

# ADAPTATIONS OF VERMETID AND SILIQUARIID GASTROPODS

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**ABSTRACT.** Most vermetids are cemented to hard substrates, and can extend the shell aperture high above the substrate. The shell can be bent sharply around obstacles, and internal septa allow it to become much longer than the soft parts. Several vermetids use these adaptations to live as facultative soft-bottom dwellers, but no species appears to be permanently adapted to this environment. In contrast, siliquariids are not cemented. *Siliquaria* lives embedded within sponges as a commensal or parasite, letting its exhalant current flow out of the shell and into the host sponge through a very long slit. *Siliquaria* is unique among gastropods in that it periodically increases the width of the shell slit and/or the cross sectional area of the whorl by cracking the whorl periphery into wedges, pushing them outward, and subsequently reattaching them together.

MOLLUSC shells that deviate from a regular, closely coiled helicospiral have often been described as bizarre, aberrant, peculiar and anomalous. The etymology of the term heteromorph, originally coined for non-spiral or loosely coiled ammonoids, bears a connotation of difference and deviation. The commonness of heteromorphs in the Upper Cretaceous has previously been interpreted incorrectly as an expression of decadence, heralding the impending extinction of the group.

To the functional morphologist, these and other 'peculiar' shapes constitute a promising subject for study, since a morphology that has been freed from geometric constraints (in this case, isometric growth) is likely to have specialized for a specific function, or set of functions, to a higher degree than a constrained morphology.

Heteromorphy, described as the deviation from a closely coiled, logarithmic spiral pattern, occurs also in gastropods, bivalves and serpulid polychaetes. Heteromorphic shells are actually an artificial aggregate of two radically different morphologies. In the first category, deviation from a logarithmic spiral is the result of an allometric growth programme, and shell morphology follows at all times a rigid morphogenetic programme. Heteromorphic ammonoids and strombid gastropods exemplify this group (e.g. Savazzi 1991; Seilacher and Gunji 1993). In the second category, shell morphology is largely under environmental control. This group contains serpulid polychaetes, vermetid and siliquariid gastropods, and a few unrelated gastropod genera (see concluding section). The shells of these organisms are usually cemented to, or embedded in a substrate, and conform to its topography. As a result, their shell geometry displays a large amount of individual variation.

Seilacher (*in* Seilacher and Gunji 1993, p. 243) mentioned briefly some of the adaptive values of shell morphology in openly coiled turritellids, vermetids and siliquariids with reference to the morphogenetic significance of allometric growth. Earlier studies on these families (Keen 1961; Morton 1965, and references therein) concentrated on Recent forms and on the morphology of the soft parts. In the present paper, special attention is paid to the adaptive and constructional aspects of shell morphology within these two families.

Not much is known of the life history and habits of these gastropods, and especially of the Siliquariidae (see below). Representatives of this family are usually scarce, and their secretive life habits make them difficult to study. Therefore, the approach normally followed for studies of functional morphology of Recent organisms, consisting of direct observations on the habits of living specimens, cannot be used on this occasion. On the other hand, plentiful Recent and fossil shell material was available for this study. In these circumstances, it is legitimate to treat Recent material

as fossils, and to apply to this material the inferential techniques developed for palaeobiological analysis.

#### MATERIAL AND METHODS

The following vermetids mentioned in this paper were collected by the author: *Dendropoma (s.s.) annulata* (Daudin), Recent, on intertidal sandstone and shells in Harrington Sound, Bermuda; *Dendropoma* sp., Recent, from shells of intertidal epibyssate bivalves on Bantayan Island, the Philippines; *Serpulorbis (s.s.) arenarius* (Linnaeus), Middle and Upper Pliocene, from several localities in the provinces of Piacenza and Asti, Italy; *Serpulorbis (Cladopoda) colubrinus* (Sowerby), Recent, on shallow subtidal coral reefs of Mactan Island, the Philippines; *Serpulorbis (s.s.) roussaei* (Vincent) on corals reefs in 3–4 m water depth near Tayud, Cebu Island, the Philippines; *Petalconchus (Macrophragma) cereus* (Carpenter), Recent, on shells from subtidal sand flats around Bantayan Island, the Philippines; *Petalconchus (M.) intortus* (Linnaeus), Middle Pliocene, from several localities in the province of Piacenza, Italy.

The siliquariids collected by the author are: *Siliquaria anguina* (Linnaeus), Recent, from unidentified sponges in 2–3 m water off Tayud, Cebu Island, the Philippines; and a Middle Pliocene *Siliquaria* from Castell'Arquato, Italy. This latter material is usually referred to in the literature as *S. anguina* (Linnaeus) (e.g. Rossi Ronchetti 1952). However, Linnaeus' species is a large Recent form from the tropical Indo-Pacific, while the Italian Pliocene species is obviously distinct, and more closely related to *S. ponderosa* and *S. cumingi* (see below). It is possible that the valid name of the Italian species is *Siliquaria ammonoides* (Brocchi). Since this nomenclatural problem lies outside the scope of this paper, the question is left open, and the Italian species is referred to herein as *S. sp.*

Unless otherwise indicated in the figure captions, illustrated specimens are in the author's collection, Institute of Earth Sciences, Uppsala University. Other repositories are the Department of Invertebrate Zoology, Swedish Museum of Natural History, Stockholm, Sweden, (abbreviated SM in the figure captions), the Department of Historical Geology and Palaeontology, Uppsala University, Sweden (As, It, UU) and the Muséum National d'Histoire Naturelle, Paris, France (MN).

Sections of specimens were prepared by embedding in epoxy resin for materialographic samples, cutting, grinding on diamond laps to avoid contamination by grit particles, polishing with cerium oxide bound on acetate laps, briefly etching with 1.5 per cent. hydrochloric acid, and gold-sputtering for SEM observation.

#### VERMETIDAE

The origin and early evolutionary history of this family are not known. As noted by Keen (1961), the earliest forms likely to belong to this family are from the Upper Cretaceous. All records from the Triassic and Jurassic (together with several records from later periods) probably refer to serpulid polychaetes.

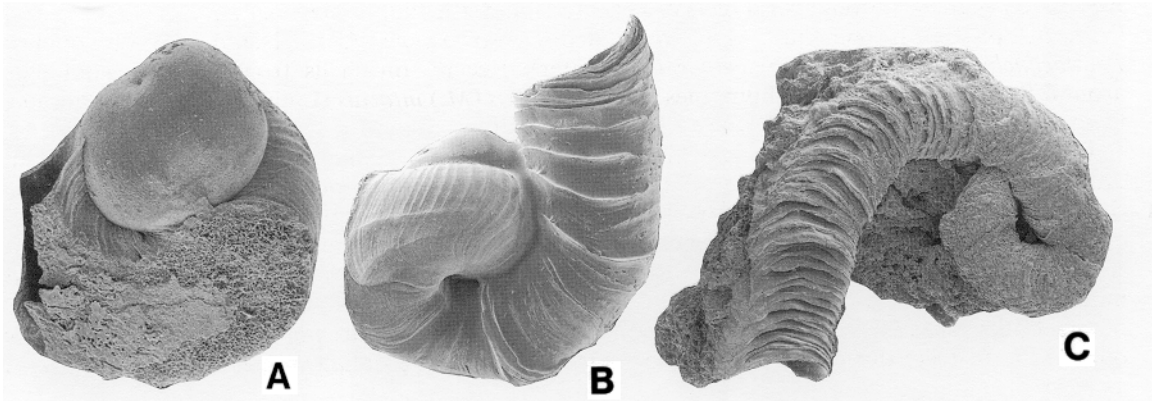
The morphological convergence between serpulids and vermetids has prompted the search for criteria to distinguish between the shells of the two groups. Shell microstructure is the safest criterion (e.g. Wrigley 1950; Schmidt 1951). Unfortunately, this character may not be preserved in fossils (especially from the Mesozoic). Vermetids differ further from serpulids in the presence of a protoconch and, usually, of internal septa or internal longitudinal ridges. Other criteria (e.g. external sculpture, colour and hardness; e.g. Mörch 1861) are unreliable or cannot be applied to fossils.

Most vermetids are loosely and irregularly coiled (always in a dextral fashion) or uncoiled, but rarely form zigzag meanders in alternating directions. This may be a result of the asymmetrical placement of the columellar muscle, inherited from regularly coiled, mobile Cerithiacea (see also discussion and references in Seilacher and Gunji 1993).

The foot of the Vermetidae is highly reduced and modified (e.g. Morton 1965). This precluded the evolutionary return to a mobile life habit.

**Cementation.** Vermetids are typically cemented to a solid substrate. The following discussion of growth and morphogenesis is based principally on the Recent *Dendropoma annulata*, with exceptions noted below.

Like most vermetids (Keen 1961), *D. annulata* lacks a veliger stage, and newly hatched larvae are mobile creepers. During this free-living stage, the shell reaches approximately 1.5 whorls (up to three to four whorls in other genera: Keen 1961; Morton 1965). Axial ribs appear toward the end of this phase. Subsequently, the shell becomes cemented to the substrate by the outer lip (Text-fig. 1A).



