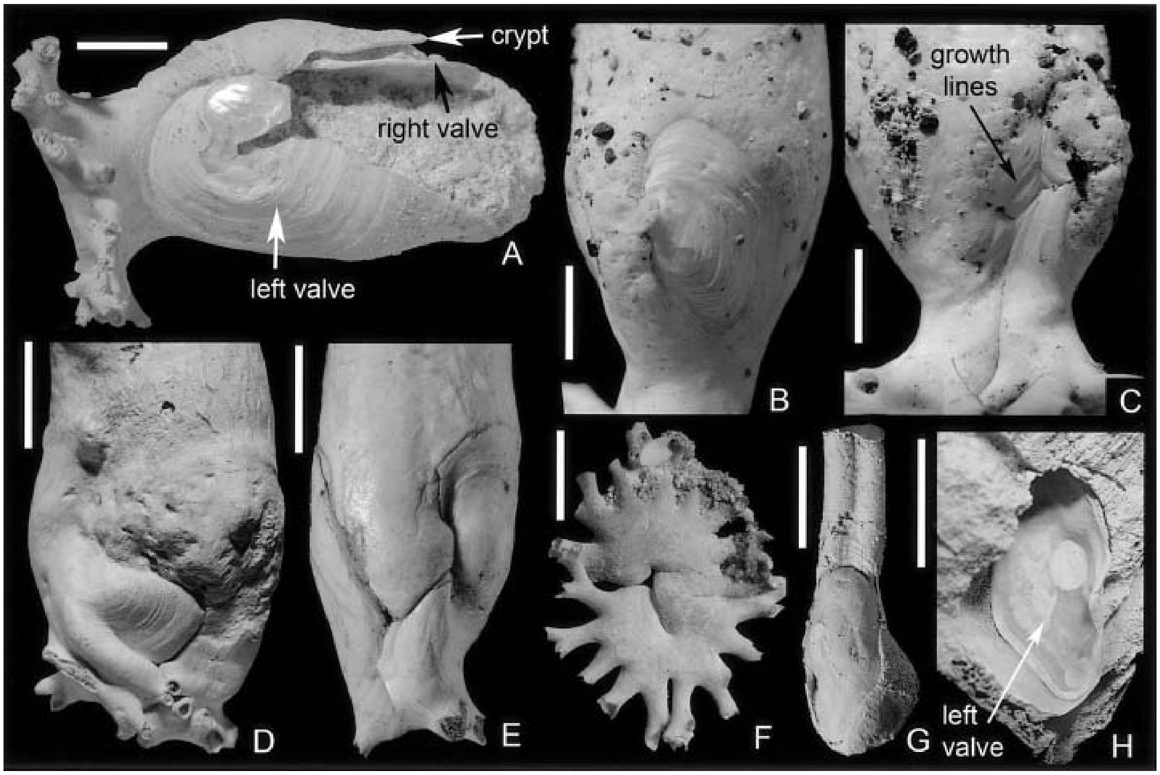

Figure 5. **A, D, F.** *Stirpulina bacillus* (Brocchi, 1814), Pleistocene, Palermo, Italy (NHM). Incomplete anterior portion of crypt (A) showing fused left valve and enclosed right valve, right view of anterior portion of malformed crypt (D) and anterior view of tubule fringe (F). **B–C.** Anterior portion of crypt of *Stirpuliniola ramosa* (Dunker, 1882), Recent, Misaki, Miura Peninsula, Japan (NSM). Dorsal (B) and right-lateral (C) views. **E.** *Stirpulina coronata* (Deshayes, 1824), Lower Barton Beds, Eocene, Barton, UK (Sedgwick Museum, University of Cambridge, UK). Dorsal view of anterior portion of crypt. **G–H.** *Bryopa lata* (Broderip, 1834), Recent, Tayud, Cebu Island, the Philippines. Left lateral view of artificial cast of borehole and left valve (G) and artificially exposed anterior portion of borehole, showing the left valve cemented to the substrate (H). Scale bars represent 5 mm.

