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TUBE FORMATION IN THE BIVALVIA – CSÖVEK KIALAKULÁSA
KAGYLÓKNÁLUM'83
BUDAPEST

ABSTRACT: The typical bivalve is more or less enclosed by two calcareous shell valves secreted by the outer mantle folds. In the wood-boring Teredinidae and the Lithophaginae the burrow is lined by either a secretion, in the case of the former, or, in the latter, by relocation and deposition of chemically etched calcium carbonate. This structurally simple tube merely smooths the enclosing wall of the burrow. A complex adventitious tube is produced, however, in representatives of the Gastrochaenacea and Clavagellacea. In the former (*Eufistulana*) the tube is separate from the shell and is secreted by reflected inner and middle folds, enlargement anteriorly being by dissolution of the basal cap and growth downwards. In the latter (*Brechites*), the true shell is tiny and embedded in a relatively enormous tube. Because the body is covered by periostracum, formation of the tube is from glands in the pedal gape, to secrete the basal perforate plate, and from the orifices of the siphons to secrete the siphonal tube. Enlargement is only possible posteriorly, with growth increments evident at the siphonal end of the tube. The most advanced members of these lineages occupy extremely narrow infaunal niches entombed within their tubes. Less specialized members of both groups (*Cucurbitula*, *Clavagella*) are borers, but possess an essentially similar anatomy, the lining of the boring being secreted in the same way as their tube-dwelling relatives. It is concluded that modifications to a boring mode of life are pre-adaptive, facilitating exploitation of other habitats, most notably a return to an infaunal life style, albeit in different ways.

INTRODUCTION

The Bivalvia have evolved an infaunal life style protectively enclosed within an antero-posteriorly divided shell, and exploiting by either deposit or suspension feeding, the rich detritus of the sea floor though some have radiated into fresh waters too. One would expect this rather passive life style to be evolutionarily conservative. This is true of the more ancient protobranch bivalves where a flowthrough system of water into and out of the mantle cavity from anterior to posterior restricts the animal to the sediment-water interface. With the development of a posteriorly located inhalant and exhalant flow system, however, particularly by the more modern filibranch and lamellibranch bivalves, the option was available for an expansion in habitat range and life styles. Some, retaining the infaunal habitat, burrow to a variety of depths – achieving protection by siphonal retraction or by deeper digging. The neotenous retention by the adults of the larval byssus in a number of predominately filibranch bivalves has allowed the exploitation of the heteromyarian endobysate and epibysate modes of life leading to the colonisation of hard surfaces and further phases of adaptive radiation. Some of the filibranch lineages have attained a monomyarian form with cementation and, for a few, relative freedom from the substrate of their birth and the capacity for swimming.

Some of the more modern predominately lamellibranch lineages have taken to a nestling mode of life with byssal attachment (again by neotenous retention of this larval feature) ensuring secure anchorage. These bivalves are predominately solitary, in contrast to the more gregarious filibranch colonisers of exposed shores. From such nestling groups have arisen the borers of, usually calcareous, soft stones (including corals), shells and wood. These borers often line their burrows with a calcareous secretion or relay the products of their erosive actions, to smooth the borehole. As examples of this life style, the Teredinidae and Lithophaginae are discussed. In, however, two otherwise boring families – the Gastrochaenidae and Clavagellidae – an adventitious tube is secreted that has permitted the adoption of, or rather the return to, an ancestral infaunal life style. How these tubes are formed and how they have permitted a return to a more primitive infaunal life mode in representatives of these families is the particular subject of this paper.

THE LITHOPHAGINAE

Less specialised members of the Lithophaginae (Mytilacea) bore calcareous, sandstone and shale rocks (Fig. 1A) and line the distal end of the burrow with calcium carbonate (Fig. 1B). Because of a fragile, smooth and polished shell, it is widely accepted (POJETA and PALMER, 1976) that boring is a chemical process though GOHAR and SOLIMAN (1963 a; b) and SOLIMAN (1969) for example believed it to be mechanical. TURNER and BOSS (1962) and WARME and MARSHALL (1969) have shown that so long as the matrix of the substrate contains

some calcium salts (> 5%), chemical erosion is possible. The active agent in the erosion process is not acidic but thought to be a calcium-chelating mucus (JACCARINI *et al.*, 1968). The secretion is produced from glands in the middle folds (Fig. 1C) (not inner folds as suggested by YONGE (1955)) and largely acts anteriorly in inhabitants of inorganic rocks and anteriorly and posteriorly in inhabitants of living corals (MORTON and SCOTT, 1980). YONGE (1955), WARME and MARSHALL (1969) and BARTHEL (1981) have asserted that lithophagines actively secrete calcium carbonate to line their borehole. There is little evidence to support this and the pallial glands hitherto described (MORTON and SCOTT, 1980) do not secrete calcium carbonate. The burrow walls are lined, instead, by a white deposit that most recent authors (NIELSEN, 1976; MORTON and SCOTT, 1980; KLEEMANN, 1980; SAVAZZI, 1982) agree is formed by dissolution of the burrow heading and which is relocated on the wall to smooth it. The same deposits are also, in coral boring lithophagines, cemented to the shell valves (Fig. 2A) where they may artificially extend them posteriorly and form a distinctive patterning often with „teeth” to interlock the valve margins posteriorly e. g. *Lithophaga pulchra* and *L. hanleyana* (KLEEMANN, 1980) (Fig. 2B). Evidence that the deposit lining the burrow is not secreted (from the siphons as suggested by YONGE (1955)) comes from those lithophagines inhabiting living corals where there is no tube produced beyond the aperture to the burrow. Rather the coral attempts to overgrow the aperture but is inhibited by a further secretion from a gland in the mantle (MORTON and SCOTT, 1980). Thus it is the coral which responds to the presence of the bivalve and not the bivalve which secretes calcium carbonate to extend a siphonal tube beyond the reach of the enclosing corals as is the case in *Gastrochaena* (Gastrochaenidae) (BROMLEY, 1978). The only possible exception to the general situation in the Lithophaginae is *Fungiacava eilatensis* inhabiting, in commensal relationship, fungiid corals (*Fungia*, *Cycloseris*, *Diaseris*) (GOREAU *et al.*, 1969; 1970; 1972). Here middle mantle folds are reflected over the shell and the animal dissolves and apparently secretes (GOREAU *et al.*, 1972) calcium carbonate to fit its burrow snugly (Fig. 3). GOREAU *et al.* (1972) did not, however, provide evidence of secretion and it is here contended that, as with other lithophagines, with so much available calcium, there would seem little reason to actively secrete more.

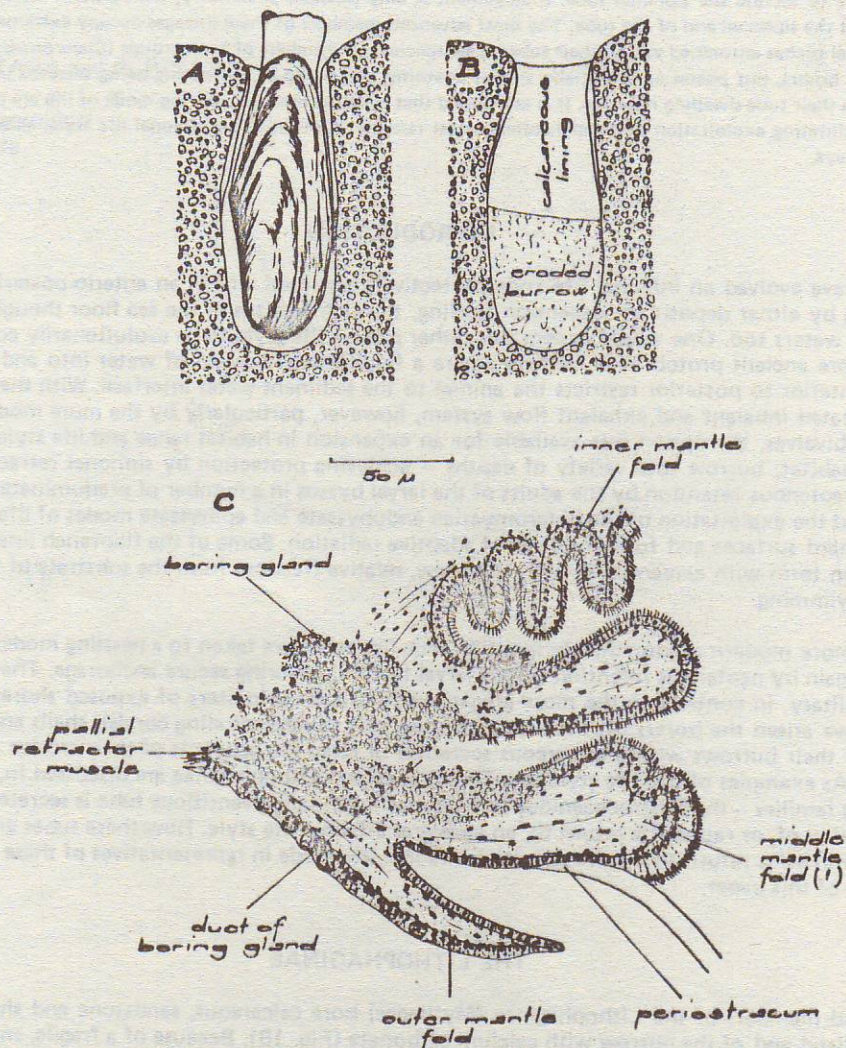


FIG. 1. The Lithophaginae. A, A specimen of *Lithophaga* in its burrow with siphons extended and attached by a byssus to the burrow wall. B, A *Lithophaga* borehole showing the eroded burrow and the calcareous lining distally. C, A transverse section through the ventral mantle margin of *Lithophaga simplex* showing the boring gland. (C, after MORTON and SCOTT, 1980).