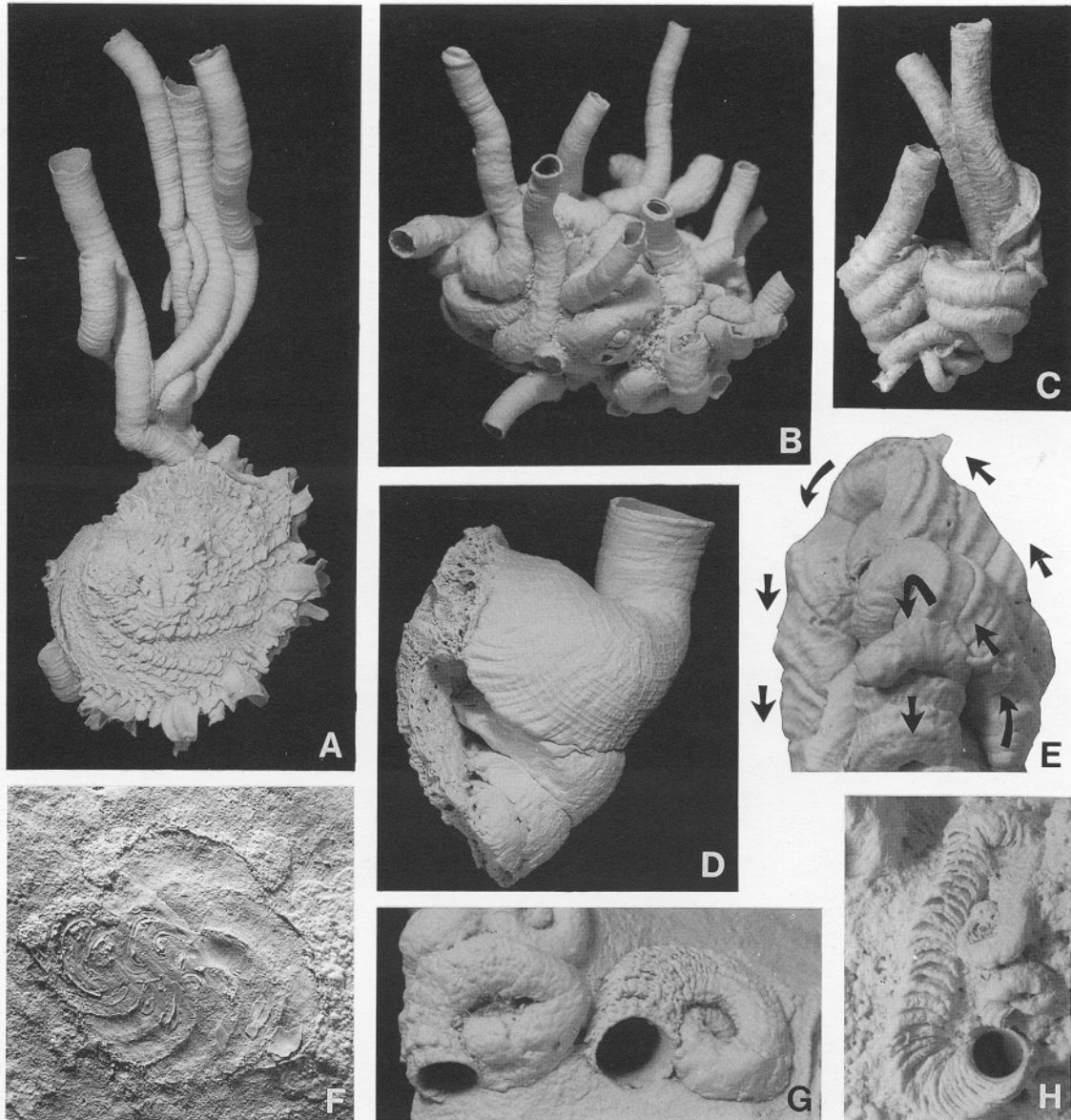
TEXT-FIG. 1. Juvenile stages of *Dendropoma annulata*, Recent, Bermuda. A, As18, larval shell with attachment scar,  $\times 80$ . B, As19, specimen showing change in coiling direction; the attachment scar is to the left,  $\times 55$ ; C, As20, specimen showing subsequent irregular growth,  $\times 18$ .

Afterwards, helical growth causes the shell aperture to lift from the substrate and to continue to grow in a regular fashion for another quarter whorl. The coiling axis then tilts approximately  $90^\circ$  and becomes roughly perpendicular to the surface of the substrate (Text-fig. 1B). This change in the mode of coiling is a constant character, and does not appear to be influenced by the orientation of the shell relative to the substrate or by the local topography of the substrate. The shell becomes again attached to the substrate, and begins to grow irregularly (Text-fig. 1C). Rough collabral frills (or different sculptures in other species) appear at this stage or shortly thereafter.

The mode of coiling of the adult shell differs in the various genera and subgenera. Typically, *Vermetus* (*s.s.*) is irregularly and loosely coiled, and adheres continuously to the substrate. Adult *V.* (*Thylaeodus*), *Trypsicha* and *Petalocochnus* (*s.s.*) are cemented to the substrate as juveniles, but afterwards pile successive whorls on top of each other to form irregular, cone-shaped shells (Text-fig. 2C; see also Seilacher and Gunji 1993). The occurrence of sudden changes in the direction of coiling, apparently caused by disturbances of the life position (Text-fig. 2E), suggests that this morphogenetic process is controlled by negative geotaxis.

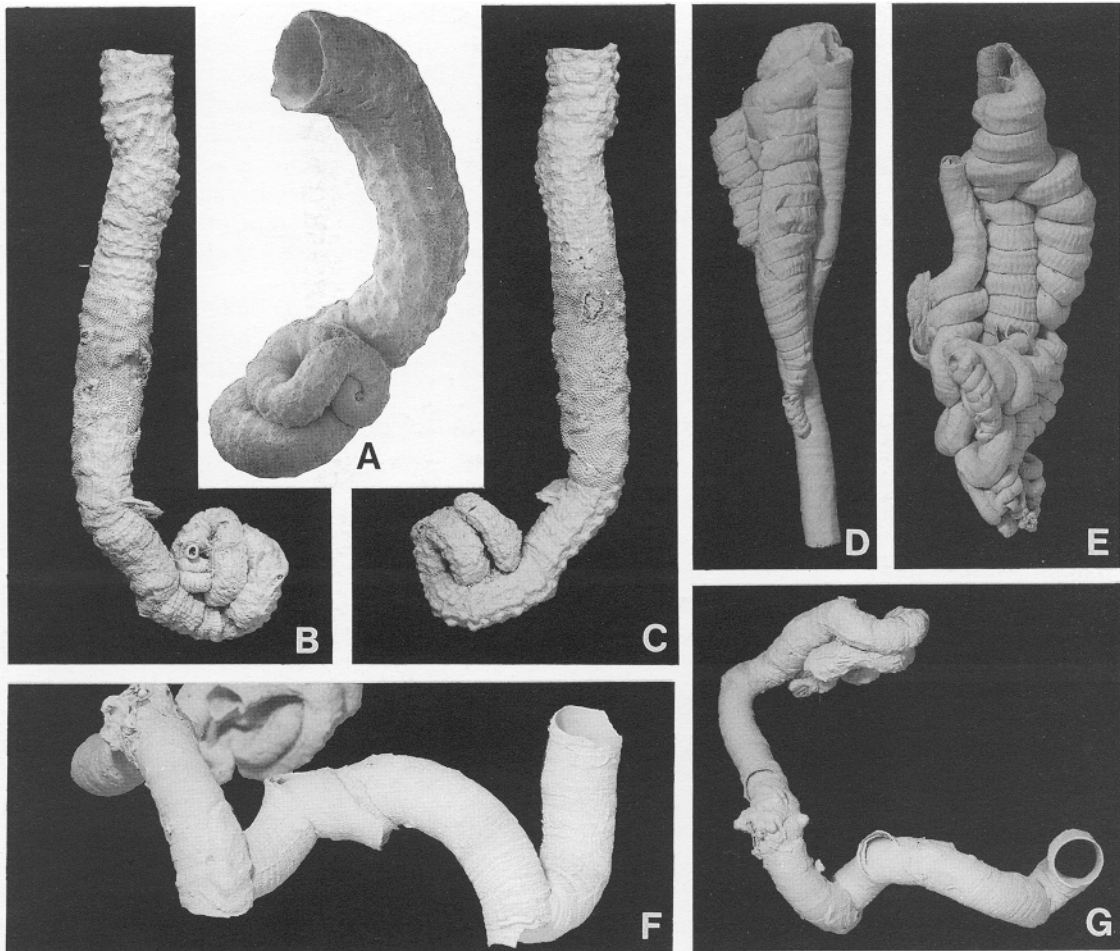
*Petalocochnus* (*Macrophragma*) is coiled in a manner similar to *Petalocochnus* (*s.s.*), but its spire is compressed sideways, and typically adheres to the substrate along one side, rather than by its apical whorls only. Juvenile *Serpulorbis* (*s.s.*) tend to coil planispirally and to remain adherent to the substrate, while coiling relaxes and becomes more irregular in adults (Text-fig. 2A–B, D). *S.* (*Cladopoda*) usually remains planispiral throughout life (Keen 1961).

At the end of growth, or at irregular intervals during growth, most vermetids build a straight, uncoiled portion of shell directed away from the substrate, called the feeding tube (Text-figs 2B–D, 3E–F). This structure carries the shell aperture high above the substrate, and therefore facilitates feeding (especially by the mucous-trap mechanism). However, feeding tubes are not cemented to the



TEXT-FIG. 2. A, *Serpulorbis roussaei* on *Chama brassica*, As21, Recent, Cebu Island, the Philippines,  $\times 0.8$ . B, *Serpulorbis riisei*, Recent, Bermuda,  $\times 1.5$  (SM). C, *Petalococonchus* (*s.s.*) sp., Recent, Bay of Bengal (SM),  $\times 1.5$ . D, *Serpulorbis colubrinus*, As22, Recent, Mactan Island near Cebu Island, the Philippines,  $\times 0.7$ . E, *Petalococonchus* (*Macrophragma*) *intortus*, It10, Pliocene, Cyprus,  $\times 2$  (UU). The arrows indicate the general direction of growth of two individuals. F, etching of the substrate (*Pinna* sp.) by *Petalococonchus* (*M.*) *cereus*, As23, Recent, Bantayan Island, the Philippines,  $\times 2$ . G, *Dendropoma* sp. semi-endolithic on *Malleus malleus*, As24, Recent, Bantayan Island, the Philippines,  $\times 2.5$ . H, *Dendropoma annulata* semi-endolithic on sandstone, Recent, Harrington Sound, Bermuda,  $\times 4$ .

substrate, and must be abandoned periodically and rebuilt. Earlier feeding tubes are apparently bored-through near their bases by the mollusc, and usually break away, leaving scars on the shell surface (Text-fig. 3F-G).



TEXT-FIG. 3. A, free-living specimen of *Serpulorbis riisei*, Recent, St Bartholomew,  $\times 9$  (SM). B–C, two views of a specimen of *Serpulorbis* sp. cemented only in its juvenile stage, Recent, Guaiquil, Ecuador,  $\times 1$  (SM). D–E, *Petalocochnus* (*Macrophragma*) *intortus*, It11–12, Pliocene, Cyprus,  $\times 1.5$  and  $\times 1.2$ , respectively (UU). The specimens in D are attached to a tube of the polychaete *Protula isseli*, and grew in the same general direction as the host. The specimens in E show a 'relay-race' growth pattern (see text for details). F–G, *Serpulorbis* sp., Recent, unknown locality,  $\times 0.8$  and  $\times 0.5$ , respectively (SM); see text for details.