Clavagella and related genera

The family Clavagellidae contains two separate adaptive (and most likely phylogenetic) lineages, called the *Clavagella* lineage and *Penicillus* lineage by Savazzi (2000). The two lineages are clearly distinct and their relationships unclear (the family could in fact be polyphyletic and the two lineages only convergent; see Savazzi, 2000). This discussion deals with the *Clavagella* lineage, which includes the genera *Clavagella*, *Stirpulina*, *Stirpuliniola*, *Bryopa* (regarded by Savazzi, 2000, as a separate lineage, but herein included in the *Clavagella* lineage because of its clearly closer affinities with the latter, rather than with the *Penicillus* lineage), *Ascaulocardium* and a few other related taxa.

The *Clavagella* lineage, with the exception of *Bryopa*, is characterised by the construction of a crypt (i.e., a secondary calcareous envelope that surrounds the soft parts; Savazzi, 1982a) at the end of a determinate growth process. After its construction, the crypt can be modified only by continued secretion at its siphonal extremity. The crypt bears an array of tubules at its anterior end, in proximity of the shell (Fig. 5A, D–F). The left valve is incorporated into the crypt and visible from the outside, while the right valve is enclosed within the crypt and free to articulate against the left one (Fig. 5A–E). The genus *Bryopa* does not build a crypt, and is an obligatory rock borer with the left valve cemented to the wall of its borehole (Fig. 5G–H).

Evolution within the *Clavagella* lineage is unclear, with tube-dwelling representatives known since the Cretaceous (e.g., Pojeta and Sohl, 1987; Pojeta and Johnson, 1995; Stallwood, 1995), facultative borers and tube dwellers since the Eocene (e.g., Cossmann and Pissarro, 1904–1913), and *Bryopa* since the Miocene (Savazzi, 2000, and references therein). However, fossil clavagellids are typically very rare, and the above record may reflect an incomplete documentation of endolithic taxa, rather than an evolutionary pattern.

The construction of the crypt takes place largely in a single episode or a short time, and most of the crypt is devoid of growth lines. However, the external surface of the crypt in the region covering the right valve shows a combination of furrows and evident growth lines (Fig. 5C–E). This shows that this region of the crypt was built gradually, and by the progressive extension of three or more separate lobes of mantle tissue folding around the edges of the right valve and gradually converging together to plug this hole in the crypt, left after the construction of the anterior portion of the crypt. This process produces parallel growth lines in the region covered by each mantle lobe, and grooves where the sides of separate mantle lobes touch each other. Abnormal crypts (e.g., Fig. 5D) sometimes show anomalous patterns of growth lines and a combination of mantle lobes different from those of normal specimens. One of these grooves typically continues in an anterior direction (lowermost in Fig. 5C), passes through the fringe of anterior tubules and ends in the pedal gape at the centre of the tubule fringe (Fig. 5F).

The literature (e.g., Deshayes, 1824, 1857; Cossmann and Pissarro, 1904–1913) contains several records and illustrations of Eocene specimens of *Clavagella* and/or related genera semi-endolithic in calcareous substrates, typically empty bivalve shells. The writer has been unable to observe any of this material, and the following description is based only on these illustrations.

These clavagellids are enclosed in a typical crypt, albeit partly embedded sideways in the substrate. Since the left valve is part of the crypt, the latter was built after this valve attained its adult size. It appears likely that the juvenile stage, shell-bearing but without a crypt, already was semi-endolithic before the construction of the crypt commenced. At this stage, the organism appears to have been cemented to the substrate by the external surface of its left valve, which is always positioned in contact with or embedded within the substrate at least in correspondence with its apical region. Thus, the juvenile became initially cemented to a calcareous substrate by its left valve, and subsequently bored through the substrate.