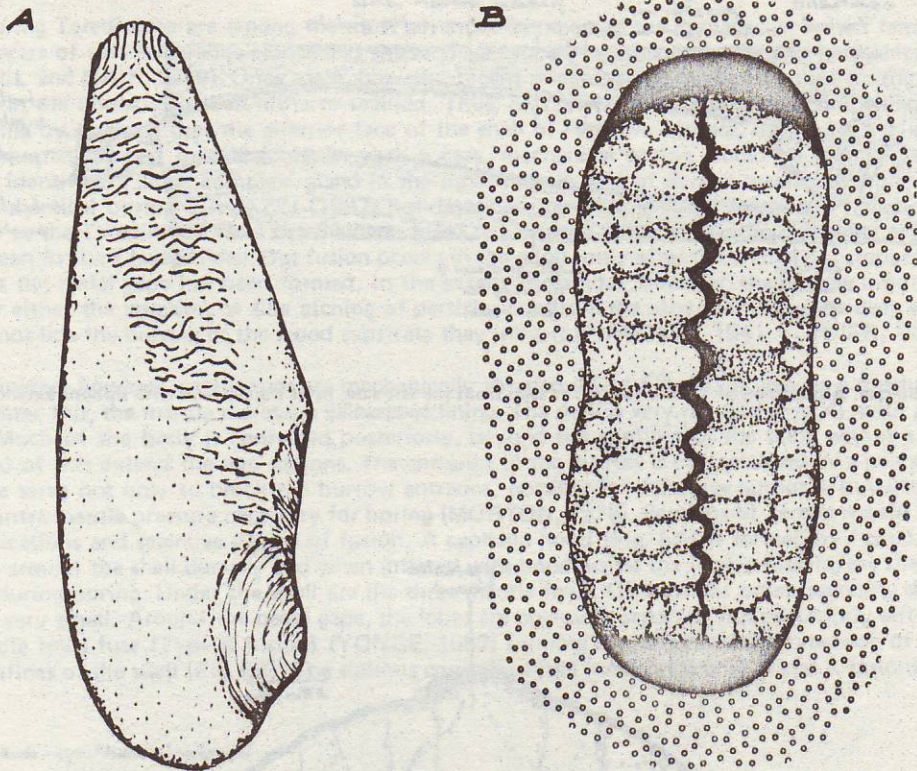


FIG. 2. The Lithophaginae. A, The shell of *Lithophaga hanleyana* as seen from the right side and showing the white calcareous material deposited on the shell in a characteristic pattern. B, The shell of *Lithophaga hanleyana* as seen from the posterior aspect, inside its burrow, with the white calcareous deposits forming interlocking teeth.

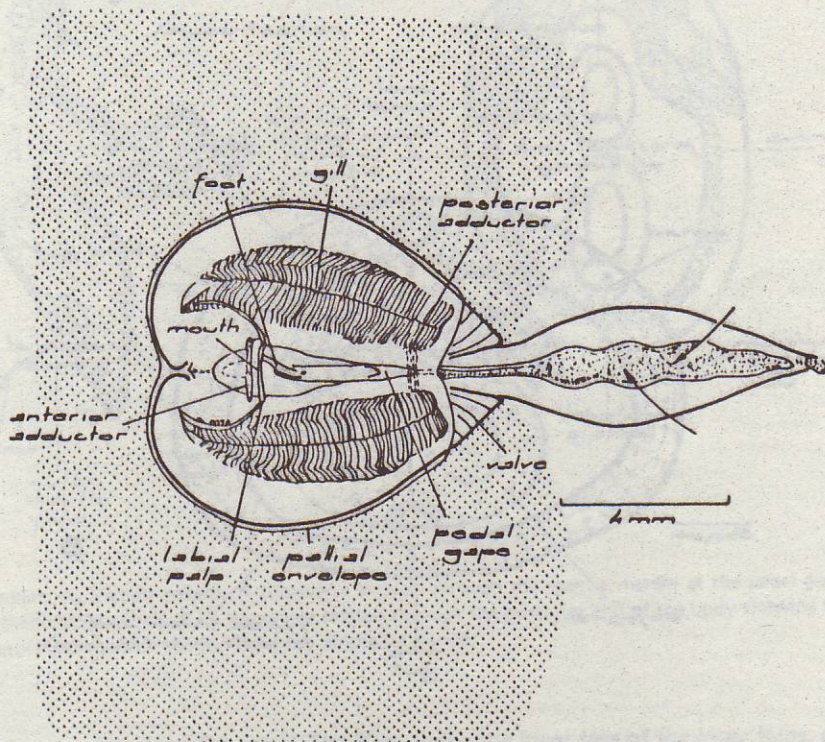


FIG. 3. The Lithophaginae. *Fungiacava dilatensis* inside its burrow and seen from the ventral aspect with the shell and pallial envelope cut away to expose the organs of the mantle cavity (after GOREAU *et al.*, 1969).

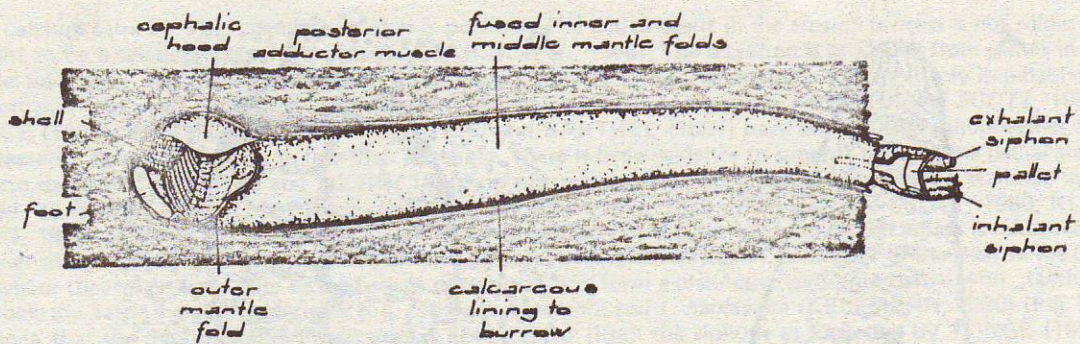


FIG. 4. The Tereidinidae. A specimen of *Teredo nautilus*, as seen from the left side, in its burrow and with siphons extended.

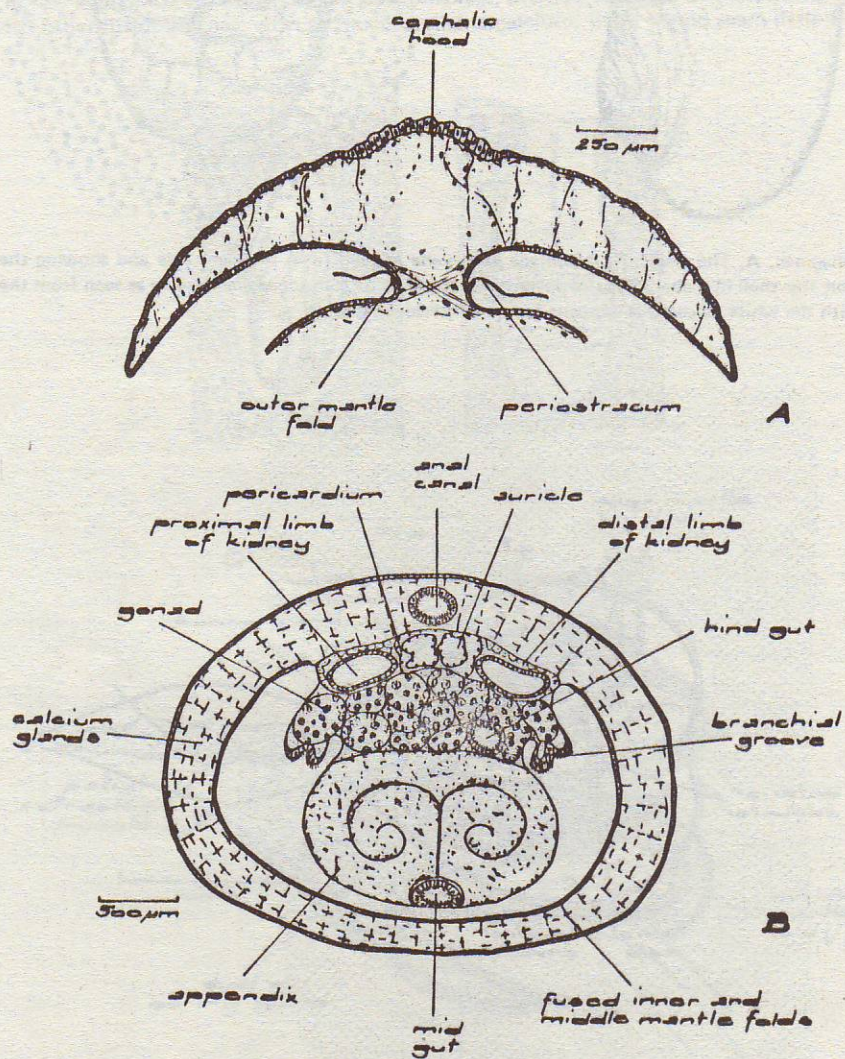


FIG. 5. The Tereidinidae. A, *Teredo nautilus*, a transverse section through the whole animal posterior to the shell and demonstrating the great thickness of the mantle with contained calcium carbonate secreting glands.