**Boring.** Vermetids are often capable of removing small amounts of material from calcareous substrates (e.g. Text-fig. 2F). The actual mechanism is unknown, but the weak radula and thin, chitinous operculum tend to exclude mechanical abrasion as the principal boring action. It is possible that this capability has evolved from a character common among closely coiled gastropods, in which a thin layer of shell material is etched from the surface of the preceding whorl, prior to cementation of this to the inner margin of the shell aperture. This may remove epibionts and outer shell layers weakened by micro-borings, thereby increasing the adhesion between adjacent whorls and enhancing the mechanical stiffness of the shell. It is likely that substrate-etching in vermetids enhances the adhesion of the shell to the substrate.

Some species etch the substrate to a larger extent, and their whorls are partly or totally embedded in it (Text-fig. 2G–H). In these cases, substrate-etching may provide the gastropod with a way to economize on the amount of shell material secreted: in fact, the shell wall lining the etched region

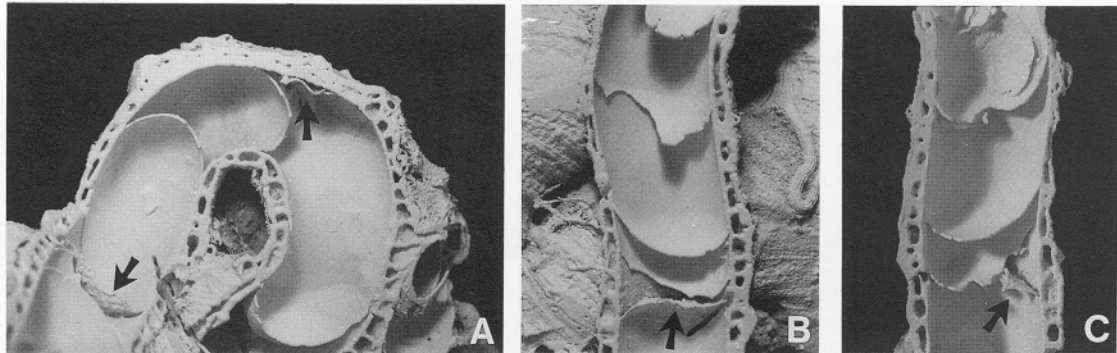
is extremely thin. Another possible function for substrate-etching is in providing a source of calcium carbonate that may allow an increased growth rate of the shell.

*Dendropoma annulata*, after reaching 5–10 mm in shell length, becomes embedded in the substrate, and its exposed region is flush with or slightly elevated from the surrounding surface of the substrate (Text-fig. 2H). This semi-endolithic habit requires the substrate to be gradually removed in order to provide growing space. In most of the observed specimens, the aperture is bent at an angle of about 90° to the direction of growth, and its whole perimeter is surrounded by shell material. In this case, periodic removal of shell material, in addition to substrate, must take place in the direction of growth. As noted by Gray (1833, p. 801), *Dendropoma*, when coiled, is often semi-endolithic in its own earlier whorls.

*D. meroclista* (see Hadfield *et al.* 1972) possesses a characteristic constriction of the shell aperture. Since the inner shell diameter increases posterior to the constriction, the constriction itself must be secreted continuously at its anterior margin and resorbed simultaneously at its posterior margin during growth, thus effectively 'moving' forward.

The Palaeogene *Elliptovermetus* was deeply semi-endolithic in calcareous substrates. For this reason, it was regarded as a subgenus of *Dendropoma* by Keen (1961). However, *Elliptovermetus* is unique in the elliptical cross-section of its whorls. It is possible that this taxon was simply convergent with, rather than related to *Dendropoma*.

*Adaptations to sessile life.* Sessile cemented organisms face two problems: overgrowth or fouling by epibionts, and erosion of the substrate. In *Vermetus* and *Spirorbis*, earlier shell portions are closed-off by a series of anteriorly concave septa deposited on the inner shell wall (Text-fig. 4). In extreme

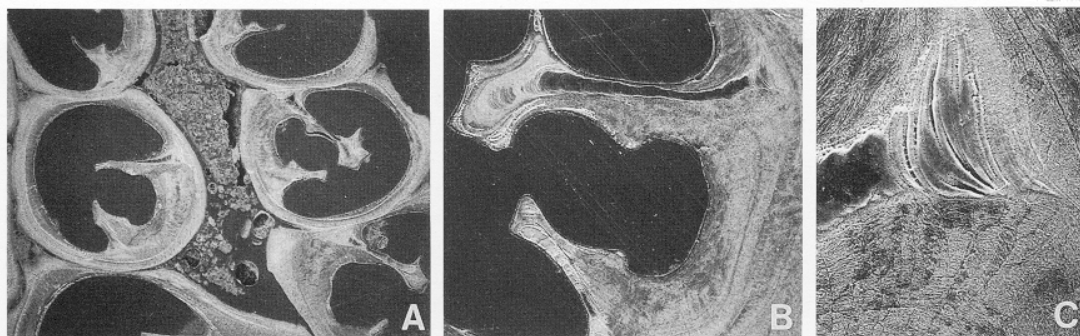


TEXT-FIG. 4. A–C, longitudinal sections of *Serpularbis* sp. (same species as in Text-fig. 3F–G), Recent, unknown locality,  $\times 1.5$  (SM). Several anteriorly concave calcareous septa are visible. Arrows indicate the remains of a few organic, anteriorly convex septa.

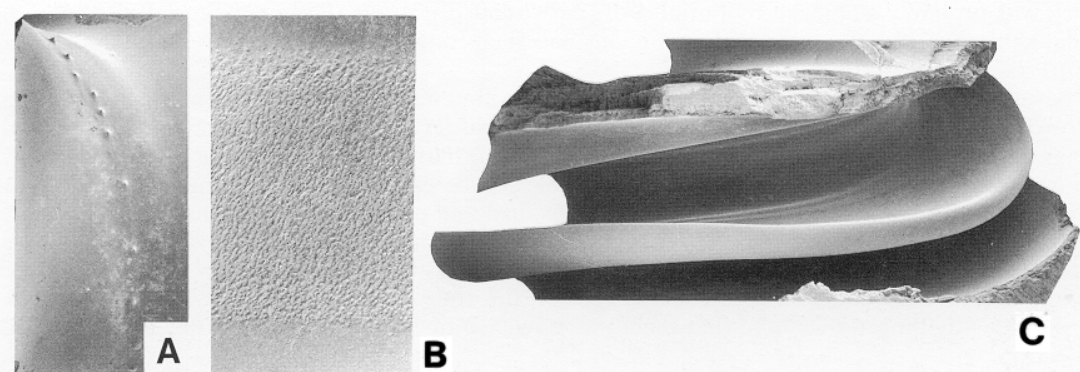
cases, the total length of the shell can be several times the length of the shell cavity. Septa are built at rather irregular intervals (Text-fig. 4), but their invariable occurrence and the approximately constant length of the body cavity in sympatric individuals suggests that construction of the septa is pre-programmed, and not triggered by external events such as shell breakage or boring.

One of the adaptive values of septa is obvious: the shell can be quickly extended to avoid overgrowth, without waiting for the soft parts to keep up with growth. Septation and fast shell growth are also indirect defences against endolithic organisms, which settle preferentially on old and worn portions of the shell. In addition, these adaptations may counteract erosion of the substrate by continuously attaching the most recent portion of the shell to a new region of substrate.

Septa are rare in *Petalococonchus*, and appear to be secreted only as a response to shell breakage or boring. Instead, this genus builds two internal ridges adherent to the columellar region of the



TEXT-FIG. 5. A–C, transversal sections of *Petalocochus intortus*, It13, Pliocene, Cyprus,  $\times 18$ ,  $\times 30$  and  $\times 180$ , respectively (UU). The apex is at top.



TEXT-FIG. 6. A–C, columellar region of *Petalocochus intortus*, It14, Pliocene, Cyprus (UU). A, spinose processes, c. one whorl inside the aperture,  $\times 8$ . B, myostracum, about three whorls inside the aperture,  $\times 50$ . C, adapical ridge (lowermost) and incipient abapical ridge (uppermost), about five whorls inside the aperture,  $\times 8$ .

inner shell wall (Text-figs 5, 6c). The two ridges display a structurally distinct, probably organic-rich core (Text-fig. 5B–C). A few smaller, secondary ridges are often located on the two main ones (Text-fig. 5B).

The extent of the two ridges is not constant throughout the shell. The following description is based on adult specimens of *P. intortus*, and therefore does not necessarily reflect a developmental sequence (which might be masked by secondary secretion and resorption). Both ridges are totally absent in the earliest whorls. The adapical ridge appears first, followed by the abapical one. After two to three whorls of approximately constant appearance, the abapical ridge gradually disappears, followed by the adapical one (Text-fig. 6c). The ridges are again absent in the last three–four whorls.

The soft parts of *Petalocochus* reflect the presence of the ridges. Unlike in other vermetids, the posteriormost region of the viscera consists of a long and narrow appendix, which apparently contains only gonad tissues (Morton 1965). The appearance of the ridges may, therefore, be associated with the onset of sexual maturity. The appendix is housed between the two ridges, and is apparently responsible for their secondary thickening, which takes place almost exclusively on their facing sides (Text-fig. 5B). The ridges appear to sustain the appendage, and may also provide a resting surface for the 'bottom' of the visceral sac near the insertion of the appendix. In the absence of septa, the ridges may therefore function in reducing the size of the soft parts with respect to the shell cavity, and in allowing the mollusc to abandon quickly earlier portions of the shell.

The inner shell wall in the columellar region bears, in the last one or two whorls, several roughly

aligned, irregularly spaced spinose processes (Text-fig. 6A). The significance of these structures is unknown. The preceding one to two whorls bear an elongated myostracum with a rough surface (Text-fig. 6B).

*Secondary soft-bottom forms.* Sessile life on the soft bottoms requires adaptations to counteract sinking into the substrate, burial by sedimentation and accidental overturning. Like many other sessile organisms, vermetids can colonize soft bottoms by attaching to objects lying on the sediment.

A Pliocene species of *Petaloconchus* (*Macrophragma*) is often attached to the tubes of the soft-bottom serpulid *Protula*. These polychaetes build a straight upward tube that may reach a few hundreds of mm in length and is anchored at its bottom by cementation to a solid substrate and/or burial in the sediment. *Petaloconchus* built a spiral shell adhering to the upward portion of the polychaete and following its upward direction of growth (Text-fig. 3D).

The vermetid in Text-figure 3B-C was attached to a small substrate in the juvenile stage. It later uncoiled and started to grow away from the substrate (as indicated by bryozoans encrusting the whole perimeter of the shell in its central portion) and probably straight upwards. At this stage, the shell was probably stabilized by burial of its early, coiled portion. The capability of attaching to solid substrates was not lost, as shown by a small shell fragment attached to the vermetid shell a short distance from its coiled portion.