In a few instances, it appears from the illustrations that most of the left valve (albeit always with the exception of its apical region) is exposed outside the substrate. As discussed by Savazzi (1982a, 1999), this is likely a consequence of the convex shape of this valve, coupled with its growth. While the juvenile left valve was cemented to the substrate, growth along the edge of this valve caused the shell margin to rotate out of the substrate, so that newer portions of the shell were exposed. This is an unavoidable consequence of the curving growth trajectories followed by points located along the edge of a coiled shell. As a consequence of this rotation and of its own growth, the free right valve followed this rotation and, from originally being exposed, became partly or totally hidden within the semi-endolithic borehole (see Savazzi, 1982a, fig. 19; Savazzi, 1999, fig. 17.13). The borehole likely was excavated chemically by mantle tissues wrapping around the body and the external surface of the right valve. Thus, the mantle was enfolding the right valve already prior to the construction of the crypt, likely in a manner comparable to that observed in the construction of the crypt (see above). A comparable morphology of the mantle likely occurs also in *Bryopa* (Savazzi, 2000).

The fact that the crypt subsequently was built as a semi-endolithic structure, including its anterior tubules and posterior siphonal tube, is a proof of chemical boring, since the freely articulating right valve could neither reach these regions nor excavate mechanically a cavity with the observed morphology. Construction of the crypt and its cementation to the substrate greatly enhanced the surface of the skeleton adhering to the substrate.

It is possible that these clavagellids typically attached themselves to a small substrate, which subsequently became detached, or destroyed by shell growth, before the construction of the crypt (Savazzi, 1982a). In this case, the facultative semi-endolithic habit described above could be the consequence of juvenile clavagellids cementing themselves ''by mistake'' to an unusually large substrate, and of the attachment not being released before the construction of the crypt.

In this context, the rock-boring habit and the cementation of the left valve of *Bryopa* to the substrate, at first sight odd, become understandable as neotenic characters inherited from tube-dwelling forms. The requirements imposed by the newly exploited endolithic habitat, on the other hand, forced further evolutionary changes. The crypt was no longer necessary and was lost almost completely, except as a calcareous lining of the siphonal region of the borehole and, in some instances, its extension in the posterior direction to form a siphonal ''chimney'' projecting from the substrate. The long time required by rock- or coral-boring made a determinate growth pattern, consisting of a quick juvenile growth followed by a metamorphosis and construction of the crypt, no longer practical. The anterior tubules likewise were no longer necessary and disappeared together with the crypt and the determinate growth pattern of which they were a part.

Since a shell cemented to the substrate would prevent the organism from moving deeper within the substrate during growth, which is a requirement of the boring habit, the shell of *Bryopa* grows mostly in the anterior direction, with the soft parts gradually vacating the posterior shell regions and effectively migrating in the anterior direction within the shell. This process leaves behind a series of parallel growth lines in the posterior region of the internal surface of the left valve (visible in the central portion of Fig. 5G). This strategy was not feasible in the right valve, because an abandoned posterior portion of this valve would prevent the siphons from passing through the siphonal canal. Thus, this region of the right valve is instead secondarily resorbed. A number of other adaptations connected with the shift from tube dwelling to rock boring are discussed by Savazzi (2000). The final result was a shell geometry and growth process unique among the Bivalvia.

Discussion

Petricolidae

Representatives of the Petricolidae are generally regarded as mechanical borers and/or nestlers in the literature (Otter, 1937; Purchon, 1955; Yonge, 1958; Ansell and Nair, 1969; Ansell, 1970; Narchi, 1974, 1975). In fact, the convergence in shell geometry of *Petricola pholadiformis* with pholadids leaves little doubt about this species being at least in part a mechanical borer. However, other authors (Bromley, 1978; Nielsen, 1986) suggested that the close fit between shell and borehole in *Petricola lapicida* is not compatible with mechanical boring, which would require ampler movements than those allowed by the borehole. Morton and Scott (1988) further described anatomical evidence supporting chemical boring in this species. Savazzi (1982b) illustrated and discussed etch marks on the external surfaces of shells of *Petricola* sp. in crossing boreholes as indirect evidence of chemical boring. Thus, both mechanisms are represented within the Petricolidae. Morton (1995) reassigned *Cooperella subdiaphana* to the Petricolidae on the basis of its anatomy, and described it as a soft-bottom dweller and a facultative builder of an agglutinated cocoon of sediment particles within soft sediments. Within the family, this habit seems to be unique to the genus *Cooperella* (Morton, 1995).

