

# CONSTRUCTIONAL MORPHOLOGY OF BIVALVES: EVOLUTIONARY PATHWAYS IN PRIMARY VERSUS SECONDARY SOFT-BOTTOM DWELLERS

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**ABSTRACT.** In contrast to the minor within-habitat improvements in shell shape and sculpture of primary soft-bottom dwellers, the transition of fixosessile rock dwellers back to soft substrates has resulted in fast and drastic morphological changes. They were facilitated by the available ecologic stepping stones that caused morphogenetic programmes—first to 'derail' (rock habitats), then to be shortened (to fit the size of dead shell habitats), and finally to extend again (in order to increase mechanical stability on soft bottoms). The third step allows only a limited number of adaptational strategies (flat, outriggered, and edgewise recliners; mud stickers; 'pickabacks') that led to convergent shell forms in different groups of bivalves. Within groups, however, phylogenetic and morphogenetic constraints, as well as the adaptational landscape, channel evolution to such a degree that it becomes difficult, at least in the fossil record, to resolve the multitude of parallel and iterative lineages.

EVOLUTIONARY discussions in modern times have often been discussed in terms of theoretical models, with the result that they become more and more detached from the everyday experience of palaeontologists engaged in stratigraphical and morphological problems. This development has forced us into divided camps: neutralists versus adaptationists, gradualists versus punctuationalists, and so on. This appears unnecessary to me. The present study builds on the conviction that evolution is an ecological process and that it is basically opportunistic. Thus I do not expect evolution to subscribe to any particular principle, but to follow the one or the other as fits the situation. In order to understand a given situation in morphological evolution, we must learn the licences, i.e. the options and constraints that are imposed on established bauplans by morphogenetic mechanisms in their approximation of an appropriate functional design, or paradigm. This is the approach of *constructional morphology*. We consider it as a method of research rather than a theoretical framework, so that it makes sense only if applied to a certain group of organisms. Nevertheless the resulting case histories are not irrelevant for theoretical evolutionary considerations. By extending our view from specific cases to larger groups, we can expect to find general patterns—not in the sense of built-in rules (because the steps are stochastic in principle), but as a reflection of the adaptive landscape and its changes in time, by which evolution is ultimately moulded.

In this approach our curiosity focuses on the familiar phenomena of convergence (if we deal with disparate origins) and of parallelism and iteration (within one group). Classical convergences, such as aberrant 'coralliform' types—including top-shaped rudist bivalves, richthofeniid brachiopods, hipponicid gastropods—are not randomly distributed in ecospace, but are concentrated in an ecological group that is here called 'secondary soft-bottom dwellers'. By this we understand forms that acquired a sedentary mode of life, usually attached to hard substrates, in a previous evolutionary step and have secondarily switched to life on areas of marine soft bottoms (sands and muds). In this new habitat they found enough food as suspension feeders, but faced the critical problem of their inherited immobility. Only very few groups, such as the swimming pectinids and limids (perhaps similarly some strophomenacean brachiopods), the burrowing actinians, and some corals managed to develop a new mode of mobility, sufficient to escape from predators and to reorient themselves.

Others went into 'pickaback' symbiosis with a mobile partner such as a hermit crab. But the vast majority solved the problem by stabilizing themselves through stable shapes and/or heavy and commonly oversized skeletons.

From the different phyla and classes included in the project, I select here the bivalves, because they are well-known and have made the transition from soft to hard substrates and back several times during their long history, such that we can hope to sample most of the different solutions. Bivalves also allow us to compare form changes in secondary soft-bottom dwellers with those in primary ones, particularly with changes that improved the ability to burrow.

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#### PRIMARY SOFT-BOTTOM DWELLERS

Molluscs probably had their origin on hard bottoms, where they could crawl in a limpet-like fashion with a broad-soled foot and protect themselves by pressing the dorsal shell against the substrate. From such ancestors, bivalved forms evolved probably with the transition to soft substrates, where the gills needed an extra protection (Vogel and Gutmann 1980). The change from a univalved to a bivalved state required only a minor change in the ontogenetic programme of calcification (Bayer 1978). Since the univalved ancestors in this case had not lost their mobility, the foot could become adjusted in the new habitat to become an effective burrowing organ. Thus, bivalves as a group can be considered primary soft-bottom dwellers that largely use the gills as a food-filter and have therefore lost typical mollusc attributes such as primary eyes and the radula.