THE TEREDINIDAE

The wood boring Teredinidae are among the most advanced members of the Pholadacea, a sister family, Pholadidae, being borers of soft calcareous stones and shales. This process is, apparently, largely mechanical (YONGE, 1963; ANSELL and NAIR, 1969). Once again, however, recent research suggests that chemical boring may be more important in the Pholadidae than hitherto realised. Thus, SMITH (1969) has provided compelling evidence of chemical boring by showing that the anterior face of the shell of *Penitella conradi*, during boring, is covered by reflected, presumably inner, mantle folds. In such a case, mechanical boring would be impossible. MORTON (1984 c) has identified a large, complex gland in the inner mantle fold of *Barnea manilensis* which may be responsible for chemical boring. SAVAZZI (1982) has described the Eocene fossil *Teredina* (Pholadidae), convergently similar to the Teredinidae. Here the shell was fused to a burrow lining of calcium carbonate – situation not unlike that seen in the Clavagellidae. But fusion occurs in the adult, only after the animal has stopped boring and a callum over the pedal gape has been formed. In the extant Pholadidae, however, the burrow is not lined, being smoothed by either the abrasion or fine etching of particles one from the other. Similarly the deep water Xylophaginae do not line the burrow of the wood substrata they inhabit (PURCHON, 1941; TURNER, 1977).

In the Teredinidae, however, soft woods are mechanically abraded (MILLER, 1924), leaving a roughened burrow wall. To counter this, the mantle secretes a calcareous lining. The shell is very reduced (Fig. 4), with a file-like anterior face. Much of the body is contained posteriorly, beyond the confines of the shell, within a pallial tube. From the end of this extend the two siphons. The entrance to the burrow is characterised by a pair of calcareous pallets. These serve not only to block the burrow entrance, possibly for defensive purposes, but also to establish the positive intra-mantle pressure necessary for boring (MORTON, 1978). Sections of *Teredo navalis* establish the pallial modifications and selective degree of fusion. A cephalic hood (Fig. 5A) is formed by fusion of inner and middle folds around the shell dorsally and when inflated with blood assists the foot in bracing the shell at the tunnel heading during boring. Under the shell are the three mantle folds. Of these the outer, secreting shell and periostracum, is very small. Around the pedal gape, the lobes are obviously separate, but posteriorly left and right inner and middle folds fuse (Type B fusion) (YONGE, 1982) forming the long posterior extension of the body beyond the confines of the shell (Fig. 5B). The siphons comprise fused inner folds only (Type A fusion).

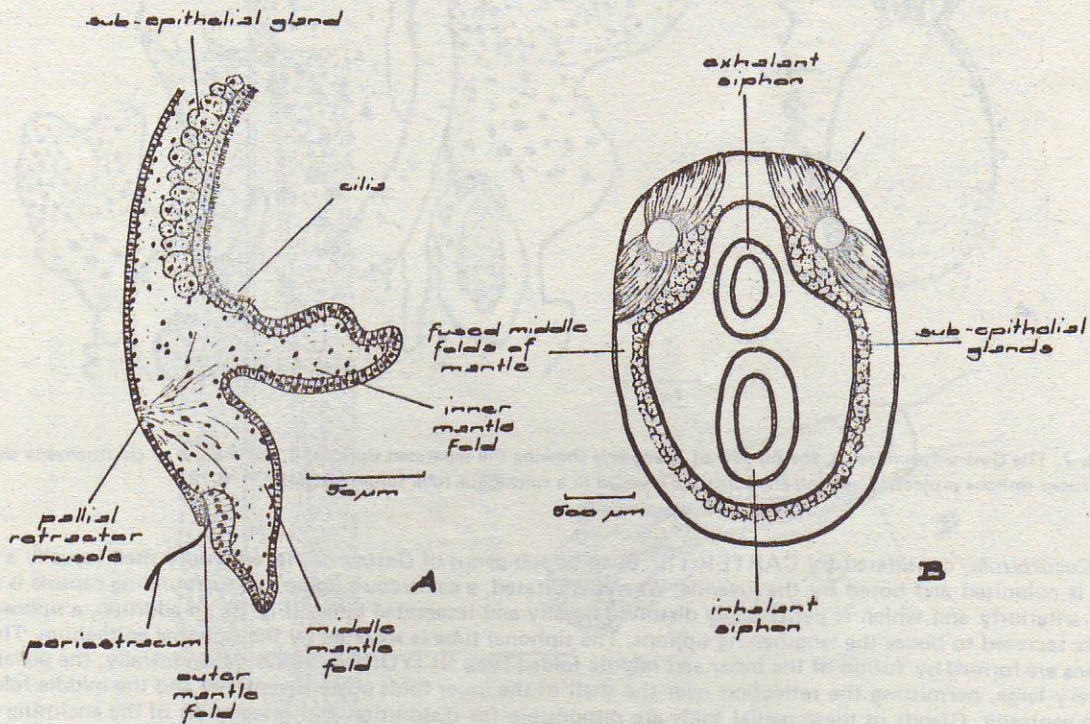


FIG. 6. The Teredinidae. A, *Teredo navalis*. A transverse section through the mantle margin at the pedal gape and showing the mucous-secreting sub-epithelial glands. B, A transverse section through the posterior end of the body showing the siphons, the pallets with their retractors and the mucous secreting sub-epithelial glands.

In the mantle are two major glandular areas. The first, lining the inner face of the inner folds, particularly in the anterior regions of the mantle cavity (Fig. 6A), discharge inwards and presumably assists in the consolidation of pseudofaeces for expulsion via the inhalant siphon. The inner and middle folds of the posterior extension to the

body are very thick and comprise a second much more extensive mass of glandular tissue that discharges a thick white secretion when cut (Fig. 5B) (TURNER, 1966). This is secreted from the outer surface and lines the boring. Thus the tube is secreted from the outer surface of the fused inner and middle folds. These same fused folds posteriorly secrete the pallets which attach to the burrow wall by muscles enabling their retraction (Fig. 6B). Similarly, the siphons, formed by fused inner folds, can also secrete calcium carbonate to form delicate tubes extending beyond the wood surface under conditions (rarely met with in nature) of calm (YONGE, 1927).

THE GASTROCHAENIDAE

The Gastrochaenidae have been reviewed by CARTER (1978), SAVAZZI (1982) and MORTON (1983 c). All three authors agree on the trends exhibited by the family. The most primitive member is represented today by *Spengleria* which appears to be a mechanical borer, the periostracum studded with spikes which abrade, further, a crevice colonised by the juvenile (CARTER and ALLER, 1975). In line with its primitive mode of boring, the shell is rather angular, thick and ridged, and the siphons are separate (Fig. 7A). More specialised conditions are represented by *Gastrochaena* in which the shell is thin with no periostracal spikes and in which boring is probably by chemical means, though PURCHON (1854) considers mechanical boring may also occur. *Gastrochaena* has the ability to secrete calcium carbonate to form a siphonal extension to its burrow so that as an inhabitant of dead coral and other calcareous substrata it can keep the siphonal orifices above the epiflora and fauna recolonising the habitat's surface (Fig. 7B) (BROMLEY, 1978).