In *Claudiconcha japonica* and *C. monstrosa* as observed in the present study (see above), the evidence of a rather close-fitting borehole that prevents both rotation of the shell about its antero-posterior axis as well as extensive gaping and other movements of the shell, together with the occurrence in calcareous substrates and the absence of significant shell wear even in hard substrates like coral, suggests a mainly or exclusively chemical boring in this genus.

As described by Morton (1977), *C. japonica* from Hong Kong is not a borer but a nestler in sediment-filled intertidal rock crevices, and is unable to enlarge the cavity in the substrate that it inhabits. The substrate is a soft metamorphosed rock, bored by the pholadid *Barnea* cf. *dilatata*. Morton (1977) mentions several crevice-dwelling bivalves found in rock crevices together with *C. japonica*, but no additional boring bivalve in this substrate. *C. japonica* is described as byssally attached in the juvenile, but no mention is made of cementation to the substrate in the adult. However, Morton (1977) reports that empty shells of *C. japonica* remain in the life position in crevices and become gradually filled with sediment or inhabited by other nestlers. The size reported for adult individuals (6 to 17 mm in shell length) is substantially smaller than that of the material collected in Japan by the writer (see above).

The remarkable difference in the life habits reported for this species, described by Morton (1977) as a nestler and in the present paper (see above) as a chemical borer, could be due to a different chemical nature of the substrate. In fact, the substrate as observed in Japan is calcareous (as proved also by the presence of *Lithophaga* sp. in the same locality), while the presence of a pholadid in the substrate from Hong Kong (Morton, 1977) is compatible with both calcareous and noncalcareous substrates. The latter, or the presence of a non-calcareous cement, could effectively prevent chemical boring, and under this condition *C. japonica* would effectively be forced to become an obligatory nestler.

Cementation of the right valve of *Claudiconcha* to the substrate appears to increase its potential to survive erosion of the substrate. In fact, several living specimens were found with the shell mostly exposed after erosion destroyed part of their boreholes, and only the cementation by their right valve prevented them from being washed away. In this respect, *Claudiconcha* is unique among boring bivalves (with the partial exception of clavagellids, see above and below) for being able to become an epifaunal, cemented, oyster-like form in the adult stage. Like oysters and, especially, representatives of the Chamidae, *C. monstrosa* is able to secondarily thicken the exposed valve in order to make it mechanically more resistant. The possible evolutionary advantage of a sessile, non-growing adult stage is discussed below.

It is unclear how lateral asymmetry evolved in *Claudiconcha*. It is remarkable, nonetheless, that the mantle folds along the ventral and posterior commissure in both species studied herein display a visible lateral asymmetry and/or substrate etching capability already in the subadult stage, while the shell is still laterally symmetric (Morton, 1977, and above). If a comparable asymmetry of the mantle tissues should be observed in other petricolid genera, this character could be regarded as the stepping stone to the evolution of lateral shell asymmetry in the family (although in itself this still would not explain the reasons for the asymmetry of the mantle).

The adult expansion of the margin of the right valve of *Claudiconcha* may be regarded as a specialisation of its external sculpture, in which one or more of the commarginal lamellae that are present throughout the subadult stage become strongly developed and adhere to the substrate.