In the molluscs, bivalved form has evolved more than once (rostroconchs, bertheliniid gastropods, bivalves); but in each case (as also in bivalved arthropods) the two valves remained connected by a less-calcified zone that acts as an elastic ligament. This is in marked contrast to the brachiopod valves, whose articulation probably evolved secondarily from two separate shells protecting the gills of a worm-like ancestor (Vogel and Gutmann 1980). Since this option has led to a crucial constraint in the further modification of the bivalve bauplan, we must first discuss the properties and modifications of the bivalve ligament.

##### *Ligaments*

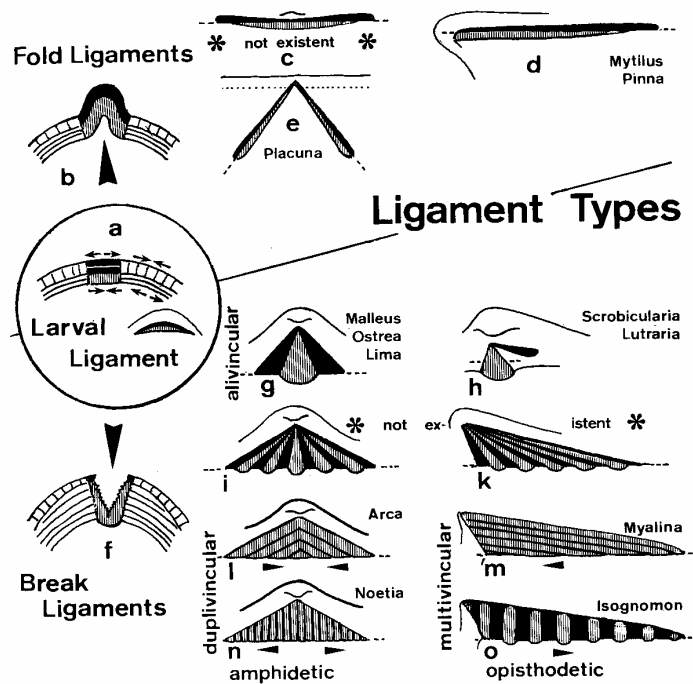
As an antagonist of the adductor muscles, the ligament elegantly serves the function of opening the valves. This problem could not be solved by hydraulics alone, because for such a function the mantle sac would have to remain closed in the open-valve position, which is incompatible with feeding. The alternative, namely opening the valves by diductor muscles, was secondarily achieved by the pholads. In this group the valves have become drilling devices, while their protective function is taken over by the hard substrate in which they bore (Röder 1977). Therefore it was possible to attach part of the anterior adductor muscle on the outside of the hinge, where it could act as a diductor and control the complicated movements of the valves much better than a lifeless ligament, which has become obsolete in this case.

The other major group in which the ligament has become reduced or lost are the rudists. Here the delegation of the opening function to parts of the adductors seems to have been attained through tooth-like projection of the myophores, with the advantage that the diductor parts remained inside the shell. This construction would approach that of articulate brachiopods, but its functional details and the possible pathways into it are not yet clear.

Returning to the structure and properties of the ligament, it should be remembered that we deal with a less calcified part of the shell that grows primarily in a similar way, i.e. with an outer layer

(apart from the periostracum) formed near the margin and an inner layer thickening the ostracum from the inside. The structure of the two layers corresponds to the stress to which they are exposed; it is fibrous (or prismatic) on the compressive and lamellar (or nacreous) on the tensional side, with the expected inversion in the ligament versus the shell. But the ideal design, in which the two layers should have corresponding thicknesses throughout the shell so that their boundary remains in the neutral zone, is impossible to produce in a growing structure, in which only the inner layer can be secondarily thickened. In the calcified shell, this defect can be compensated by overdesigning. In the ligament, however, it becomes critical. A second constraint stems from the fact that the ligament consists of non-living material. Thus its elastic properties do not change with the dimensions of the growing shell and they may also deteriorate by ageing.

Text-fig. 1 shows ways in which the two constraints are coped with in various types of ligaments. Major 'tricks' are (1) the breaking of the outer layers, with fresh material being continuously produced in the functional zone and (2) the regular introduction, or maintenance, of separate generative zones for the outer layer apart from the outer shell margin. Text-fig. 1 also demonstrates that the new generative zones do not grow as predicted by the model of spiral shell growth (text-fig. 11-κ), but in ways that allow to maintain, at all stages, the same absolute distances between them along the hinge line. We assume that these distances are optimized against the constant elastic properties of the two ligament materials. The ligament also imposes strong constraints on shell geometry. For instance, *fold ligaments* limit not only the secondary thickening of the shells, but also