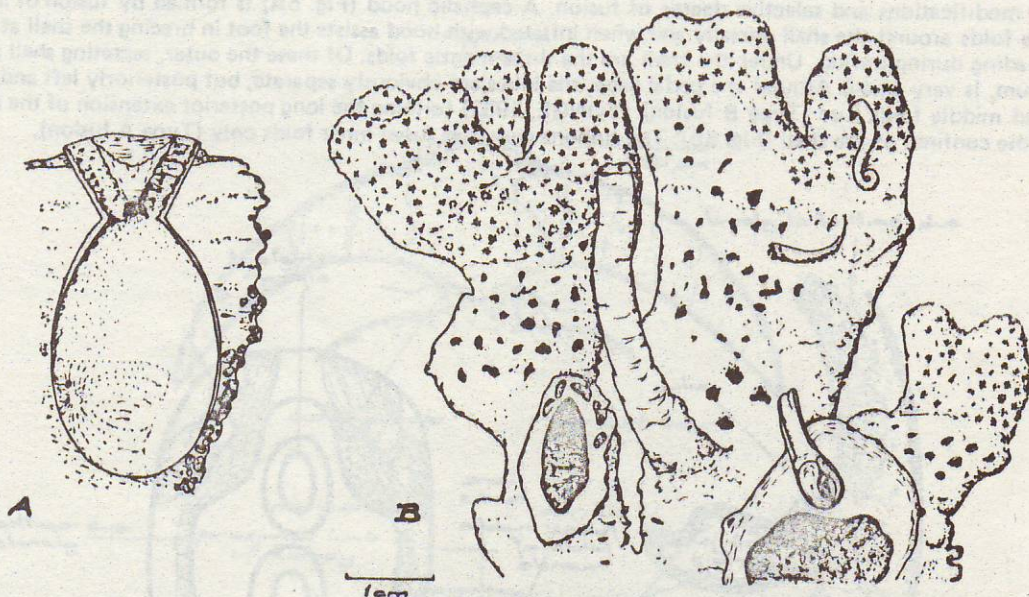


FIG. 7. The Gastrochaenidae. A, the burrow of *Spengleria* showing the separated siphons. B, the burrow of *Gastrochaena* showing the fused siphons projecting beyond the substrate encased in a calcareous tube (after BROMLEY, 1978).

In *Cucurbitula*, considered by CARTER (1978) to be sub-genus of *Gastrochaena*, an empty shell (usually a bivalve) is colonised and bored by the juvenile. When penetrated, a calcareous „igloo” or surrounding capsule is secreted anteriorly and which is periodically dissolved basally and resecreted larger (Fig. 8). In addition, a siphonal tube is secreted to house the lengthening siphons. The siphonal tube is secreted by the siphonal epithelium. The siphons are formed by fusion of the inner and middle folds (Type B) (YONGE, 1982). Mid-ventrally, the pedal gape is very large, permitting the reflection over the shell of the inner folds postero-ventrally and the middle folds antero-ventrally. Glands in these pallial folds are responsible for dissolution and resecretion of the enclosing calcareous capsule (MORTON, 1982).

The fossil *Kummelia* is very similar to *Cucurbitula*, both in shell and tube form, but is free of a solid substrate and was apparently infaunal, encased in an adventitious tube (CARTER, 1978; MORTON, 1983c). The tube, however, has regular growth increments. This is in direct contrast to the extant, most specialised, gastrochaenid, *Eufistulana*. The tube is long, with no obvious growth increments, and is four-layered. The shell and contained tissues occupy the basal swollen region and the very long siphons extend to the only, distal, orifice in the tube (Fig. 9A). The tube, presumably, lies buried in subtidal deposits, the siphonal orifice extending above the surface. The siphonal region of the tube is separated from the basal region by an oval septum (as in *Cucurbitula*) (SAVAZZI, 1982). The inner layer of the tube, distal to the septum, is secreted by the siphonal epithelium (Fig. 10A). The siphons are formed by fusion of type B (YONGE, 1982). The outer layers of the tube are secreted by glands in

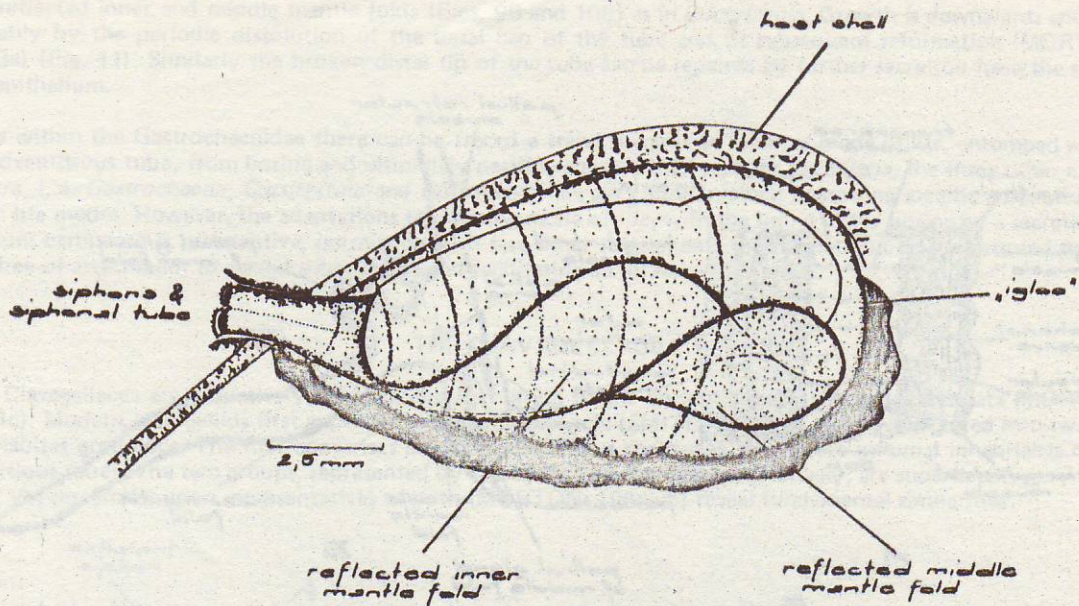


FIG. 8. The Gastrochaenidae, *Cucurbitula cymbium*. A specimen, as seen from the right side, enclosed within its „igloo” and with inner and middle mantle folds reflected over the shell (after MORTON, 1982).

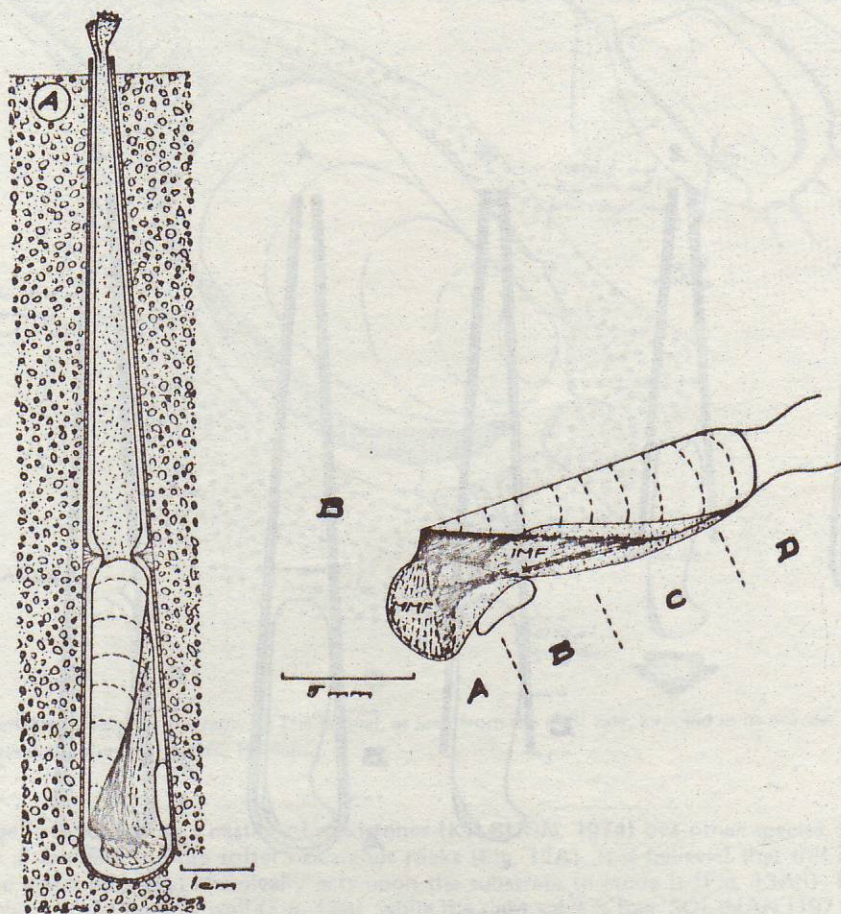


FIG. 9. The Gastrochaenidae, *Eufistulana mumia*. A, The animal in its postulated position in the sediment. B, The animal as seen from the left side showing the reflected inner (IMF) and middle (MMF) mantle folds areas of the mantle (A-D) possessing different gland types which secrete successive layers of the adventitious tube (after MORTON, 1983a).