Several vermetids are cemented in the juvenile stages, but become uncoiled and unattached during growth, and lie freely on or within the sediment. The cluster of two specimens in Text-figure 3F-G was cemented to a substrate (probably a piece of wood) that decayed during the juvenile stage, as shown by the fact that the attachment scar visible on the early whorls is missing in the adjacent regions of later whorls. One of the two specimens died and partly broke off, while the second was evidently collected alive. The approximately flat outline of this cluster causes it to have two stable orientations on a horizontal surface. The zigzag geometry of the last portion of shell and the numerous scars of feeding tubes directed in opposite directions (Text-fig. 3F) show that the organism was frequently flipped over, and that each time it reacted by building a feeding tube in the upward direction.

Certain soft-bottom vermetids are less dependent on the presence of a suitable substrate. A few species are commonly non-cemented, or possibly attach to substrates not larger than their protoconchs (Text-fig. 3A). These forms lie freely on or within soft sediments, and are small and irregularly shaped. As in other secondary soft-bottom dwellers, miniaturization, probably coupled with a short life span and early sexual maturity, may represent a stepping-stone into the new environment. The onset of reproduction at an early stage would decrease the risk of premature death from the hazards of sessile life on unstable sediments. All these species, however, are also known to cement facultatively to large substrates in the manner typical of vermetids.

Septation is an excellent preadaptation to sessile life on soft sediments. In addition to preventing smothering by sedimentation or overturning, this character allows the shell to achieve a large size, and therefore a large surface area, without increasing shell weight excessively. This reduces the chances of sinking into the sediment and of accidental disturbance. At the same time, shell growth can take place without the need for the soft parts to increase correspondingly in length. Not surprisingly, the shell portion closed off by septa is especially long in soft-bottom species.

A cluster of several individuals of the same species as the one shown in Text-figure 3F-G, probably collected from soft sediments, was sectioned. In addition to numerous anteriorly concave calcified septa, traces were found of a few organic septa, anteriorly convex, immediately preceding a calcareous septum, and apparently extending backwards into a lining of the inner shell walls (Text-fig. 4). These organic septa are apparently a membrane secreted before the shell chamber was sealed off. This membrane may retard or prevent the closed-off chamber from being filled with sediment pouring in through small borings (in fact, early whorls are heavily bored by clionid sponges, with openings on the outer and, sometimes, inner shell surfaces). The anteriorly convex geometry of the organic septa may be a result of shrinking, either during the life of the mollusc, or as a result of desiccation after collecting. A tantalizing, but still unproven, possibility is that the organic septa



may have contained bubbles of gas, decreasing the specific gravity of the shell and preventing it from sinking into a soft sediment. Field observations on the contents of the closed-off chambers in this and similar species will be necessary to test this hypothesis.

Several vermetids form monospecific clusters of tubes, occasionally of considerable overall size. Sometimes, these aggregates are not cemented to solid substrates but lie on soft sediments (e.g. see Mörch 1861). A large size is a common adaptational strategy in secondary soft-bottom dwellers (e.g. oyster-like bivalves; Seilacher 1984). Large organisms are stable because their bulk makes them difficult to dislodge. The same goal is achieved by a cluster or colony of small individuals attached to each other. This is the case in soft-bottom colonial corals and nodular calcareous algae.

Aggregates of vermetid tubes may also be regarded as mud-floats or snow-shoes, since their low specific gravity (compared with most oysters, corals and calcareous algae) makes sinking unlikely. As in solitary soft-bottom vermetids, shell septation becomes highly adaptive in this context by reducing shell weight and preventing sediment from filling empty shells. Thus, empty vermetid tubes retain their mud-floating function, and provide a stable substrate for subsequent generations.

In a few cases (especially in the genus *Petalococonchus*), juveniles settle on the uppermost portions of an older individual, and continue its upward growth (Text-fig. 3E). This 'relay-race' mode of growth may be an effective way to counteract rapid sedimentation, and has also been observed in soft-bottom oysters (e.g. Chinzei *et al.* 1982, fig. 4).

#### SILIQUARIIDAE

Unlike vermetids, most siliquariids are not cemented to a substrate but live (or, presumably, lived) embedded within sponges. Aside from this, very little is known of the life habits of this family. The earliest siliquariids are from the Middle Triassic.

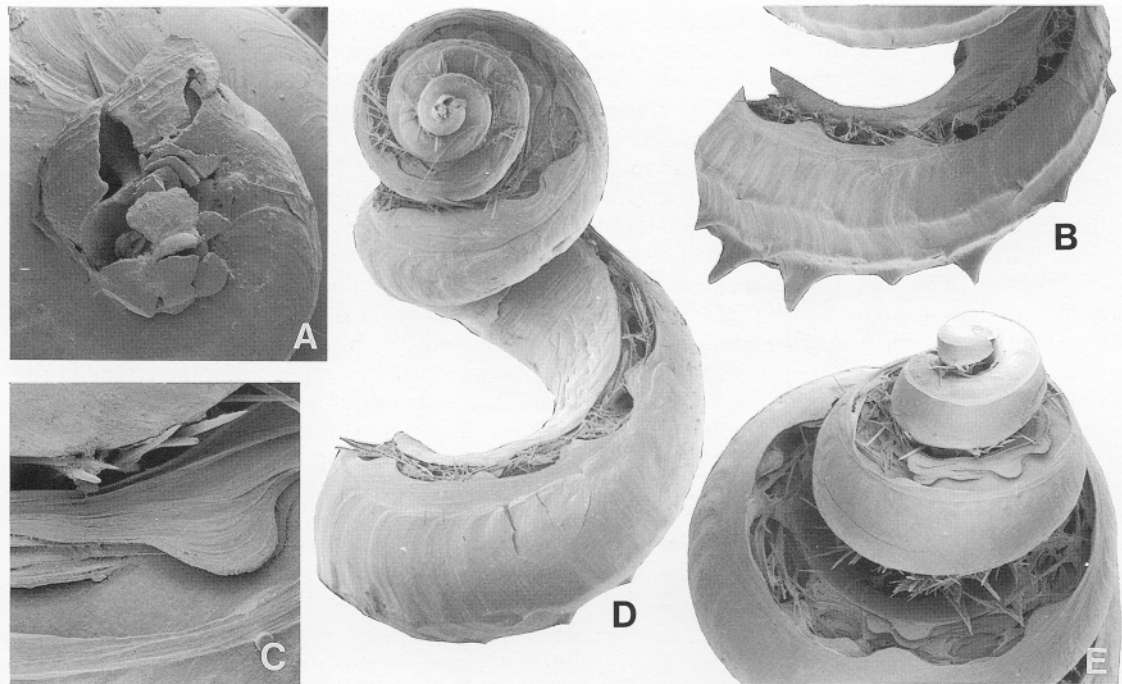
Most siliquariids possess an elongated apertural slit along the right side of the spire. This slit may remain open for several whorls, and sometimes spans the entire length of the shell cavity.

*Growth.* Several specimens of *Siliquaria anguina* were available embedded in their host sponges. It proved exceedingly difficult to clean these specimens without breaking the larval shell. The only intact protoconch collapsed when coated for SEM observation (Text-fig. 7A). Observations with a light microscope prior to coating showed a very thin, translucent shell composed of two to three whorls, significantly smaller than the larval shell of most vermetids and bearing a weak pustulose sculpture changing into an axial sculpture on the last whorl. At this stage, probably representing a free-living habit, the shell has no slit. Subsequent growth takes place without the change in orientation of the coiling axis observed in all vermetids.

Juvenile *Siliquaria* probably settle on a suitable sponge and become embedded passively by growth of the host. At this point, the shell starts to assume its adult shape and sculpture, and the slit originates as a broad sinus (Text-fig. 7A, D-E). The slit on the first 1-3 post-larval whorls is closed by a secondary deposit of shell material level with the surrounding regions of the shell (Text-fig. 7A, E). In later whorls, the edges of the slit are thickened by several subsequent layers, and the slit is closed by a final 'ceiling' deeply sunk within the slit (Text-fig. 7C, E).

The first few whorls are rather closely coiled, and adjacent whorls sometimes touch each other. Even in these cases, there is no cementation between successive whorls. Later whorls are coiled loosely but always visibly. Unlike vermetids, which are capable of bending their shell sharply, *Siliquaria* appears unable to 'manoeuvre' in close quarters. Instead, its whorls are wound laxly around obstacles, and the shells of intertwined individuals can usually be moved with respect to each other. The aperture projects slightly from the substrate, as shown by common encrustations by epizoans in the apertural region of live-collected specimens.

The earliest post-larval whorls are thickened secondarily and the apical region is closed by a septum. Occasionally, several septa are present. They are highly concave in the anterior direction, rather than approximately hemispherical like in the Vermetidae, and may occupy a quarter whorl or more.