Pholadidae and related taxa

Most Pholadidae produce a callus in the adult stage (e.g., Fig. 4A–B, D–F), but normally the callus either fuses along the mid-line, thereby immobilising the valves (e.g., *Teredina*) or is not fused along a dorsoventral line running through its central portion (e.g., Fig. 4B, D). In the latter case, the gap between the two sides of the callus is bridged by periostracum (which also lines the inside of the callus). This structure retains some flexibility and still allows the posterior commissure to open and close. In both cases, the shell and callus are laterally symmetrical.

Since the pedal gape becomes largely or completely closed, the bivalve most likely can no longer cleanse the borehole from mud and other detritus by flushing water out of the pedal gape. *Parapholas* and other pholads rely on a set of flexible periostracal shingles (Fig. 4B, C) to act like a seal to prevent detritus from becoming lodged between the shell and borehole by entering through the siphonal opening of the latter.

Seen in this context, the laterally asymmetric callus of *Jouannetia* is an alternative design to allow the posterior commissure to articulate in the adult stage. In this genus, a flexible bridge of periostracum between two lateral calluses would not be suitable, because the effective hinge line of the shell (i.e., the line between the dorsal and ventral condyles) is close to the posterior commissure. As a result, a modest amount of valve articulation in this region would be accompanied by a much higher amount of articulation at the pedal gape, which cannot be accommodated by stretching a sheet of periostracum. In ‘‘normal’’ pholads, instead, the situation is the opposite: the dorsal and ventral condyles, being closer to the pedal gape than to the posterior margin, cause a lesser amount of relative movement of the valves in this area than at the posterior extremity of the shell.

Unlike other pholadids (e.g., *Parapholas*, pers. obs., and *Aspidopholas*, Fig. 4E, G), *Jouannetia* does not produce a calcareous lining of the borehole walls. Thus, this genus cannot decrease the diameter of the siphonal opening of the borehole. The siphonoplax may be functional in this context by protecting the posterior region of the shell (which, in *J. globulosa*, is quite thin) from predators.

In *J. cumingii*, the siphonoplax has the added function of extending into the siphonal canal of the borehole and preventing the almost spherical adult shell from accidentally rotating within the borehole, which could cause the posterior commissure to become misaligned with the siphonal canal and prevent the extension of the siphons through the latter structure. This explains the spike-like shape of this feature. Although a spike on each valve conceivably could work just as well as a single one, a second spike might restrict the possible amount of commissural gape without providing additional advantages, especially in irregularly bent siphonal canals.

In *J. globulosa*, the shell is pear-shaped rather than spherical, and if the borehole of this species is flask-shaped as it is reasonable to assume, the above problem does not exist. Thus, the siphonoplax in this species retains a more conservative geometry and function.

The evolutionary origin of valve asymmetry in the Pholadidae remains to be discussed. In fact, the subadult and adult shells of most pholads are bilaterally symmetrical. The few exceptions are found in *Jouannetia* and in *Nettastomella*, in which the posterior extremity of the right valve extends past the posterior margin of the left one. The ontogenetic pattern and adaptive significance of this character in *Nettastomella* are unclear, but it appears to be an integral part of the shell rather than a siphonoplax, and the result of a gradual construction process, because it shows distinct growth lines and is not morphologically different from the rest of the shell.

As discussed above, bilateral symmetry of the valves is encouraged by shell rotation within the borehole, as well as by the fact that a laterally symmetrical shell applies the same pressure against the substrate on both margins of the pedal gape, thus avoiding undue mechanical stress on the attachment of the foot to the substrate. Therefore, any deviation from this symmetry may be expected to have a special adaptive value.

In this context, it is important to note that the shell of juvenile pholadids shortly after the settlement of the veliger and in the earliest phases of the boring process is laterally asymmetric (Ito, 1999, unpublished MS, and references therein). In particular, the posterior adductor muscle is oblique and allows the posterior margin of the right valve to overlap that of the left valve when the posterior commissure is adducted. In turn, this allows a higher amount of opening of the anteriorly located pedal gape, which is functional in the boring process. Other laterally asymmetrical characters also occur at this growth stage, e.g., the right ventral condyle is ball-shaped and fits into a corresponding socket of the left condyle. Thus, lateral asymmetry already is part of the pholadid *Bauplan*, and this potential resource could be tapped into (perhaps neotenically) during the evolution of *Jouannetia*.