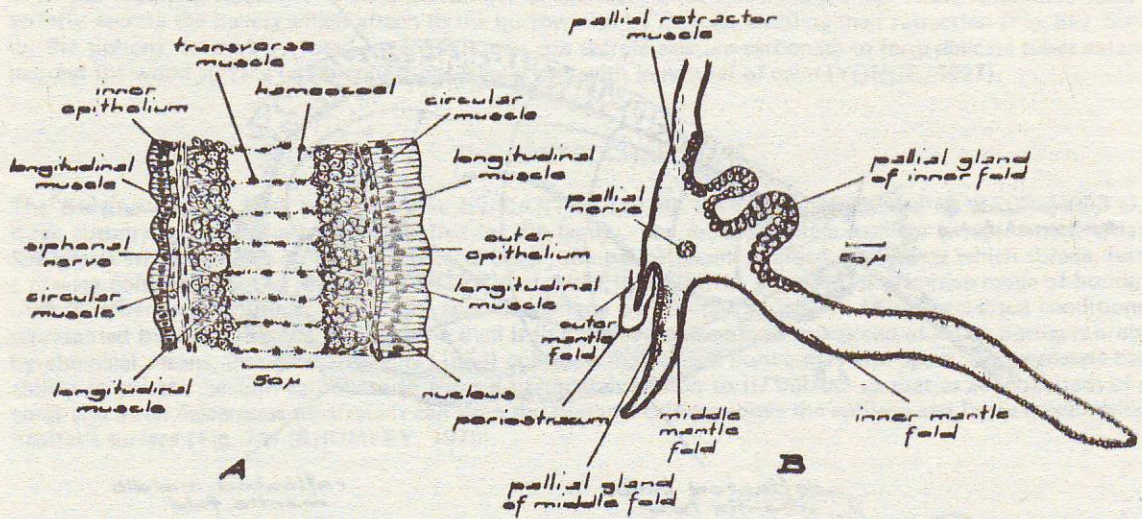


FIG. 10. The Gastrochaenidae, *Eufistulana mumia*. A, A transverse section through the siphonal wall and B, a transverse section through the mantle margin at the pedal gape showing glands in the inner and middle folds (after MORTON, 1983a).

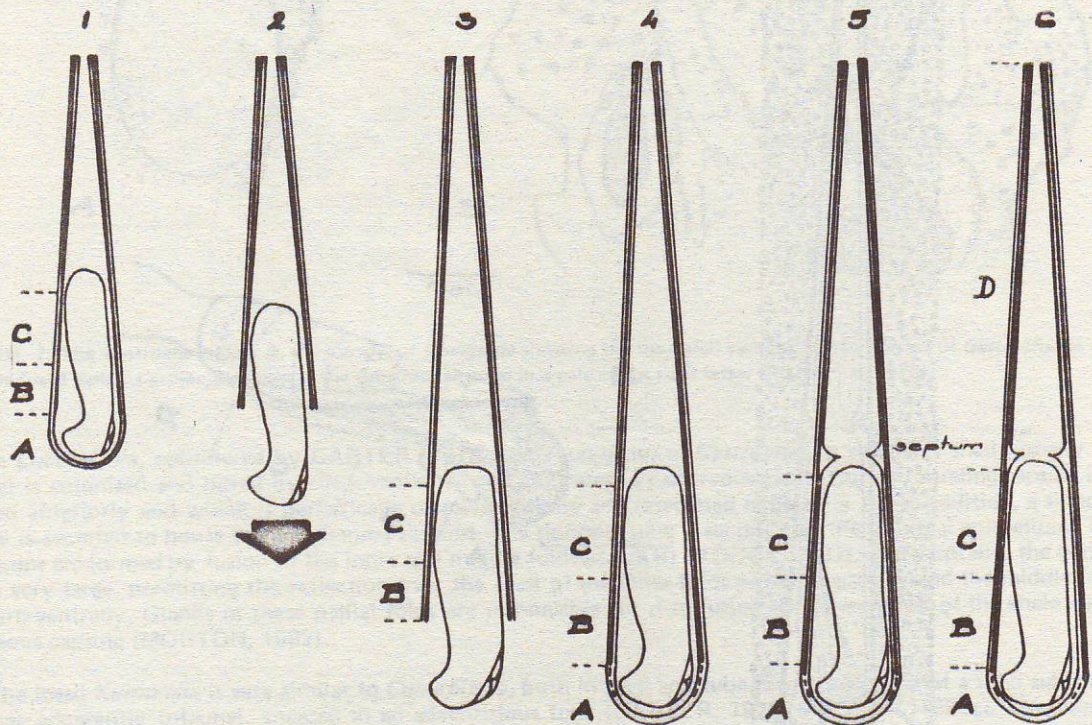


FIG. 11. The Gastrochaenidae, *Eufistulana mumia*. The postulated process (1-6) of tube formation. The letters A, B, C, and D, refer to the four secretory regions of the mantle shown in Fig. 9 (after MORTON, 1983a).

the reflected inner and middle mantle folds (Figs. 9B and 10B) as in *Cucurbitula*. Growth is downwards and presumably by the periodic dissolution of the basal cap of the tube and its subsequent reformation (MORTON, 1983a) (Fig. 11). Similarly the broken distal tip of the tube can be repaired by further secretion from the siphonal epithelium.

Thus within the Gastrochaenidae there can be traced a trend towards an infaunal mode of life, entombed within an adventitious tube, from boring and ultimately nestling ancestors. Except for *Spengleria*, the three other extant genera, i. e. *Gastrochaena*, *Cucurbitula* and *Eufistulana*, are very similar, albeit possessing specific adaptations to their life modes. However, the adaptations to a boring mode of life, with the lining of the boring by a secretion of calcium carbonate is preadaptive, permitting with few other refinements the formation of a tube around the body, free of attachment to a solid substratum, and facilitating an infaunal life style.

THE CLAVAGELLACEA

The Clavagellacea are a relatively modern, aberrant group of the ancient sub-class Anomalodesmata (MORTON, 1981c). Modern clavagellids first appeared in the late Mesozoic (SMITH, 1962a;b) and have radiated into two major habitat groupings. The first comprises borers of calcareous rocks, the second are infaunal inhabitants of adventitious tubes. The two groups, represented by *Clavagella* and *Brechites* respectively, are superficially very different, yet researches upon representatives of both (MORTON, 1984a;b) reveal fundamental similarities.

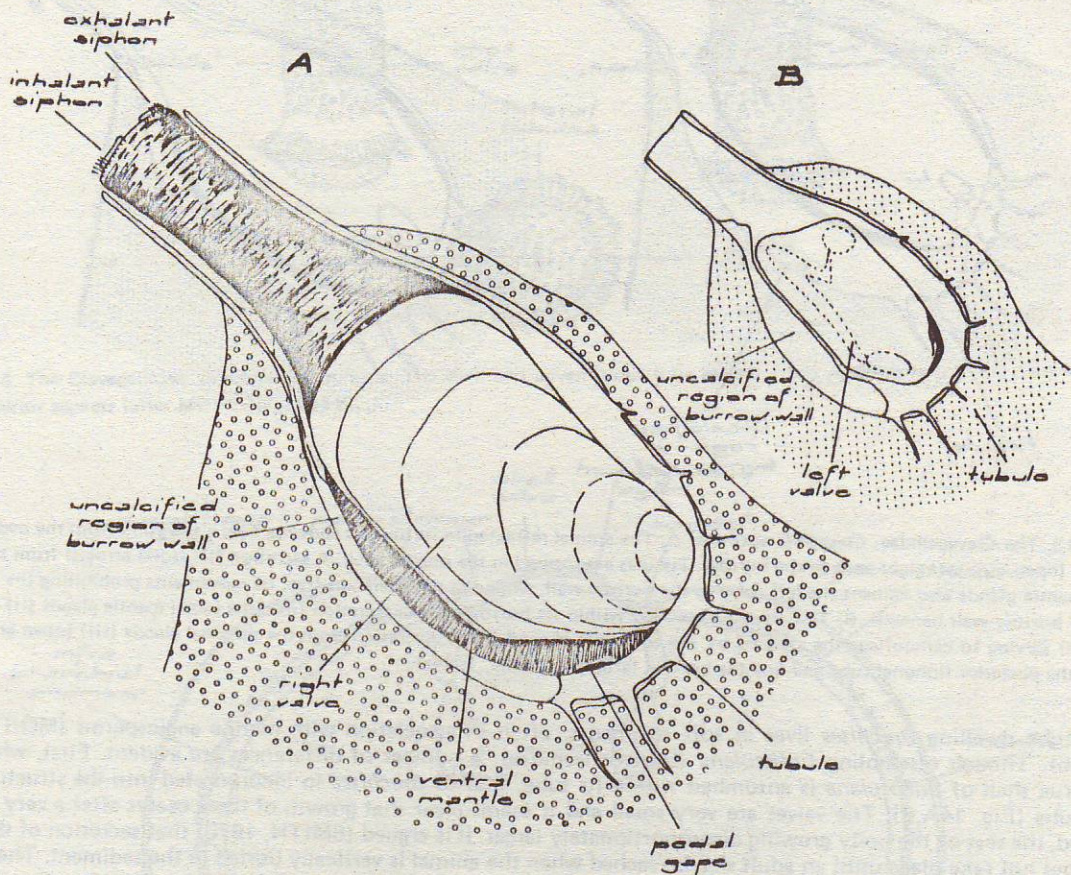


FIG. 12. The Clavagellidae. *Clavagella australis*. A, The animal, as seen from the right side, exposed in its burrow. B, The left valve attached to the burrow wall (after MORTON, 1984a).