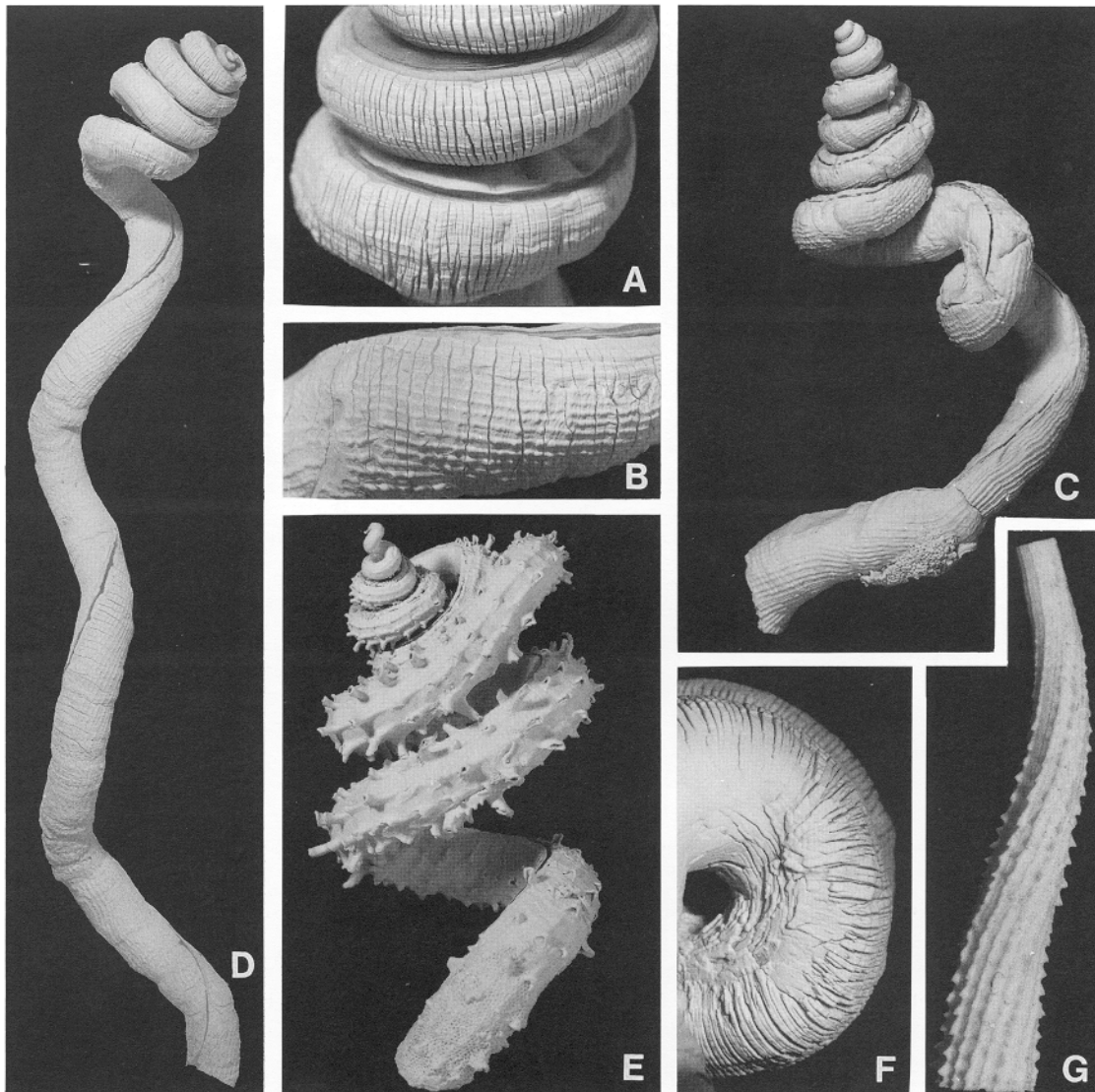
TEXT-FIG. 7. A–E, early whorls of *Siliquaria anguina*, Recent, Cebu Island, the Philippines. A, As26, collapsed protoconch,  $\times 100$ . B, As27, onset of spiny sculpture,  $\times 8$ . C, As28, secondarily closed shell slit,  $\times 75$ . D, As26, juvenile shell, showing slit filled with sponge spicules (same specimen as in Text-fig. 7A),  $\times 16$ . E, As28, early whorls of juvenile specimen, showing the changes in morphology of the shell slit,  $\times 16$ .

*Adaptations to embedding.* *Siliquaria* can apparently adapt to the growth rate of its host sponge by varying the degree of translation of the shell aperture about the coiling axis and by changing the direction of growth (Text-fig. 8C–E). This is responsible for the rather irregular aspect of siliquariid shells.

In *Siliquaria*, the shell slit remains open for the whole length of the shell cavity, which in adult *S. ponderosa* (Text-fig. 8D) spans over 90 per cent. of the total shell length. In *Pyxipoma*, on the other hand, the slit is open for no more than half of the shell length (and often considerably less). A corresponding slit in the mantle faces the shell slit (Morton 1951). The mantle slit of the Siliquariidae is not homologous to the superficially similar mantle slit of vermetids, which is present only in females, functional in brooding, located in a different position and not matched by a shell slit. The gill of *Pyxipoma* is as long as the shell and mantle slits (Morton 1951). The same probably applies also to the much longer slits in *Siliquaria*.

It is very likely that the shell and mantle slits and the extremely elongated gill of the Siliquariidae are coadaptations to life within sponges. Morton (1951) proposed a function for these structures in eliminating waste products of the gastropod. However, my observations on *S. anguina* show that the slit is partly filled with sponge tissues and spicules (Text-fig. 7B, D). Any particulate material ejected by the mollusc through the slit should clog it in a short time. In addition, the mouth and anus of *Pyxipoma* (and, presumably, *Siliquaria*) are located close to the shell aperture, and faeces and other waste products are therefore discharged conveniently there.

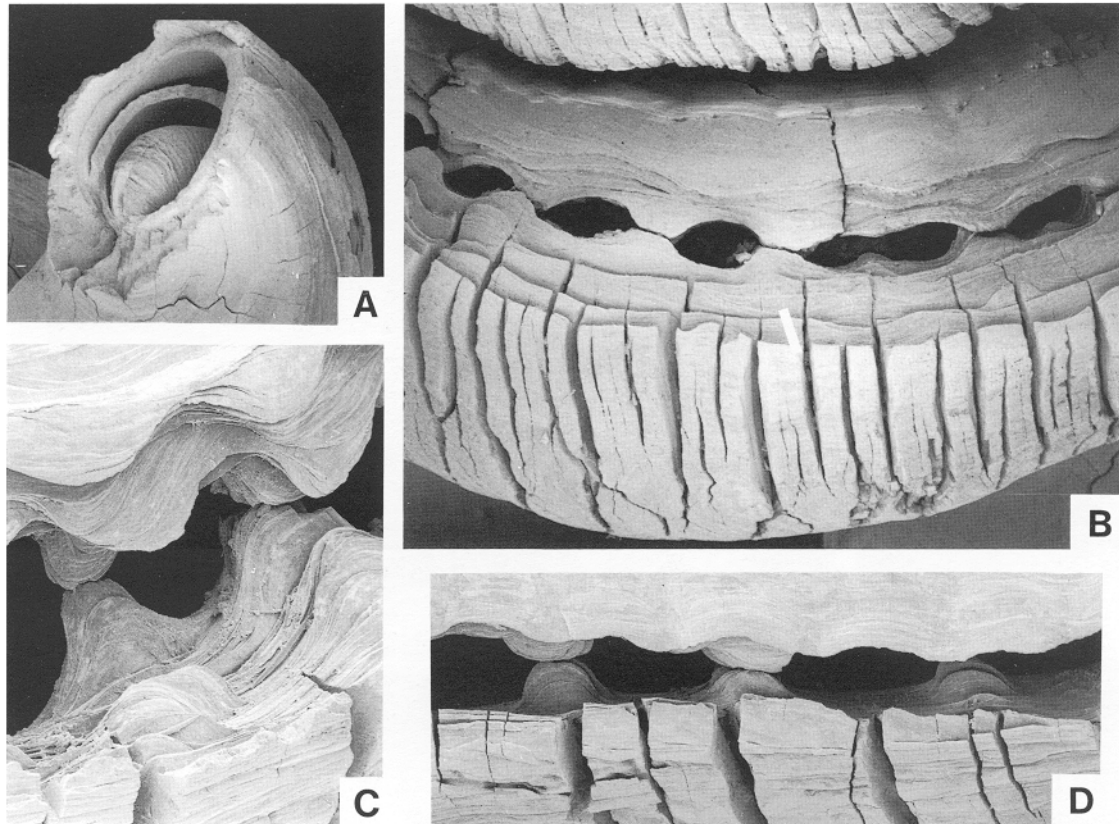
A passage of solid matter (e.g. fragments of sponge tissues) from the host into the mantle cavity of the gastropod appears unlikely. Although this might conceivably provide a source of food for the gastropod, it is unlikely that the mantle tissues and/or ctenidia are sufficiently strong to extend into the slit and tear apart pieces of sponge facing the shell slit. In addition, the region of the mantle



TEXT-FIG. 8. A–B, *Siliquaria ponderosa*, Recent, unknown locality,  $\times 3$  (SM); details of outer surfaces of the whorls in coiled (A) and uncoiled (B) regions. C, *Siliquaria cumingi*, Recent, Awaji-shima, Japan,  $\times 1.5$  (SM). D, *S. ponderosa* (same specimen as in Text-fig. 7A–B),  $\times 0.7$ . E, *S. anguina*, As25, Recent, Cebu Island, the Philippines,  $\times 1.3$ . F, *S. ponderosa* (same specimen as in Text-fig. 6A–B, D), umbilical view, with transversal and longitudinal crack patterns,  $\times 3.5$ . G, *Pyxipoma brevifissurata*, Middle Eocene, Paris Basin, France,  $\times 3.5$ .

cavity facing the slit houses the exhalant current. Any materials entering the slit would therefore be carried to and ejected from the shell aperture without passing through the ctenidia. The same consideration tends to exclude a water current passing from the sponge to the mollusc. Moreover, such a current would be of little use to the mollusc, since it would consist of water that has already been strained of food particles by the sponge.

The remaining alternative is a water flow from the mantle cavity of the gastropod into the canal system of the sponge. In contrast with the other alternatives, this would provide obvious advantages for the gastropod. Two interpretations are possible. If the slit is connected to the exhalant canals



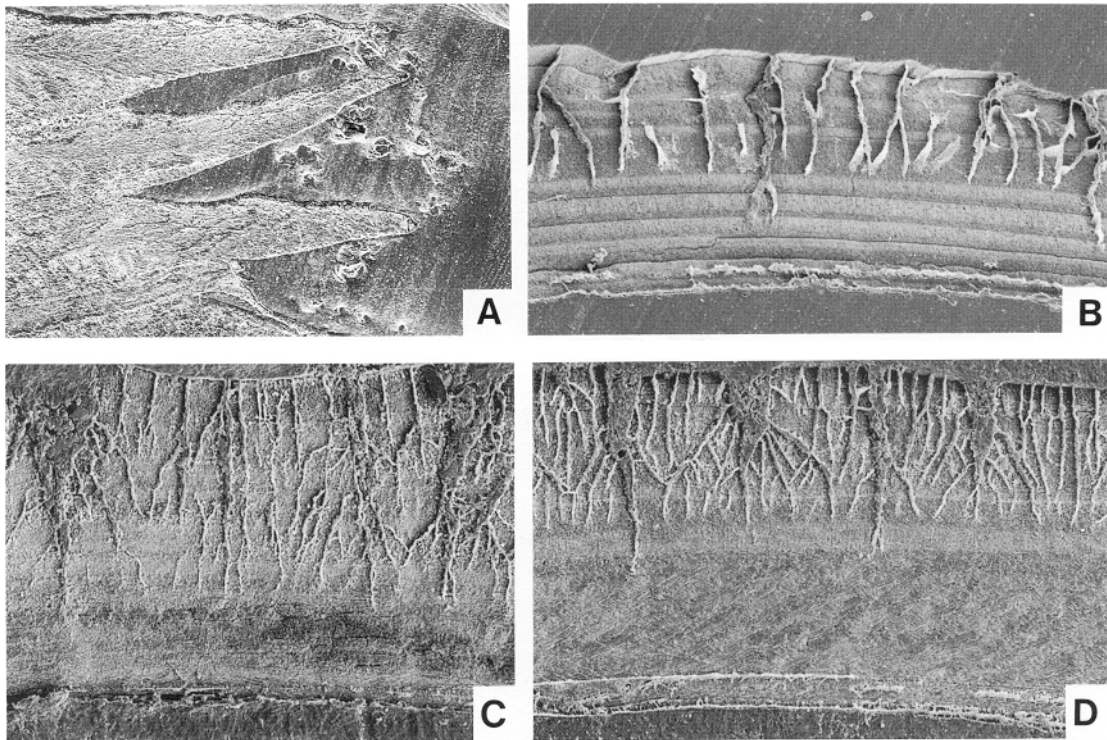
TEXT-FIG. 9. A–B, *Siliquaria* sp., Pliocene, Diolo, Italy. A, It15, septa in apical region,  $\times 8$ . B, It16, secondarily enlarged slit and whorl,  $\times 16$ . C–D, *Siliquaria cumingi*, Recent, Awaji-shima, Japan (SM). C, detail of denticles along facing margins of the shell slit,  $\times 60$ . D, detail of shell slit,  $\times 40$ .