The shell of the Teredinidae is comparable in general proportions to that of *Jouannetia* and to the early post-larval shell of pholadids (above references). It also shows a partial overlap of the valves, and consequently a slight lateral asymmetry, in its posterior region. The Teredinidae are clearly related to the Pholadidae and probably an evolutionary offshoot of the latter (e.g., Turner, 1969). Their shell biomechanics is different from that of the Pholadidae in several respects (Röder, 1977), including the fact that the soft parts of the Teredinidae are much larger than the shell itself, and therefore the posterior commissure of the shell in this family can never close completely.

Clavagellidae

The cementation of the left valve to the substrate in facultatively boring species of *Clavagella* has been interpreted as an adaptation to decrease the likelihood of the organism being accidentally buried or placed in an unfavourable orientation to carry out its respiratory and feeding functions (Savazzi, 1982a, 1999). Attachment to a small substrate is a common strategy among soft-bottom marine invertebrates to decrease the sensitivity of juveniles to comparable disturbances (Savazzi, 1982a, 1999, and references therein). Although adult tube dwelling clavagellids are believed to possess the capability for hydraulic burrowing within soft sediments, this activity likely is restricted to increasing the depth of the crypt in the sediment, and does not include reburrowing after exposure on the surface of the substrate or after major changes in the orientation of the crypt (Savazzi, 1982a, 1999).

The affinities and origins of clavagellids are unclear. At present it is not possible to state with certainty whether they evolved from soft-bottom or endolithic forms. Both ideas have been proposed (e.g., Savazzi, 1982a; Pojeta and Sohl, 1987), and both have their merits and drawbacks. It is possible that cementation of the apical portion of the left valve to a solid substrate is common (or at least that it was common in the Palaeogene), either as a relic from an earlier epifaunal or endolithic habitat or as a primary stabilising adaptation to life within soft sediment. As discussed by Savazzi (2000), the obligatory endolithic habit of *Bryopa* is probably a secondary adaptation derived from tube-dwelling ancestors, with juvenile cementation of the left valve to a substrate being used as the "stepping stone" to the endolithic habitat. This does not exclude, however, that the ancestors of the *Clavagella* lineage were endolithic, and that cementation of the left valve, as well as facultative boring, are inherited from these endolithic ancestors. In this case, *Bryopa* would represent an instance of secondary return to the original life habits of the group, a general evolutionary pattern that has been documented in several other bivalves (albeit as a secondary return to soft bottoms, rather than hard substrates; Seilacher, 1984).

The apparent lack of an adult, non-boring stage in *Bryopa* (or at least, the lack of morphologic adaptations that would allow one to identify such a stage) suggests that this genus grows and bores continuously, or at least that it has a much extended growing and actively boring phase, compared to its likely crypt-building ancestors.

Comparison of *Claudiconcha* and *Clavagella*

Although there are obvious differences in the soft parts and life habits of *Claudiconcha* and the *Clavagella* lineage, it is instructive to compare the adaptations of the two taxa with respect to cementation to the substrate. While *Clavagella* and *Bryopa* cement to the substrate by the external surface of part of or the whole left valve while the latter is still growing in a regular fashion, *Claudiconcha* does so only after the end of the regular growth process, and exclusively by the irregularly shaped margin of the right valve.

The expanded right margin of *Claudiconcha* can be regarded as analogous to the crypt of the *Clavagella* lineage, rather than to its shell. Clavagellid crypts, including those of non-boring representatives of both the *Clavagella* and *Penicillus* lineages, often are cemented to clasts (e.g., Fig. 5B–C, G), including large shells and rock substrates. The similarity between the right valve margin of *Claudiconcha* and the anterior region of the crypt in the *Clavagella* lineage extends to the fact that both grow in a gradual manner and display growth lines (Fig. 1C, 5C) while enveloping the free valve.