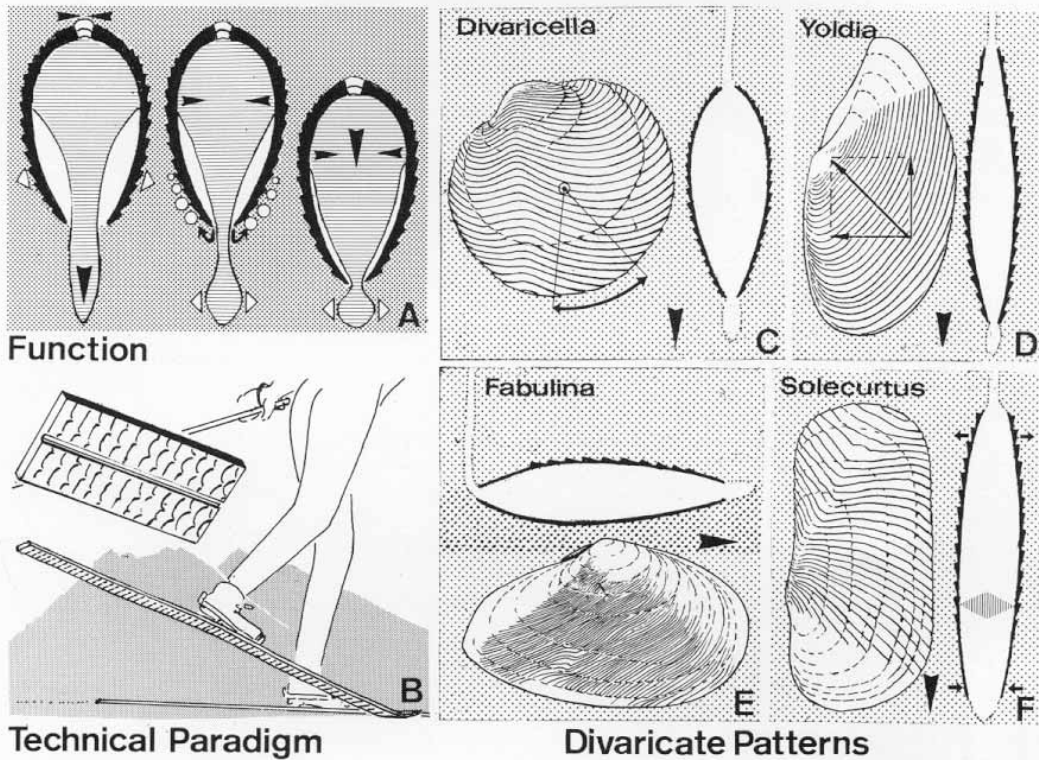


TEXT-FIG. 1. Only fold ligaments remain functional throughout their lengths; in break ligaments the functional parts of the two layers alternate along the hinge. Note that seemingly straightforward solutions (C, G, H) are not represented because of geometrical or mechanical constraints (from Seilacher 1981, modified).

shell curvature. In the theoretically simplest case, in which this type of ligament would extend amphidetically on both sides of the umbo (text-fig. 1c), shell curvature would be reduced to zero. It is therefore not represented. Also, the evolution of inequilateral, prosogyre shells in this group has probably as much to do with the space conflict between the two umbones in the case of a non-expandable ligament, as with an endobenthic, burrowing mode of life.

It should be noted that seemingly non-breaking ligaments are nevertheless affected by growth deformation. This is most obvious in modern *Pinna* (text-fig. 8), where the cross-sectional angle of the hinge becomes widened beyond the yield of the ligament during ontogeny. As a result the ligament is broken in the apical part of all specimens and the separated apices become scissored in a regular way (the left apex always slips dorsally over the right one), with internal flexible septae compensating for the inevitable damage. In this case the ligament will start to break from the inside—an interesting analogue to the rostroconch hinge. It would be interesting to study whether in this case the animal is able to repair the damage by deposition of new ligament material from the inside.

## BURROWING SCULPTURES



TEXT-FIG. 2. Ratched sculptures reduce back slippage while the shell acts as a penetration anchor for the probing foot. Deviations from the paradigm of the cross-country ski reflect the rocking and opening of the valves (C-E) and their pivoting in F. In horizontal burrowers (E) burrowing sculptures are stronger on the upper valve to compensate for reduced resistance of the sediment layer on top (A from Trueman and Ansell 1969, C-F from Seilacher 1972, modified).

*Break ligaments*, on the other hand, are split from the outside. They not only allow, but require a certain amount of shell thickening and also permit the growth of highly vaulted valves. Nevertheless inequivalvity is common, because it reduces the space problem of the opposed umbones and because it agrees with the pleurothetic mode of life, which is common in epibenthic species. Inequivalves are also limited by the requirement that an equal amount of ligament should break on both valves. Another way out of the umbonal space problem is the transition, during ontogeny, from convex to concave curvature in the flatter valve of inequivalves such as *Gryphaea*.