of the sponge, the exhalant current of the gastropod would mix with the exhalant stream of its host. In this case, the adaptive value of the slit would be of reducing or avoiding the need for the mollusc to maintain an exhalant current following the extremely long and narrow path back to the shell aperture along the mollusc mantle.

A completely different effect would be achieved if the sponge tissues facing the shell slit of *Siliquaria* contain ostia or inhalant canals. In this case, the pumping action of the sponge would suck water from the mantle cavity of the gastropod. The resulting draft would continuously force new water into the shell aperture and through the ctenidia. In this case, *Siliquaria* might take advantage of the feeding activity of the host sponge and partly impair it (by feeding the host with strained water), with no corresponding advantage for the host. This habit could therefore be characterized as parasitism. Also this arrangement would reduce or avoid the need for the exhalant current to reach the shell aperture.

The topological relationships of *Siliquaria* and the tissues of its host have never been studied. In the available material of *S. anguina*, openings in the shell slit often seem to correspond to 'holes', or channels, in the sponge tissues (Text-fig. 7B, D). However, it is not possible to decide whether these holes are inhalant or exhalant canals.

The above interpretations could be verified in living material by observing whether the exhalant current of *Siliquaria* leaving the shell aperture is weaker than the corresponding inhalant current. A connection between the water systems of the mollusc and its host could be detected by injecting

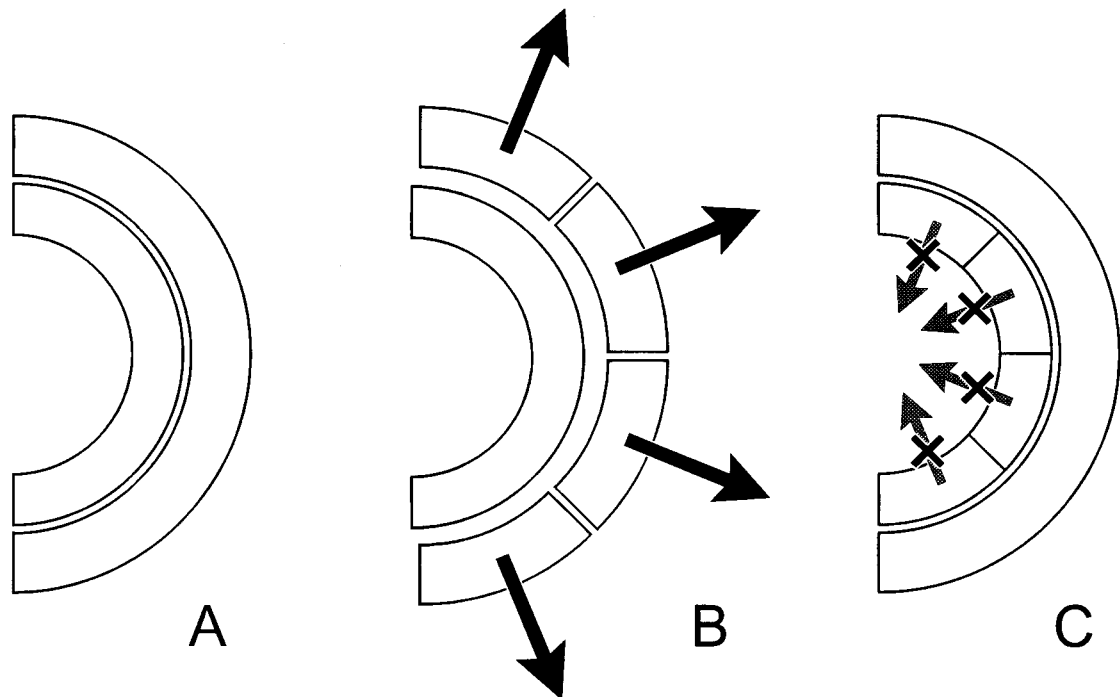


TEXT-FIG. 10. A, *Siliquaria anguina*, As29, transversal section of inner margin of the shell slit, Recent, Cebu Island, the Philippines,  $\times 160$ . The small bodies located between the frills of the slit edge are transversally sectioned sponge spicules. B–D, *Siliquaria* sp., It17–19, longitudinal sections of the outer periphery of the shell whorl, Pliocene, Diolo, Italy,  $\times 100$ ,  $\times 150$  and  $\times 150$ , respectively. The cracks are filled with embedding resin, and stand up in relief after chemical etching.

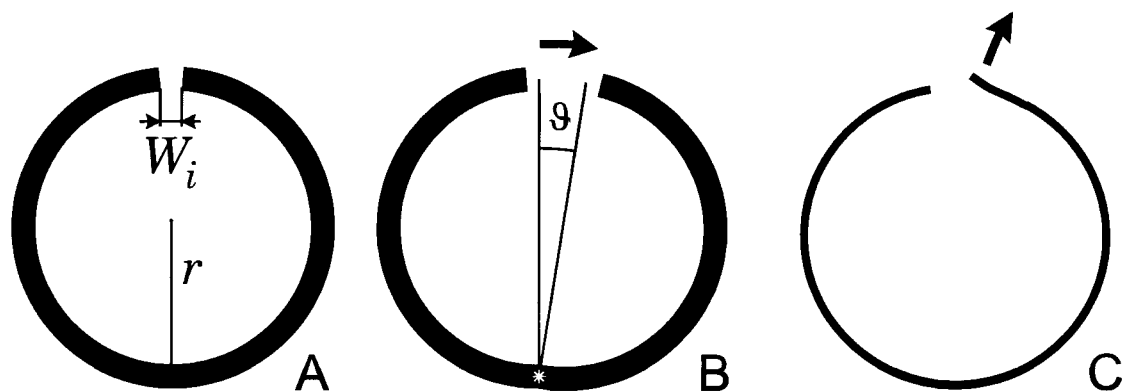
a soluble tracer in the inhalant stream of *Siliquaria*, and looking for the tracer in the exhalant stream or in the tissues of the sponge. Only a cytological examination, however, will show whether *Siliquaria* is commensal or parasitic on its host sponge.

Two types of shell sculpture are represented in *Siliquaria*. Most species, including *S. ponderosa* (Text-fig. 8D), *S. cumingi* (Text-fig. 8C) and *S. sp.* (Text-fig. 9), appear smooth or lightly sculptured at a superficial examination. On the other hand, a small group of species, including *S. anguina*, possesses long and fragile fluted spines (Text-figs 7E, 8B). This last type of sculpture is extremely effective in anchoring the shell within its host sponge (as easily experienced by trying to extract representatives of these species from their substrate). The spines may also have a simultaneous function as shock absorbers, by breaking under the impact of objects tossed by waves, and thereby protecting the shell in a manner analogous to the function proposed for echinoid spines (Strathmann 1981). Obviously, this function applies only to spines located close to or above the surface of the host sponge. The spiny *Siliquaria* are invariably thinner-shelled and more fragile than the smooth ones. Typically, spines are absent in the earliest whorls (Text-fig. 7D–E).

A close examination of the 'smooth' species of *Siliquaria* reveals a unique relief pattern consisting of deep, narrow cracks starting at the right rim of the slit and running up to  $180^\circ$  around the whorl in a roughly axial orientation (Text-figs 8A–B, F, 9B, D). These cracks cross the growth lines, and must therefore be a secondary feature. Since the cracks are wider near the surface, they must have appeared at the outer shell surface and extended progressively to deeper, secondary shell layers while the shell was gradually thickened. In *S. ponderosa* (but not in the other species observed for



TEXT-FIG. 11. Secondary enlargement of the slit in *Siliquaria* can take place by cracking into wedges and expansion of the outer half of the whorl (B versus A), but not of the inner half (C).



TEXT-FIG. 12. A, schematic cross-section of shell whorl in *Siliquaria*. B, the same after cracking and expansion. C, a thin shell wall can flex in the neighbourhood of the slit. See text for details.

this paper) a second pattern of cracks, perpendicular to the first one, occurs in the region of the whorl diametrically opposite to the slit (Text-fig. 8F).

Sections of the cracks in a plane parallel to the shell slit reveal that each of the major cracks visible at the shell surface branches toward the interior of the shell (Text-fig. 10B–D). The samples in the figures were embedded in epoxy resin, and the resin filling the cracks stands out in relief after etching. Major cracks are often intercalated by a hierarchical system of progressively shallower and narrower cracks (Text-fig. 10C–D). The smallest of these cracks do not branch, or show only an

incipient branching. There is no visible difference in shell structure between the cracked and non-cracked regions. This, together with the fact that the spacing and orientation of cracks is slightly irregular, suggests that the location of each individual crack is not predetermined. Rather, the cracks probably become distributed in a self-organizing fractal pattern controlled by the local relief of strain in the immediate neighbourhood of each crack.

In a few cases (Text-fig. 10C), the outer shell surface between two major cracks is convex (in a manner reminiscent of mud cracks), possibly as a result of accumulating stresses within the shell material, rather than being the result of actual shrinkage of the outer layer. The increase in the radius of curvature of the whorl periphery, resulting from expansion of the shell slit (see also below), could be the source of these stresses. Accumulating stresses may also be adaptive in facilitating cracking and thereby in reducing the amount of pressure the mollusc must apply to the shell walls. In fossils, the presence of stresses in the shell material results in occasional post-mortem cracks of the inner margin of the shell slit (Text-fig. 9A-B). Cracks in this region are absent in live-collected Recent specimens.