Clavagella mullerae is described as a nestler of sandstones (KILBURN, 1974) but other species, e. g. *C. australis* (MORTON, 1984 a) are able to bore softer calcareous rocks (Fig. 12A). It is believed that this is achieved by a secretion from the pedal gape that chemically acts upon the substrate to erode it (Fig. 13A;I). The left valve of *Clavagella* is attached to the burrow wall (Fig. 12B), while the right valve is free. SOLIMAN (1971), however, believed that boring was a mechanical process. SAVAZZI (1982) accepted this but suggested that although initial attachment was by the left valve, helical growth caused the shell to rotate, so that most of the left valve is exposed (which it is not) while the right bores into the substrate. In no other cemented bivalve does such „helical“ growth occur (YONGE, 1979). Moreover I simply cannot see how mechanical boring can be achieved in such a si-

tuation and, to the contrary suggest that valve attachment must preclude such a mechanism. Attachment is, rather, by the selective secretion of a glue from radial mantle glands developed in the middle folds of the naked tips of the siphons on the left side only (Fig. 13A;II) (MORTON, 1984a). In other anomalodesmatans the radial mantle glands serve to glue sand grains to the posterior borders of the shell and siphons for camouflage e. g. *Periploma angasai* (MORTON, 1981). The siphons of *Clavagella* too are camouflaged in this way (Fig. 13B;II) but the most significant function of the glands, with regard to an understanding of how adventitious tube of *Brechites* is constructed, is the gluing of the left valve to the burrow wall. Also located in and discharging via the siphonal tips is an extensive gland, thought to secrete a protective calcareous tube around the siphons (Fig. 13B;III). This secretion presumably pours down over the fused periostracum covering the siphons (formed by fusion of Type C (YONGE, 1982)) to unite with the burrow, the internal surface of which it also coats, except under the free right valve. The radial mantle glands possibly also secrete the glue which attaches material to the outside of the tube assisting in the camouflage of this too. Thus *Clavagella* is thought to chemically erode a burrow and to protectively house its siphons in a tube of its own secretion.

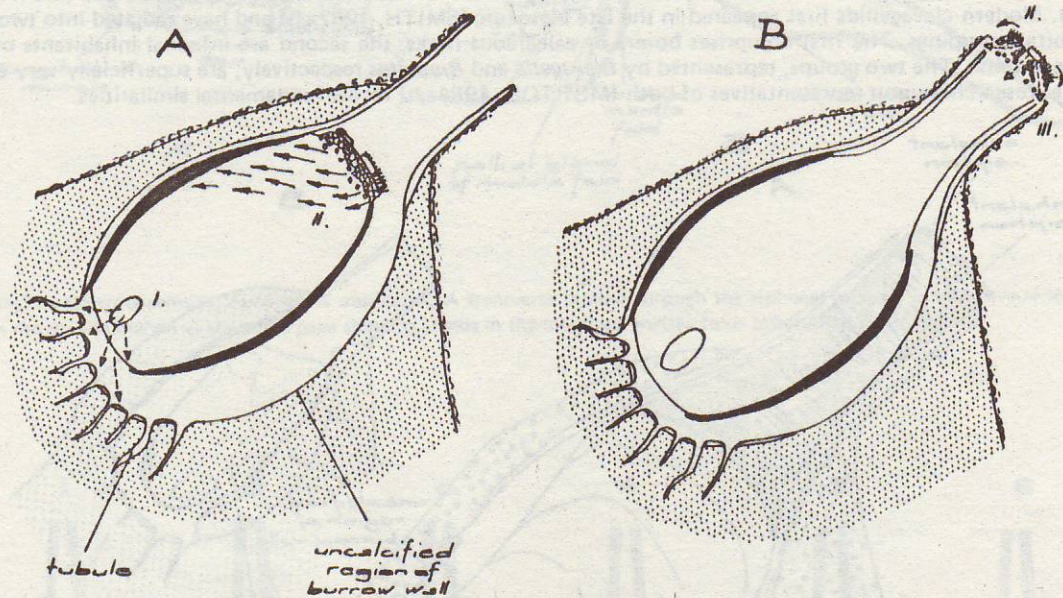


FIG. 13. The Clavagellidae. *Clavagella australis*. A, The animal retracted in its burrow showing how a secretion from the pedal gape (I) (open arrows) might enlarge the burrow. Tubules are formed in the porous rock. A secretion (II) (solid arrows) from the radial mantle glands also cement the left valve to the burrow wall, while the right remains free, its movements prohibiting the lining of the burrow wall beneath. B, The animal expanded within its burrow with a secretion from the radial mantle glands (II) (solid arrows) serving to camouflage the siphons by the adhesion of sand grains. Secretion from the siphonal glands (III) (open arrows) form the posterior siphonal tube and line the burrow (after MORTON, 1984a).

The tube dwelling *Brechites* lives in soft sediments, often in association with marine angiosperms (MORTON, 1983b). Though resembling *Eufistulana* (Gastrochaenidae), a number of differences are evident. First, whereas the true shell of *Eufistulana* is entombed within its tube, that of *Brechites* is incorporated into the structure of the tube (Fig. 14A,B). The valves are very small and it seems clear that growth of these ceases after a very short period, the rest of the body growing disproportionately larger. It is argued (SMITH, 1978) that secretion of the tube does not take place until an adult size is reached when the animal is vertically buried in the sediment. The tube unites with the true shell because secretion is over the surface of the periostracum that covers the entire animal due to extensive mantle fusions of Type C (YONGE, 1982) (as in *Clavagella*) involving the inner surfaces of the outer as well as the middle and inner folds (Fig. 15). SAVAZZI (1982) and MORTON (1984 b) both believe that the basal perforate plate (Fig. 14C) is produced first from a gland in the anterior region of the mantle cavity discharging via the pedal gape. Perforations in the basal plate result from a local inhibition of secretion caused by inflated papillae on the mantle. Perforated tubules are of two types, those on the surface of the plate and those at its margin. Through these perforations mantle fluids are expelled from the mantle cavity causing the animal to sink into the sediment with growth of the tube distally (SAVAZZI, 1982). They may also allow entry into the mantle cavity of subsurface waters containing nutrients (MORTON, 1984b). The distal part of the adventitious tube is secreted from the siphons, the secretion pouring down over the periostracum and uniting with the basal plate at the flare of lateral tubules. Growth increments to the tube occur around the siphonal end in the form of „plaited ruffles” (SMITH, 1976). The postulated method of tube secretion is shown in Figure 16. The tube of *Brechites* therefore is secreted in a manner similar to the way the burrow is eroded (i. e. via a secretion from the pedal gape) and the siphonal tube is constructed in *Clavagella*. This, however, is completely different from that of both the Teredinidae and the Gastrochaenidae.

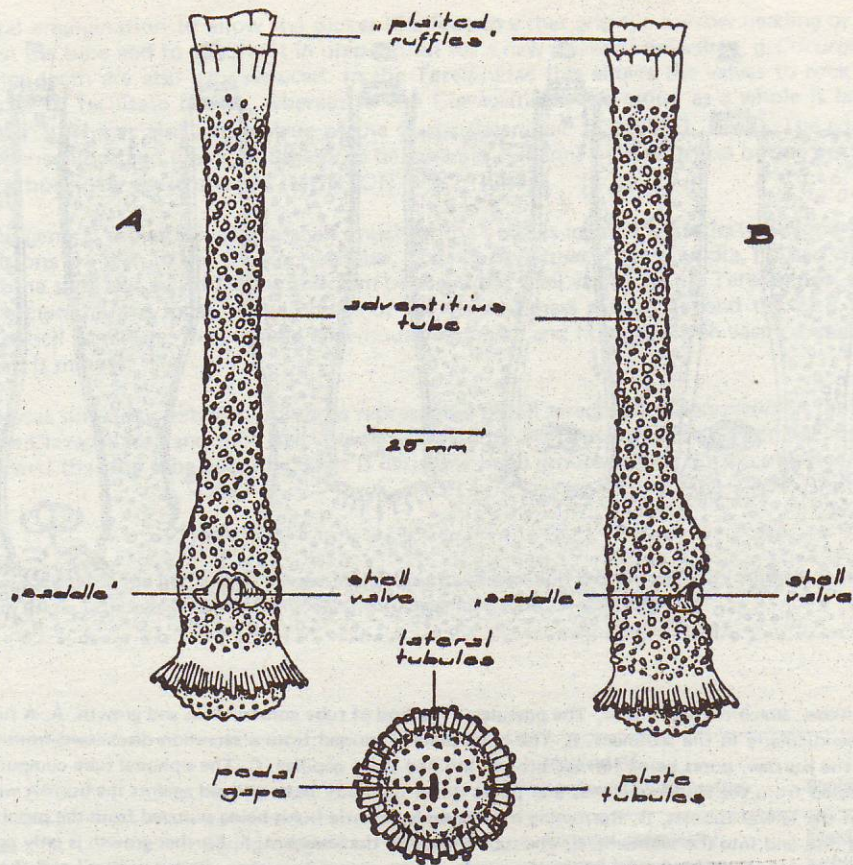


FIG. 14. The Clavagellidae, *Brechites vaginiferus*. The shell and adventitious tube as seen from A, the dorsal; B, the right and C, the anterior aspects (after MORTON, 1984 b).