An obviously successful compromise is the ligament design found in many heterodonts (text-fig. 1H). Here the two ligament layers are widely separated for increased lever on both sides of the hinge axis and breakage is not excessive. The resulting limitation of shell curvature also agrees with the streamlining required by a burrowing mode of life, while umbonal collision can be avoided by a prosogyrous growth programme. Another possibility to avoid this collision is an ontogenetic switch to higher curvatures in both valves after a flattened umbo has been produced in the early stages (*Circe*).

We shall come back to ligamental problems in our discussion of secondary soft-bottom dwellers.

#### *Shell adaptations to burrowing*

On soft bottoms the ability to burrow has a major bonus, because it reduces predation pressure, while allowing for various modes of nutrition such as suspension feeding, epistratal and intrastratal sediment feeding, and even carnivorous habits. The mechanical principles of soft-substrate burrowing have been analysed by Trueman and Ansell (1969). The most effective design is represented by worm-like organisms. As primary soft-bottom dwellers in the strictest sense they have evolved a cylindrical hydraulic body that combines ideal streamlining with the possibility to glide through the sediment almost as easily as along its top. Here, the peristaltic thickening and contraction of body sections transform the push-and-pull action into a seemingly continuous process. In bivalve burrowing, however, functions are divided between the different parts of the body (text-fig. 2). The foot, as a hydraulic structure, alternatively thins into a probe and thickens into a protraction anchor. Correspondingly, the shell is expanded as a penetration anchor during the probing of the foot and becomes partly closed when it is pulled behind. In this phase friction can be further reduced by the ejection of water from the front end and the resulting fluidization of the sediment around the shell.

This mode of burrowing was so successful that it has been maintained by all bivalves that remained in soft substrates. They also have never reduced the shell, because it serves not only for protection, but also supports the necessary filter chamber. In boring bivalves, however, these two functions were taken over by the hard substrate, so that the shell could be transformed into a boring instrument without being constrained by additional tasks (Röder 1977).

In burrowing bivalves evolutionary trends in shell morphology are thus limited to minor modifications that improve the burrowing function. For instance, *shell geometry* tends to become more streamlined and elongated as species burrow deeper and reach more compacted sediment (Stanley 1970).

Another common trend is the evolution of *burrowing sculptures* (Jefferies *et al.* 1981; Savazzi *et al.* 1982) in shallow burrowers (text-fig. 3). Like the profiles of cross-country skis, they reduce back slippage of the shell while it serves as a penetration anchor and produce minimal friction while it is being pulled forward. The effectiveness of such ribs obviously depends on their profile, which should be ratcheted. But experiments (Savazzi 1981b) have shown that their dimensioning is also important. If the ribs are too low, sediment grains will be little affected; if they are too high, grains in the grooves will slip as a whole against the outside sediment, so that effectivity diminishes again.

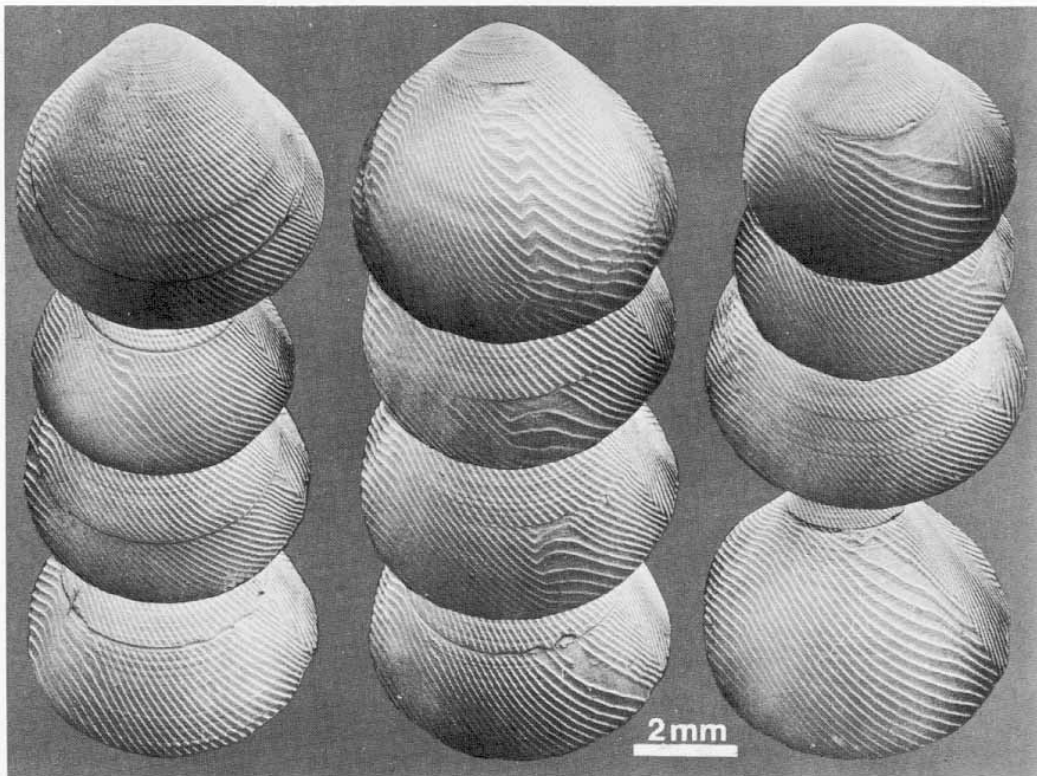
On this basis one can formulate the paradigm for burrowing ribs in the following way (Seilacher 1973):