Other asymmetrical borers

Pedum (Pectinidae) is primarily a nestler, rather than a true borer (Yonge, 1967; Savazzi, 1998). However, it is included in this discussion because its shell often shows the type of mechanical wear that indicates it is able to modify the cavity within living coral that it inhabits. *Pedum* owes its lateral asymmetry to its epifaunal ancestors reclining onto their right valve and to the necessity of attaching the shell to the substrate by a byssus passing through a byssal notch in the right valve. Together with *Bryopa* (see above), this is an exception to the rule that lateral asymmetry is associated with determinate growth, albeit a less important one because *Pedum* cannot be regarded as a true borer.

Reasons for determinate growth in endolithic bivalves

Endolithic bivalves face the constant risk of being exposed to predators and accidental damage by erosion of the substrate. Most of them react to erosion by deepening their borehole and/or secreting secondary calcareous structures that protect and hide the exposed shell portions (e.g., Carter, 1978; Savazzi, 1982a, 1994, 1999). These structures have apparently evolved from a calcareous lining deposited on the walls of the borehole to consolidate the substrate and narrow the siphonal opening of the borehole. Therefore, it may appear surprising that boring bivalves in three unrelated families have evolved in a seemingly opposite direction and adopted a determinate growth pattern with a sessile adult stage that can neither change its position within the substrate nor secrete secondary structures external to the shell (except at the siphonal extremity of the shell or crypt).

The adaptive justification for this strategy may lie in the fact that boring in hard substrates requires a substantial amount of energy, and giving up this activity frees this energy for reproductive purposes. Thus, even though the average life span of the organism may be reduced by an enhanced vulnerability to erosion of the substrate, the net result may still be an increased reproductive success. Coupled with further adaptations that enhance the chances of survival to erosion, like attachment to the substrate in *Claudiconcha* and extreme secondary shell thickening in *C. monstrosa*, the resulting adaptive strategy is obviously viable, as shown by its multiple parallel evolution.

Conclusions

In *Claudiconcha* (Petricolidae), cementation by the expanded edge of the right valve in the adult allows this genus to survive after the shell is mostly exposed by erosion of the substrate. In this respect, the adult stage is comparable to oyster-like cemented epifaunal bivalves.

In *Jouannetia* (Pholadidae), the asymmetric anterior callus allows articulation of the valves in order to open and close the posterior commissure, while the asymmetric siphonoplax protects the posterior commissure from predators and, in *J. cumingii*, is specialised to prevent the spherical adult shell from accidentally rotating within the borehole, and thus the posterior commissure from becoming misaligned with respect to the siphonal canal of the borehole. Since the bivalve is unable to restore actively a proper position within the borehole because of the callus, this adaptation is of obvious value.

Palaeogene *Clavagella* facultatively cemented to the substrate by the left valve and subsequently bored the substrate chemically before building a crypt as the last stage of a determinate growth pattern. *Bryopa* appears to have inherited this attachment by the left valve, but has secondarily lost the crypt and its anterior fringe of tubules and reverted to a continuous growth pattern (or at least, to an extended growing phase and a lack of morphologic characters marking the adult stage).

The adaptive value of lateral asymmetry in boring bivalves is as varied as the taxonomic and evolutionary background of the asymmetric forms. Two general patterns emerge: (1) Lateral asymmetry of the shell is associated with one valve being attached to the substrate, or being prevented to move with respect to the substrate, and (2) it is associated with determinate shell growth, and arises only in the adult, non-growing phase.

There is a partial convergence between *Claudiconcha* and *Clavagella*, which are the only boring bivalve genera to attach to the substrate by one valve. The clavagellid *Bryopa* appears to deviate from the second of the above patterns in lacking an identifiable adult, non-growing stage.

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