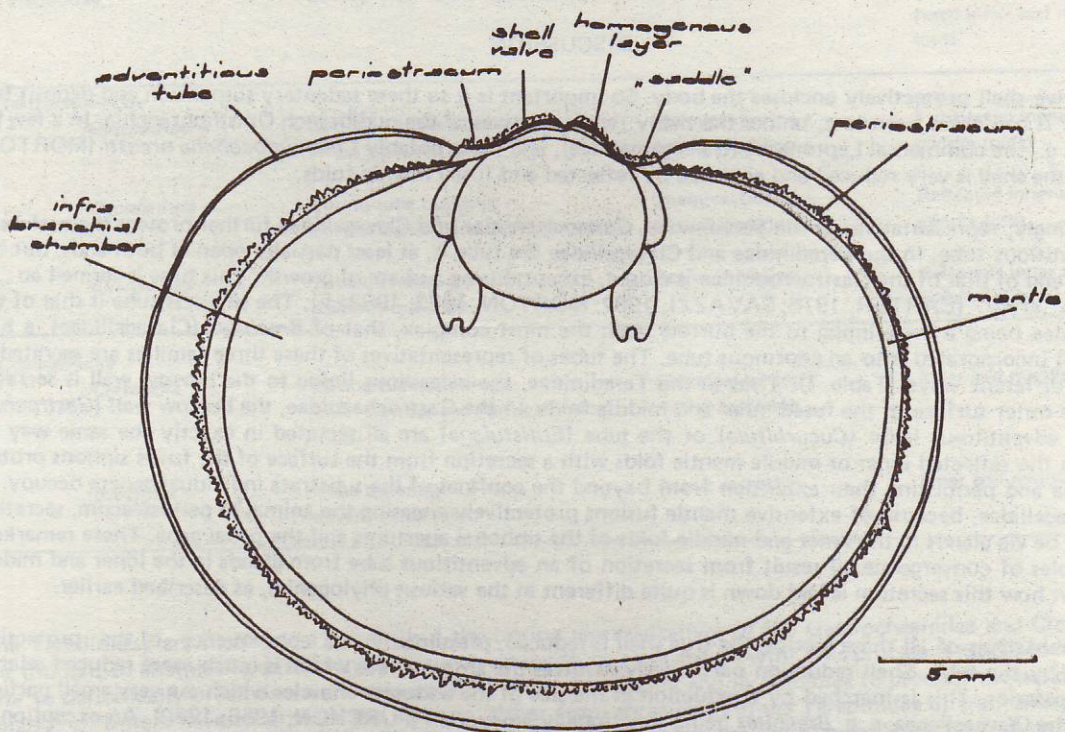


FIG. 15. The Clavagellidae, *Brechites vaginiferus*. A generalised section through the adventitious tube and body in the region of the true shell showing how the tube is secreted over the extensively fused mantle and periostracum (after MORTON, 1984b).

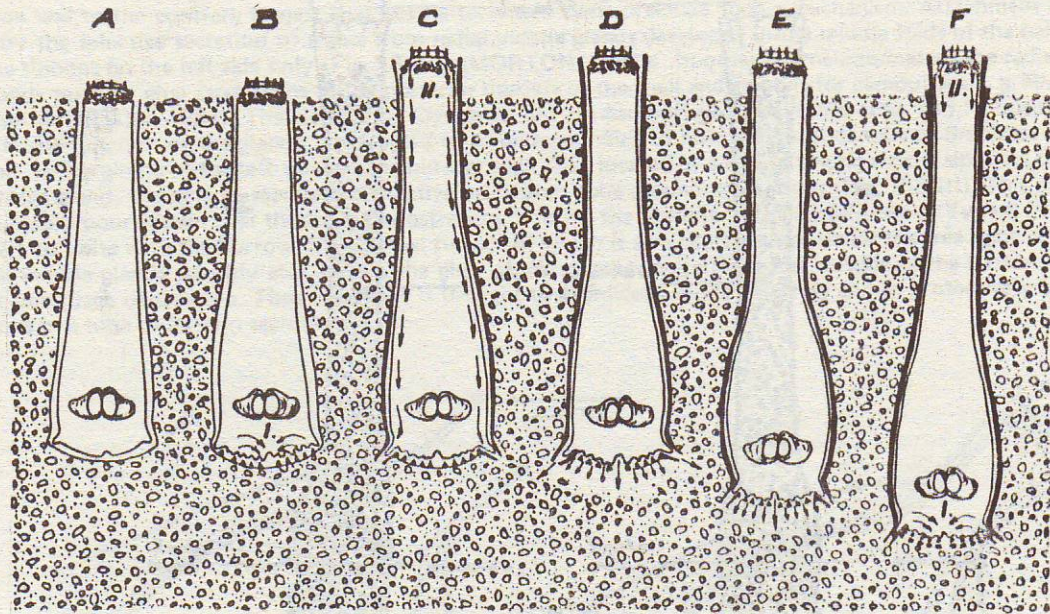


FIG. 16. The Clavagellidae. *Brechites vaginiferus*. The postulated method of tube construction and growth. A, A tubeless post juvenile lies buried perpendicularly in the sediment. B, The basal plate is formed from a secretion discharged from the pedal gape and lines the base of the burrow, pores being formed around inflated basal papillae. C, The siphonal tube component of the adventitious tube is secreted from the siphonal glands and pours down the body to be pressed against the burrow walls and united with the basal plate at the lateral tubules. D, Burrowing is achieved by mantle fluids being pumped from the pedal gape, through the pores of the basal disc and into the sediment. E, The tube sinks into the sediment. F, Further growth is only possible posteriorly by secretions of the siphon glands down inside the original tube to produce the „plaited ruffles” and the layered shell. Further secretion anteriorly seals the lateral tubules but not the plate tubules.

DISCUSSION

The bivalve shell protectively encloses the body. So important is it to these sedentary suspension and deposit feeders that it has never been lost, unlike the many representatives of the nudibranch Opisthobranchia. In a few bivalves, e. g., the commensal Leptonacea (Galeommatidae), and most notably *Chlamydoconcha orcutti* (MORTON, 1981b), the shell is very reduced and enclosed by reflected and fused mantle folds.

Contrastingly, representatives of the Teredinidae, Gastrochaenidae and Clavagellidae further protect themselves in an adventitious tube. In the Teredinidae and Clavagellidae the tube is, at least partially open at both ends, but the anterior end of that of the Gastrochaenidae is closed, except during a phase of growth. This tube is termed an „igloo” or a „crypt” (CARTER, 1978; SAVAZZI, 1982; MORTON, 1982; 1983a,b). The simplest tube is that of the Teredinidae being a mere lining to the burrow wall: the most complex, that of *Brechites* (Clavagellidae), a tiny true shell incorporated into an enormous tube. The tubes of representatives of these three families are secreted in entirely different ways (Table 1). Thus in the Teredinidae, the calcareous lining to the burrow wall is secreted from the outer surface of the fused inner and middle folds. In the Gastrochaenidae, the burrow wall (*Gastrochaena*), the adventitious igloo (*Cucurbitula*) or the tube (*Eufistulana*) are all secreted in exactly the same way by glands in the reflected inner or middle mantle folds with a secretion from the surface of the fused siphons protecting these and permitting their extension from beyond the confines of the substrata individual genera occupy. In the Clavagellidae, because of extensive mantle fusions protectively encasing the animal in periostracum, secretion can only be via glands in the inner and middle folds of the siphonal apertures and the pedal gape. These remarkable examples of convergence all result from secretion of an adventitious tube from glands in the inner and middle folds. But how this secretion is laid down is quite different in the various phylogenies, as described earlier.