1. They should be ratcheted with the gentle slopes in burrowing direction.
2. Their strike should be at right angles to burrowing direction.
3. Their height should correspond to the grain size of the burrowed sediment.
4. In highly vaulted bodies the profile may be smoothened in the most projecting surfaces, where forward friction is most critical.

The approximation of this paradigm has been studied in many groups of burrowers (bivalves, gastropods, crustaceans, trilobites, lingulid brachiopods, calcichordates; see Jefferies *et al.* 1981 for a summary). In the view of constructional morphology, these examples are interesting not only because of their palaeobiological and palaeoenvironmental implications. They may, by significant deviations from the physical paradigm, also reveal the constraints imposed by a particular bauplan or morphogenetic program.

In bivalves the major constraint is implied in their accretionary mode of shell growth. In the theoretical model of spiral shells (Raup 1966), growth conformable sculptures are either radial or concentric. None of the two can have the same strike relative to burrowing direction all over the shell. This dilemma can be lessened by emphasizing radial or concentric ribs, or both, in the parts of the shell, in which they happen to run in the right direction (Seilacher 1973, fig. 2). More difficult is the task to maintain the same rib dimensions during growth.

Thus it is not surprising that many bivalves programme their burrowing ribs with a principle (Waddington and Cowe 1969; Meinhardt, in preparation) that is dependent on a time function rather than being dictated by the geometry of spiral growth (text-fig. 3). This 'divaricate principle' (Seilacher 1972), familiarly expressed in mollusc colour patterns, but also in arcoid ligaments, is better suited for the task at hand. First, it provides not only one, but two coordinate strike directions in a V-shaped fashion. Secondly, the asymmetry is also provided, as seen in corresponding colour patterns. Thirdly,



TEXT-FIG. 3. Shell outline and divaricate rib pattern of *Strigilla pisiformis* from Miami (Florida) correspond to the *Divaricella* Type (text-fig. 2c). The regular fashion in which traumatic gaps in the pattern regenerate indicates that this pattern is formed by a diffusive inhibitor/activator system (SEM photos by H. Hüttemann).

the spacing (and consequently rib height) is largely growth-independent, so that a near-optimal scale can be maintained with less difficulty. Thus the alternative, but less efficient solution of allometrically reducing the height of the ribs relative to their distance (Savazzi 1981a, 1982a, b) is not necessary in this case.

In spite of their fabricational flexibility, actual divaricate burrowing ribs *deviate* in significant ways from the cross-country ski paradigm. The rib distance, for instance, is negatively allometric, but still increases with growth in absolute measure (Seilacher 1972, fig. 6). This indicates that the underlying morphogenetic principle is not completely growth-independent. More surprising is the fact that these ribs do rarely run truly perpendicular to burrowing direction. This has to do with the fact that bivalve shells are not used like cross-country skis. Shells with a rounded outline (*Divaricella* type, text-fig. 2c), perform a rocking movement (Stanley 1969), which is also reflected in their V-shaped rib pattern. The dividing line between the two sets of ribs, however, does not run in burrowing direction, but is rotated from it counter-clockwise in left view. An analogous rotation is observed in the more elongated shells of the *Yoldia* type (text-fig. 2d), in which only one set of divaricate ribs is developed. This rotation makes sense, if we consider the opening of the valves during the probing phase: the observed rib direction corresponds to the resultant of the opening and the backslippage vector. A third group (*Macoma* type, text-fig. 2e) resembles the previous one in outline and rib pattern, but is sculpturally inequivalve. It comprises species that burrow along horizontally in a flat position as they graze the sediment surface with their ingestion siphons. Their reduction or omission of burrowing sculptures on the lower valve compensates for the higher friction exerted by the sediment below the shell as compared to the thin and less compacted sediment cover on top of it.