Restricting the cracks to half of the shell wall prevents the shell stiffness from being compromised. The exclusive occurrence of the cracks on the right side of the shell slit is the result of an obvious geometric constraint. In a dextrally coiled shell (Text-fig. 11A), cracking the right margin of the slit allows the wedge-shaped fragments of the shell to separate as they move away from the slit (Text-fig. 11B). This is the cause of the progressive widening of the cracks during ontogeny. If cracks were located on the inner margin of the slit, instead, the shell wedges would be compressed together when pushed laterally away from the slit (Text-fig. 11C), which would prevent their movement.

As an analogue, architectural arches composed of wedge-shape bricks or stones bear their own weight, as well as the weight of overlying masonry, thanks to the fact that the shape of the arch transforms weight into a lateral force pressing adjacent wedges together. Applying an upward force to the arch, instead, would cause its wedges to separate and the arch to collapse.

That the spacing of cracks in *Siliquaria* is related to the amount of shell coiling is shown by the fact that cracks are less dense in shell portions displaying a large amount of uncoiling (Text-fig. 8B versus A). In these portions, widening of the slit results in a lesser amount of reciprocal distancing of the shell wedges. At a limit, transversal cracking would not be necessary at all to widen the slit in a straight portion of shell.

Secondary widening of the slit takes place in two stages. First, the shell is cracked, perhaps by hydrostatic pressure within the mantle tissues, and the wedges are pushed outward. Subsequently, a secondary layer of shell material is secreted on the inner side of the expanded shell, cementing the fragments together. The process is repeated periodically, and at each stage the cracks propagate to the latest shell layer. Obviously, this process would be impossible in a free-living mollusc, because the shell would literally fall to pieces. However, the sponge tissues surrounding the shell form a resilient container that holds the pieces in place until cemented together.

The pressure necessary to break the shell into wedges does not increase appreciably with shell thickness, since the cracks need only to propagate through the last layer of deposited material. It cannot be excluded that expansion of the slit is preceded by partial resorption of part of the inner shell layer. However, the very presence of cracks indicates that resorption of the inner shell layer is not total.

The outward displacement of the right side of the whorl broadens the slit and increases the cross sectional area of the whorl. A quantitative evaluation of these effects can be attempted by means of a simple geometric analysis (Text-fig. 12). I assume that half of the circumference of the whorl is pushed outward (arrow in Text-fig. 12B), pivoting at a point located 180° away from the slit (asterisk in Text-fig. 12B), i.e., where the second pattern of cracks, parallel to the slit, is located in *S. ponderosa*. For small angles of rotation, the cross-sectional area of the whorl and its volume increase by:

$$I \cong \frac{(2r)^2 / 2 \sin \theta}{r^2 \pi} 100.$$

where  $I$  is the percentage increase in area or volume,  $r$  the whorl radius, and  $\vartheta$  the angle of rotation. On the other hand, the width of the slit (and hence its open area) increases by:

$$W \cong \frac{2r \sin \vartheta}{W_i} 100,$$

where  $W$  is the percentage increase in width and  $W_i$  the initial width.

As an example, from measurements of a specimen of *S. ponderosa* we can take an initial inner whorl diameter of 7.8 mm and a slit width of 0.8 mm. Based on the above formulas, rotation of the outer half of the whorl by  $5.7^\circ$  would cause a 10 per cent. increase in the width of the slit and a mere 1.6 per cent. increase in the cross sectional area and volume of the whorl. Actually, a considerable secondary thickening of the shell takes place, as necessary to cement the shell wedges together after each expansion. Therefore, a small displacement of the shell wedges causes the cross sectional area of the whorl to remain constant or actually decrease during growth. This is the situation observed in *S. ponderosa* and *S. cumingi*. In these species, the only significant effect of shell cracking is to widen secondarily the shell slit.

In the Pliocene *S. sp.*, the shell slit was sometimes widened to a greater extent. In these cases, shell material was added along the inner and/or outer margins of the shell slit, apparently to counteract an excessive increase in width of the slit (Text-fig. 9B). In these cases, a significant secondary increase of the cross sectional area of the whorl, computed at 10–15 per cent. (or occasionally more) took place. This secondary increase in the volume of the shell cavity might have provided room for larger gills and/or gonads, or may have facilitated the respiratory currents. Therefore, shell cracking and expansion may have a different adaptive value in different species.

*S. sp.* and *S. cumingi* do not possess the longitudinal pattern of cracks observed in the larger and thicker *S. ponderosa*. In the first two species, the shell is thinner, and shell wedges apparently flex along their entire length, instead of breaking at their base as in *S. ponderosa*. Consequently, a mechanism is needed to prevent these resilient wedges from returning to their original position and close the shell slit once the mollusc stops applying a pressure from within the shell. This function is provided by rounded denticles projecting in facing positions from each side of the slit and touching each other in its middle (Text-fig. 9B–D). Once the facing denticles are separated by pressure within the shell and new shell material is added at their tips, the shell slit is forced to remain open. Significantly, denticles are absent in *S. ponderosa*.

The shell slit of siliquariids has been described in the literature as either being continuous (like in *S. ponderosa*) or consisting of a series of aligned holes (as in *S. cumingi* and *S. sp.*). This description is misleading, since the tips of facing denticles touch each other, but (unlike in the gastropod *Haliotis*), are not cemented together. This allows the denticles to separate at a subsequent growth stage, in order to allow further widening of the slit (Text-fig. 9C). It may be noted that the tips of facing denticles must be slightly separated during their construction, in order to allow mantle lobes to adhere to these regions. Once the mantle retracts from these regions, release of the internal pressure within the shell causes the resilient shell wedges to close the small gaps between the tips of the denticles. This causes an inevitable small 'loss' in the achieved increase of the width of the shell slit and/or whorl.

Transversal cracks, albeit much shorter, narrower and more broadly spaced, are also present in the spiny species *S. anguina* (faintly visible in Text-fig. 7B, D). This species is characterized by a thin shell. The higher flexibility of the shell wall may allow the wedges to flex outwards in proximity of the slit edge (Text-fig. 12C), allowing the cracks in this species to be shorter and less frequent. It is also possible that the minimal amount of secondary enlargement of the slit in *S. anguina* has no adaptive significance, and that the cracks in this species are a vestigial character, left over from earlier evolutionary stages. This is suggested also by the fact that the denticles along the sides of the slit are shaped and spaced irregularly, and sometimes do not occur in facing pairs.

It may be objected that shell resorption would be a more effective way to broaden the slit. However, resorption would necessitate mantle tissues to adhere periodically to the edges of the slit,



possibly narrowing or closing it. If *Siliquaria* is dependent on the shell slit for expulsion of the exhalant current, as suggested above, this could impair the flow of water through the ctenidia for an unacceptable length of time. Adhesion of the mantle to the sides of the slit may also be prevented by invasion of this area by sponge tissues (e.g. Text-figs 7B, D-E, 10A).

A further explanation of the peculiar mechanism of secondary cracking could be that shell resorption may not be available (and, in fact, is not observed) in the siliquariid Bauplan. Lastly, no amount of secondary resorption could allow the increase in cross-sectional area of the whorl provided by shell cracking in Pliocene *S.* sp. (see above).

*Other siliquariids.* *Pyxipoma* differs from *Siliquaria* in its much shorter shell slit. The association of *P. weldii* with sponges is comparable to that of *Siliquaria* (Morton 1951). *Pyxipoma* never reaches large sizes, a factor that may be connected to its relatively shorter gill and slit.

Specimens of *P. brevifissurata* (Deshayes) from the Eocene of the Paris Basin are extremely uncoiled (Text-fig. 8G). Some fragments are practically straight, but remnants of the original dextral coiling are still detectable as a twisting of the sculpture around the shell surface. The morphogenetic significance of this character was discussed by Savazzi (1990a). The spiny sculpture and lack of cementation scars suggests life within sponges, but the very short and narrow slit might indicate the lack of a parasitic association like the one proposed for *Siliquaria*, or a lesser reliance on the feeding current of the host.

The Eocene genus *Agathirses* possessed a series of perforations instead of a slit. Each perforation originated as a shallow sinus at the shell margin. Only one or a few perforations were open simultaneously. The rest were closed secondarily by a calcareous plug. The gradually uncoiling shell, spiny sculpture and apparent lack of cementation scars suggests a life habit embedded in a sponge or a comparable organism.

*Stephopoma* differs from other siliquariids in living attached to rock surfaces (Morton 1951). This form is not truly cemented, but rather lives loosely embedded in the layers of encrusting epibionts that cover the substrate. This genus lacks a shell slit, and feeds by ciliary currents as well as ctenidial sweeping (Morton 1951). Unlike the Vermetidae, the shell of *Stephopoma* is not septate, and consequently the length of the soft parts imposes a limit on the maximum shell length. Also unlike the Vermetidae, dextral coiling in *Stephopoma* is always evident, even in the openly coiled portions.