In representatives of all these groups, the true shell is reduced, presumably as a consequence of the protection afforded by the tube. Shell reduction particularly involves the anterior face which is much more reduced relative to the posterior. This is matched by a reduction in the size of the adductor muscles which are very small particularly in the Clavagellacea, e. g. *Brechites* being functionally amayarian (PURCHON, 1956; 1960). An exception to this are members of the Teredinidae where the adductors are disproportionately large, notably the posterior, and rich in blood. This is because in these mechanical borers powerful adduction is required to scrape wood fragments from the burrow heading (TURNER, 1966). The shells of such bivalves are modified in other ways too, notably

an antero-ventral emargination to allow the sucker-like foot to either grip the burrow heading or to closely oppose glands against the tube and to dissolve it in preparation for a new phase of growth, e. g. *Cucurbitula* (MORTON, 1982). The hinge teeth are also very reduced. In the Teredinidae this allows the valves to rock about a median dorso-ventral axis to facilitate boring, whereas in the Clavagellidae, the group as a whole is largely edentulous (MORTON, 1981c). This is also largely true of the Gastrochaenidae (CARTER, 1978). The edentulous condition in the Gastrochaenidae and Clavagellidae could be taken as evidence of mechanical boring but current opinions suggest chemical boring by these bivalves (MORTON, 1982; 1984a).

In line with the general reduction of the shell, much of the body is located posteriorly beyond the shell margins. Simplest conditions are seen in the Gastrochaenidae. Thus in *Eufistulana*, the ctenidia, housed within the siphons, extend beyond the shell but can still be withdrawn between the shell valves. In the Teredinidae, virtually the whole length of the ctenidia and most of the organs of the visceral mass extend beyond the shell. In *Brechites* (Clavagellacea), the shell is minute, the ctenidia enormously elongate and housed within vastly expanded siphons. The visceral mass too is minute.

The morphological similarity between borers as represented by all teredinids, *Cucurbitula* in the Gastrochaenidae, *Clavagella* in the Clavagellacea and tube dwellers represented by *Eufistulana* (Gastrochaenidae) and *Brechites* (Clavagellacea) suggests that the tube-dwelling habit is derivable in all groups from a boring ancestor.

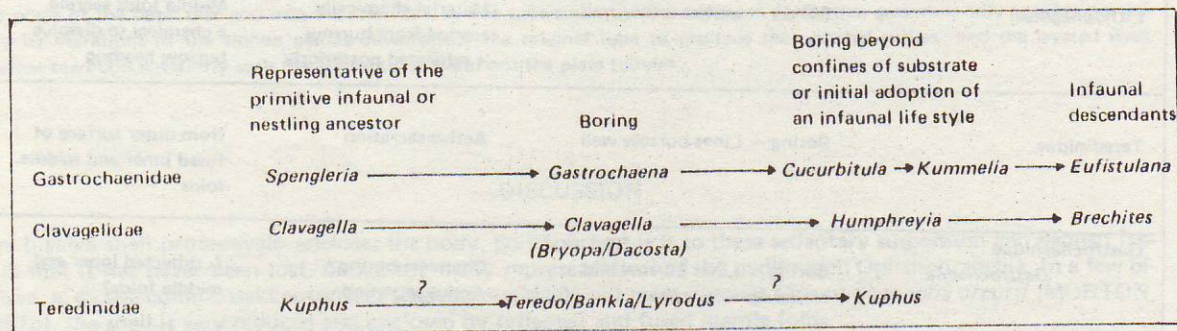
TABLE 1. A comparison of the life styles, the methods of burrow formation and the secretory epithelium involved in burrow or tube construction in the Lithophaginae, Teredinidae, Gastrochaenidae and Clavagellidae.

	Life style	Method of burrow/tube formation	Secretory surface
Lithophaginae	Boring — Lines burrow wall	Material chemically eroded from burrow is relocated posteriorly	Middle folds secrete a chemical to dissolve burrow heading
Teredinidae	Boring — Lines burrow wall	Active secretion	from outer surface of fused inner and middle folds
Gastrochaenidae			
<i>Gastrochaena</i>	Boring — Lines burrow and forms siphonal tube	Chemical boring + Active secretion	? reflected inner and middle folds?
<i>Cucurbitula</i>	Boring/tube building — Forms "Igloo" and siphonal tube	Chemical boring + Active secretion	Reflected inner and middle folds
<i>Eufistulana</i>	Tube building — Forms adventitious tube	Active secretion	Reflected inner and middle folds
Clavagellidae			
<i>Clavagella</i>	Boring/tube building — Lines burrow and forms siphonal tube	Chemical boring + Active secretion	inner and middle folds
<i>Brechites</i>	Tube building — Forms adventitious tube	Active secretion	inner and middle folds

The Teredinidae are mechanical borers, but the boring representatives of the Gastrochaenidae and Clavagellidae are thought to chemically extend the burrow downwards, to cater for growth. This process is modified in *Eufistulana* to periodically break down and resecret the crypt proximally and in *Brechites* to produce the basal plate. Similarly, all borers have to protect the siphons, either from abrasion as in the Teredinidae or from overgrowth by enclosing corals or other encrusting organisms as in the Gastrochaenidae and Clavagellidae, by ensheathment in a tube of calcium carbonate. In *Eufistulana* and *Brechites* this process has been greatly exaggerated to produce an adventitious tube to house extraordinarily long siphons.

Though methods of tube secretion in the Gastrochaenidae and Clavagellidae are different, secretion is typically from inner and middle folds (Table 1). This is also true of the Teredinidae and, possibly significantly it is glands in the middle folds of *Lithophaga* which are secretory (MORTON and SCOTT, 1980), though in *Barnea* (Pholididae), pallial glands which may assist in boring occur in the inner folds (MORTON, 1984). SAVAZZI (1982) argues that tube building is restricted to the lamellibranch bivalves in which there is a high degree of mantle fusion and thus that pallial adaptations to facilitate a burrowing mode of life in these „higher“ bivalves are responsible for successful boring and tube secretion. Whereas it is true that tube building is restricted to the lamellibranch bivalves – Teredinidae, Gastrochaenidae and Clavagellidae, I cannot see how extensive ventral mantle fusion is necessarily a pre-requisite for this. Thus in *Eufistulana*, inner and middle folds are reflected over the shell to form the tube. There is no reason why similar folds in a lithophagine should not be similarly reflected, indeed in *Fungiacava*, such a fold is (GOREAU *et al.*, 1969). If there is any fundamental difference between the Lithophaginae and other phylogenies of borers and tube builders it is that in the former, there is no ventral fusion to form a discrete tubular inhalant siphon. This apparently makes it impossible for a complete tube to be secreted housing (as in the Gastrochaenidae) greatly elongate siphons or (as in the Teredinidae and Clavagellidae) the, similarly elongate, siphons plus a posterior extension of the mantle beyond the confines of a very reduced shell and containing many of the organs of the body. Moreover, for the Lithophaginae, exclusively occupying burrows within rock containing some calcium carbonate there would seem to be little reason for the active secretion of more when it is chemically eroded as a paste which simply requires relocation to line the shell and burrow wall. For the other lamellibranch borers there is a need to secrete calcium carbonate, most importantly to house and protect the siphons projecting beyond the habitat surface. In those lithophagines inhabiting living corals the siphons are thought to be protected from the nematocysts of the coral polyps by an inhibitory secretion from the siphons themselves (MORTON and SCOTT, 1980).

TABLE 2. Functional stages in the evolution of an adventitious tube dwelling bivalve from a boring ancestor in the Gastrochaenidae and Clavagellidae. The status of *Kuphus* in the Teredinidae as either a primitive borer or a specialised tube dweller is questioned.



Adventitious tube building in *Eufistulana* and *Brechites* have therefore arisen independently as a result of modifications in a boring ancestor to line its burrow and protect the siphons. This extreme example of convergence, but with the tube produced in subtly different ways, suggests that the boring mechanism, with burrow lining, is pre-adaptive for the ultimate evolution of a free living descendant, infaunally entombed within a tube (Table 2).

TURNER (1966) suggests that the infaunal *Kuphus*, boring mangrove roots and subsequently forming a tube in the mud is primitive. This may be so, but bearing in mind the above, it does seem possible that it could equally be highly specialised being derived from a simpler, boring, teredinid, that has subsequently adopted a life style more reminiscent of *Eufistulana* and *Brechites*. Though *Kuphus* has been little studied, such an observation is supported by SAVAZZI (1982) who suggests that the anterior end of the tube is closed. Whether or not the tube remains open during growth or is closed and periodically eroded and re-secreted, following a further phase of growth, is unknown and requires investigation.

ÖSSZEFOGLALÁS

A fúrógagylók esetében a kivájt üreget vagy egy szekrétum (Teredinidae), vagy kalcium-karbonát (Lithophaginae) béleli ki. Ezen esetekben a cső szerepe csupán az üreg falának simábbá tétele. Ennél bonyolultabb, járulékos csövet fejlesztenek a Gastrochaenacea és a Clavagellacea képviselői. Az előzőknél (*Eufistulana*) a cső elkülönül a héj-

tól, a második csoportnál (*Brechites*) a valódi héj nagyon kicsi és bele van ágyazva a viszonylag nagyméretű csőbe. Mivel a kagyló testét periostracum borítja, a csövet a láb és a szifó mirigyei választják ki.

Összegzősképpen elmondható, hogy a fúró életmód révén a kagylók új élőhelyeket képesek meghódítani. Ezzel egy szesszilis jellegű életformához térnek vissza, egymástól eltérő módon.

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