The occurrence of divaricate burrowing ribs in most groups of endobenthic bivalves indicates that the underlying morphogenetic principle is generally available. All the more it is surprising that not all burrowing species make use of this possibility. Instead, we find smooth, radially or concentrically ribbed and tuberculated forms in the same niche. Obviously, there are alternative solutions to the adaptational problem as well as constraints related to other functions that exclude one standard interpretation.

It might be mentioned that the case of divaricate burrowing ribs has been repeatedly cited by modern neutralists (e.g. Gould and Lewontin 1979) in their critique of the traditional adaptationist camp. In fact, I am still inclined to believe that most divaricate colour patterns are primarily neutral, or non-functional features in the sense that any other arrangement would do as well. This is suggested by the fact that in life the patterns remain hidden in the sediment or under a thick periostracum and that they are extremely variable in contrast to the few species, in which such patterns demonstrably have a mimetic function. A similar evolutionary relationship was assumed in the sculptural expression of divaricate morphogenetic programmes. I see this switching into a more rigorously selected function of a pre-existing, or pre-disposed structure as an interesting mechanism, but not as a general or even predominating mode of evolutionary change.

## SECONDARY SOFT-BOTTOM DWELLERS

Bivalves were extremely successful as soft-bottom filter feeders. Nevertheless, many groups have left the soft bottom to become hard-bottom dwellers again; but since the burrowing foot could not evolve back into a crawling sole, they became sedentary. The pathway into a fixosessile niche was wide open to bivalves due to their mode of nutrition and the general presence of byssus as an organ for larval attachment (Stanley 1972). The paedomorphic retention of this attachment (and in some instances its replacement by cementation of the shell to the hard substrate) throughout life led to the reduction of the foot. It also led to the high intraspecific variability in shell shape that is characteristic of oyster-like, cemented forms and for species whose byssal attachment to rocky substrates is similarly rigid.

It is the evolution of such fixosessile rock dwellers back to soft-bottom habitats that I address here. This step is particularly interesting for a number of reasons:

1. The major adaptational problem implied is straightforward: to make up for the inherited loss of the foot in an environment devoid of adequate anchoring ground.

2. This evolutionary habitat change has happened in so many instances among bivalves as well as in other sessile groups, that we have a good chance to do comparative studies and to sample a wide variety of possible pathways.

3. It is in this group (for which we use the terms 'secondary soft-bottom dwellers') that we find the largest number of bizarre forms—quite in contrast to the primary soft-bottom dwellers discussed in the previous paragraph.

Thus our first question will be, what allowed the extreme and rapid changes of established bauplans in this particular situation? This question is relatively easy to answer. It has primarily to do with the ecological stepping stones that facilitate this change. Corresponding to the rule that an established system tends to adapt to changing conditions first by developing a cover under which the old functions can continue, the pioneer species will attach to hard substrates that are available on soft bottoms, i.e. to dead shells of other organisms. The only morphological change (the 'cover') necessary is progenetic reduction of adult size by shortening the life cycle ('miniaturization stage'). This stepping stone remains to be used during early ontogenetic stages by most of the species that do become independent of such anchoring grounds as they grow up. This makes it difficult, in the fossil record, to distinguish the miniaturized pioneers from juvenile stages of secondary soft-bottom dwellers in the strict sense.

The miniaturization stage is critical, because the following evolutionary step implies a considerable change of selection pressure and also a switch from an  $r$ - to a  $K$ -strategy. Independence from an adequate anchoring ground can be gained in three different ways:

1. By developing a *new mode of mobility*, such as the ability to swim up (pectinids, limids, and possibly some Strophomenacea), to crawl (certain corals and bryozoans), and to burrow (soft-bottom sea anemones; *Penicillus*, fig. 11). Among the pelecypods, only attached Arcacea seem to have been able to re-activate the foot for this purpose (Thomas 1976).

2. By establishing symbiotic 'pickaback' relationship with a mobile partner. The shelter-building associates of hermit crabs and of some worms are familiar examples.

3. By mechanically stabilizing the body by shape, weight, and size.

Among bivalves the third solution has been the one predominantly used. Therefore we will focus our discussions on this 'strategy'. In doing so, we first deal with the forms that were originally cemented, then discuss byssally attached forms, and finally borers.