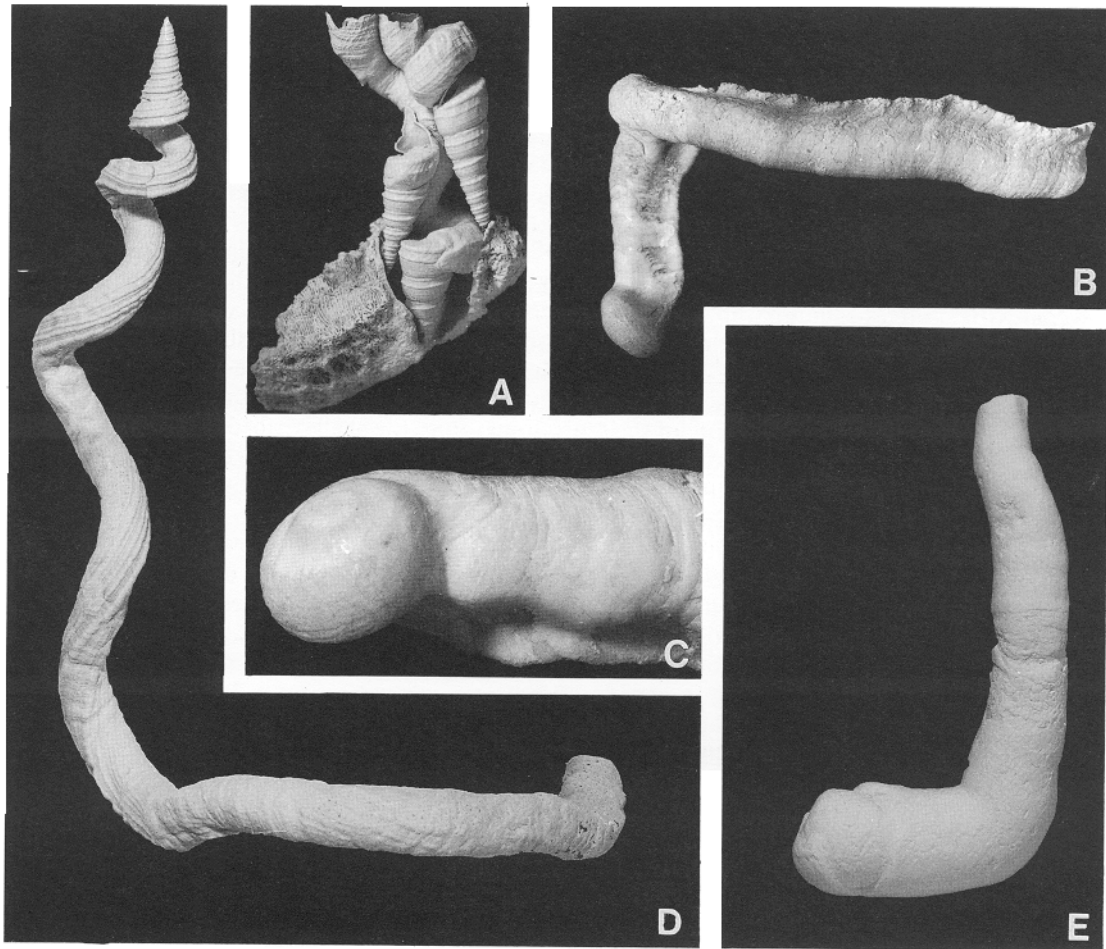
Judging from the illustration by Cossmann (1912, pl. 10, fig. 29), the Miocene '*Vermetus*' *circumlobatus* appears to possess many regularly spaced, slightly flaring traces of sinuses in a position corresponding to the siliquariid slit. These traces are too small and numerous to be the scars of broken feeding tubes. It is possible that this species is actually a siliquariid related to *Agathirses*.

None of the above forms displays the secondary shell-cracking pattern described in *Siliquaria*.

#### OTHER ATTACHED GASTROPODS

The turrnellid *Vermicularia* is convergent with the Vermetidae in the habit of cementing to a solid substrate (Morton 1953; Gould 1968, 1969). Unlike the Vermetidae, however, *Vermicularia* has a relatively large free-living, regularly coiled stage (Text-fig. 13A, D). In addition, this genus can remain facultatively at the free-living stage by retaining its juvenile life habit (Gould 1968). *Vermicularia* builds internal septa only in the first shell whorls, usually as a response to boring by clionid sponges. In these cases, the septa usually continue forward into a thick lining of the inner shell wall that may extend for several whorls and reduces considerably their inner cross sectional area (pers. obs.). Usually, these septa do not reduce substantially the length of the shell chamber with respect to the total shell length.

A few Eocene species referred by Cossmann (1912) to *Vermicularia* (*Anguillospira*) are septate and completely uncoiled. They might be vermetids, rather than turrnellids. Since they appear to lack attachment scars, they probably were obligatory soft-bottom dwellers. A few other forms, also referred to *Vermicularia* by Cossmann (1912), resemble this genus but show only an incipient



TEXT-FIG. 13. Other Recent attached gastropods. A, *Vermicularia spirata* attached to coral, Harrington Sound, Bermuda,  $\times 1.5$ . B-C, *Magilus antiquus*, Mauritius,  $\times 0.5$  and  $\times 1.2$ , respectively (MN). D, *Vermicularia lumbricalis*, Senegal,  $\times 0.7$  (SM). E, the tube-dwelling bivalve *Teredina personata*, Middle Eocene, Grignon, France,  $\times 1.2$ . This specimen shows a conspicuous secondary elongation of the crypt at its siphonal extremity.

uncoiling, or (in the subgenus *Casimiria*) possess closely coiled whorls with a broad umbilicus. Since these forms display neither attachment scars nor the irregular development that should be expected from completely sessile forms, they may represent different life habits. It is possible that the resemblance of these forms to *Vermicularia* and to each other is due to convergence, and that they represent a polyphyletic evolutionary trend within the Turritellidae.

The coralliophilid *Magilus* cements its shell to colonial corals and becomes embedded by growth of the host. Its shell uncoils irregularly, much like a vermetid but without cementation scars (Text-fig. 13B-C), and becomes filled secondarily with a solid, very heavy deposit, leaving a short conical cavity for the soft parts. The regularly coiled apical whorls of *Magilus* are much larger than in *Vermicularia* (Text-fig. 13C). However, it is likely that *Magilus*, like most coralliophilids, is also essentially sedentary during the regularly coiled stage.

The coralliophilid *Rapa* becomes embedded in soft coral. The shell of *Rapa*, however, is regular or only slightly irregular. The only shell character that may be related to its life habit is the very elongated, ventrally closed siphonal canal present in a few species. Other coralliophilids attach to

soft corals by folding the margins of the aperture around thin coral branches (e.g. see Kosuge and Suzuki 1985).

The Hipponicidae are permanently attached to a substrate (typically a mollusc shell) by a calcareous plate, probably not homologous to an operculum, secreted by the foot. The Miocene *Rothpletzia rudista* is an extremely specialized hipponicid attached to nodules of calcareous red algae lying on soft sediments (Rothpletz and Simonelli 1890). The foot plate is deeply cup-shaped and much larger than the shell proper, which is flattened into a broad cone (in fact, the original description regarded the foot secretion as an apically cemented shell, and the true shell as an operculum; Rothpletz and Simonelli 1890). The soft parts and the shell margins were continuously elevated above the surface of the substrate by growth of the foot secretion and by septation of its internal cavity. *Rothpletzia* may be regarded as morphologically convergent with rudist bivalves.

The shell of the Silurian tubinid *Semitubina sakoi* was embedded in a symbiotic colonial coral. In the adult shell of *S. sakoi*, the last whorl was openly coiled and extremely thin-walled (Kase 1986). Other tubinids possess long and slender spines, comparable to the sculpture of *Siliquaria anguina* (see Knight *et al.* 1960). It is likely that these gastropods were embedded within sponges, hydroids or other organisms. The regular (albeit uncoiled) shell geometry of these forms suggests that they were mobile epifaunal forms carrying a relatively small encrusting host, rather than sessile forms like the Siliquariidae.

The Carboniferous pseudozygopleurid *Helminthozyga* possessed a regularly coiled shell in the juvenile stage, but later in ontogeny became irregularly uncoiled in a manner reminiscent of *Vermicularia* and *Siliquaria*. *Helminthozyga* does not appear to have been cemented to a substrate. It is possible that, like *Siliquaria*, it was sessile and embedded within a larger organism.

#### CONCLUDING REMARKS

The adaptations that enable cemented vermetids to survive fouling, overgrowth and shell breakage appear to be reasonably good preadaptations to the evolution of free-living forms. In fact, several vermetids can live facultatively in soft-bottom environments, but no Recent or fossil species can be characterized as an obligatory soft-bottom form.

Vermetids can be compared with tube-dwelling bivalves (Savazzi 1982). Several genera of Gastrochaenidae, Teredinidae, Pholadidae and Clavagellidae have evolved into secondary soft-bottom dwellers, either as a facultative or obligatory life habit. These bivalves build calcareous envelopes, or crypts, that completely encase the soft parts and isolate them from the surrounding sediment except for siphonal and, sometimes, accessory openings. The shell may be free within the crypt, or one or both valves may be attached to it. The siphonal extremity of the crypt can be secondarily extended in length (Text-fig. 13E). This allows the organism to avoid smothering by sedimentation and to react to disturbances of life position by changing the direction of growth, and therefore has essentially the same adaptive significance as growth of the vermetid shell at its aperture.

Tube-dwelling bivalves have no analogue of the septation observed in vermetids. Instead, these bivalves react to burial or encroaching epibionts by extending their siphons. This is enabled by the higher efficiency of the gills in most boring and tube-dwelling bivalves, compared with gastropods. The Lithophaginae are the only boring bivalves that react to overgrowth of the substrate (typically, a living coral) by moving in the posterior direction and filling the anterior region of the borehole with meniscus-shaped layers of secondary lining (e.g. see Krumm and Jones 1993). This filling material could be regarded as a potential preadaptation to life on soft bottoms, like septation in the Vermetidae. However, the Lithophaginae did not evolve into soft-bottom forms, probably because the lesser efficiency of their gills did not allow the development of long siphons (cf. Savazzi 1982).

The Siliquariidae possess morphological adaptations partly resembling those of the Vermetidae. However, the obligatory association with sponges of most siliquariids may have constituted an evolutionary closed-alley that prevented the radiation of these gastropods into the soft bottoms. Association of the Coralliophilidae with coelenterates, together with the heavy nature of the

secondary filling in *Magilus*, may have had a similar constraining effect on the evolution of this family.

The secondary enlargement of the shell slit and/or cross sectional area of the whorl in *Siliquaria* has no parallel among gastropods. However, a few bivalves are known to modify their shell geometry secondarily by cracking selected portions of their shells and moving them relative to each other (Chinzei *et al.* 1982; Savazzi 1990b). Secondary cracking also takes place in the pseudoligamental region of rostroconchs. In all these cases, only one crack (or bundle of cracks) is present in each valve or shell. In contrast, the shell of *Siliquaria* typically cracks into several hundred wedges during growth.

Siliquariid gastropods have been largely neglected by both taxonomists and functional morphologists. As shown by this paper, these gastropods display several extremely peculiar characters, some of which need to be confirmed by studies on living specimens. So far, only one siliquariid species has been observed alive (Morton 1951), and its morphology and life habits are atypical of the family.

The general failure of attached gastropods to mimic the evolutionary pathways of bivalves (e.g. see Seilacher 1984) and become secondary soft-bottom dwellers may be explained, at least in part, by the constraints imposed by earlier evolutionary 'choices' (see above). An additional reason may be that gastropods have evolved into hard-bottom sessile organisms later than bivalves (mostly in the late Mesozoic and/or early Cenozoic for gastropods, *versus* the late Palaeozoic and Mesozoic for most bivalve lineages). Therefore, the time available for the evolution of secondary changes of life habits in these gastropods has been considerably shorter than in bivalves, and competition for the soft-bottom niches may have been correspondingly harder.

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