#### CEMENTED STOCKS AND THEIR SOFT-BOTTOM DERIVATIVES

Most cemented bivalves are monomyarian (oysters, spondylids, *Placunopsis*, plicatulids); but the dimyarian Chamacea, Rudists, and fresh-water 'oysters' (*Etheria*) show that this is not a necessary relationship. We shall here use the Ostreacea for reference, because this is the most varied group. Thus the principal adaptational strategies can be discussed in oyster examples and analogous adaptations in other groups be listed as convergences.

##### *Morphogenetic consequences of cementation*

Since cementation is the task of the growing mantle edge, the commissure has to fit snugly to the substrate. This means that the relief of the substrate is moulded on the outside not only of the attached valve ('immuration', Voigt 1968), but also of the free valve—in this case as a positive transformed by the spiral growth geometry ('xenomorphism'). The control of substrate topography on growth is also expressed in the outlines of cemented shells, which tend to be irregular and highly variable. This ecotypic 'derailment' of a regular growth programme may facilitate a subsequent switch to novel programmes.

Cemented growth may continue in this fashion throughout life; but in many cases the commissure will eventually lift-off the substrate in order to facilitate water circulation, to widen the shell cavity, and to defend against overgrowth. This is also the case in the miniaturized soft-bottom pioneers growing on other shells. The mode in which the attached valve lifts the commissure, predetermines



the general geometry of growth during subsequent soft-bottom adaptations (text-fig. 4). Thus elevation of the posterior margin induces an helicospiral exogyrid form, of the ventral margin the planispiral gryphaeid growth, and of the whole shell including the hinge the saccostreid cone shape. Other modifications during the lift-off include the alectryoniid plication of the commissure and retarded calcification giving the free valve a higher flexibility.

These differences can be observed in juvenile stages of advanced forms, but also in minute ancestral forms. It is probably no coincidence that small and thin-shelled epizoic versions appear stratigraphically below the large free forms in *Lopha* (Middle Triassic; Seilacher 1954) and in *Exogyra* (Lower Toarcian; Seilacher 1982a). The same is true for *Plicatula* (*P. spinosa*; Domerian). A systematic search should also document the miniaturized epizoic ancestors of other groups such as rudists.

#### *Recliners versus 'mud stickers'*

Among the possible strategies of mechanical stabilization two groups should be distinguished, although they may be not sharply separated. In the first and more common case ('recliners' = Liegeformen; Dacqué 1921) the animal essentially rests on the substrate; in the second the shell itself acts as an anchor in the sediment. In the absence of active burrowing, anchorage inside the sediment must be acquired passively and will therefore evolve preferentially in quiet environments with a relatively high sedimentation rate ('mud stickers'). The difference between the two life forms is expressed in shell shapes and opening mechanisms, but also in shell structures. Only the recliners follow the strategy of heavyweight structures that is so much in contrast to the lightweight skeletons of mobile organisms.

The strategy of 'mud (or sand) stickers', being a response to sedimentation is also valid for living substrates. Therefore it is not surprising to find related forms living in mud and in sponge or coral colonies (*Streptopinna*, text-fig. 9; *Vermicularia*; *Pyrgoma*).

#### *Cup-shaped recliners*

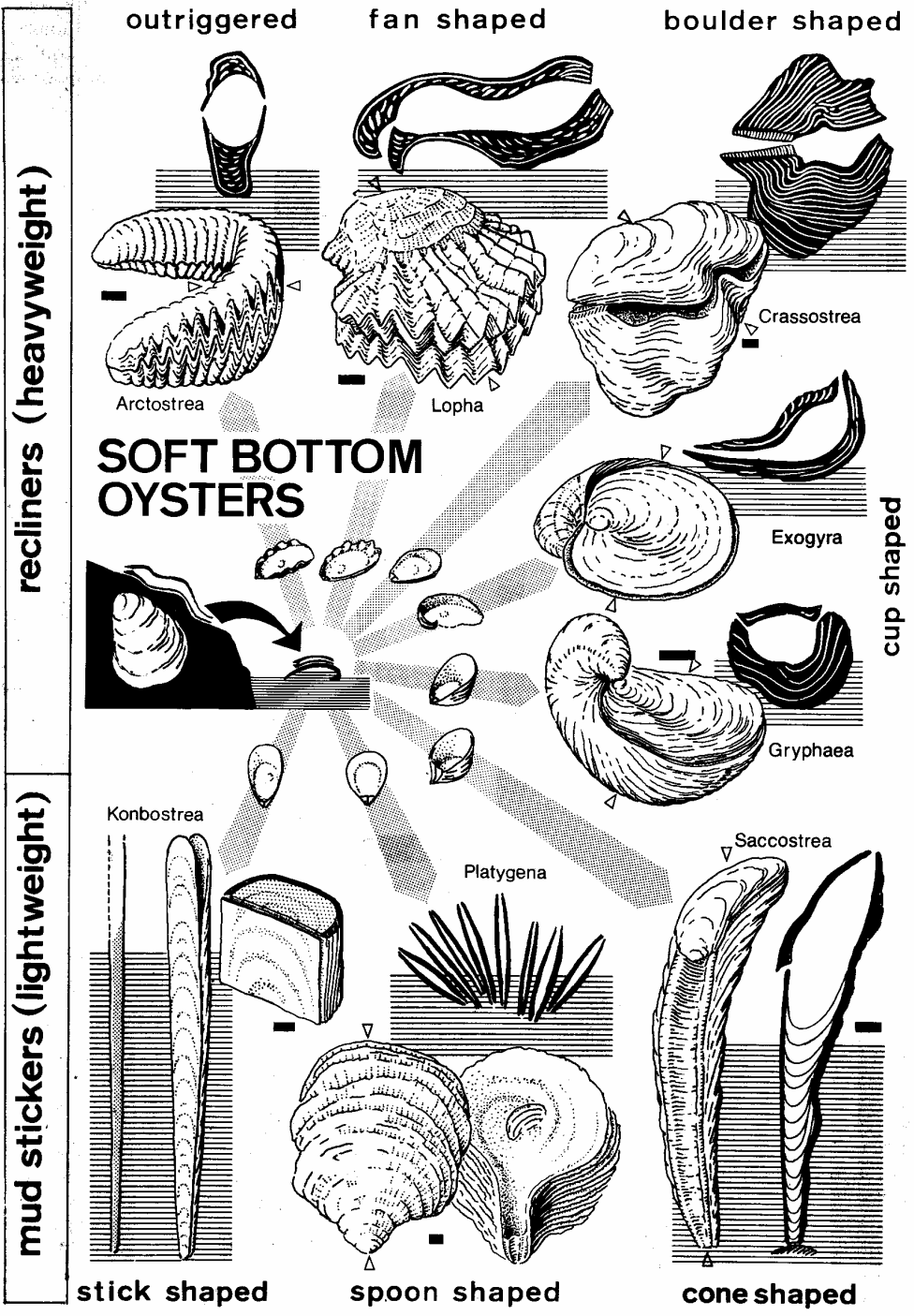
Probably no invertebrate has received as much attention in terms of functional morphology and evolution as *Gryphaea* (Hallam 1982). The geometrical inequivalvedness is induced in the juvenile stage, when the attached valve starts to grow up from the initial anchoring ground into a cup, inside which the free right valve nests with a flexible shell margin—a relationship which may also be expressed in adult forms (*Cubitostrea*), whose left valve shows regular radial ribs, while the right valve remains smooth. The resulting gryphaeid curvature of the left valve allows excessive deposition of dense shell material in the umbonal region, which serves as a balance to keep the animal in the right position. The inequivalvedness also permits the umbo of the left valve to expand without getting in conflict with the opposed umbo. The umbonal problem can be even better avoided in the helicospiral exogyrid version, but nevertheless the excessive thickening of the lower valve is maintained.

*Convergences.* As shown by Stenzel (1971), gryphaeid shells have evolved repeatedly from attached oyster stocks. Similar growth forms can also be observed in other cemented groups, such as *Spondylus* and *Chama*. In all of them it is the attached valve that forms the cup. This is in marked contrast by byssally attached groups (bakevelliids, inoceramids, anomiids), in which it is the valve originally facing the substrate that becomes the lid in cup-shaped recliners (see below).

#### *Boulder-shaped recliners*

Extreme shell thickening in both valves is characteristic for several species of *Crassostrea* (text-fig. 4) in the upper Cretaceous and the Tertiary. During the later part of their lives they continue to thicken the shell without further growth of the soft body, so that the shell cavity is only a small fraction of the whole shell volume. For geometrical reasons, the ligament must also continue to grow during this stage, resulting in a high ligament area with nearly parallel sides. In addition to the excessive shell thickening and unusual size (up to 25 cm in diameter), a very dense shell structure contributes to increase the stabilizing weight of the oysters.

It may be more than coincidence, that the most spectacular 'storm tells' (Seilacher 1983), some of



them reaching 20 m in thickness (Bender 1968) have accumulated through event condensation during regressive intervals from this type of oyster.

*Convergences.* Although this seems to be a straightforward strategy, no comparable adaptations can be quoted from other pelecypod groups, which probably could not match the oyster's rate of shell and ligament production.

#### *Fan-shaped recliners*

Another possibility to stabilize the shell is its expansion into a flat fan shape. Adhesion to the sediment may be further increased by strong sculptures (radial ribs, spines, foliate concentric ribs). In

TEXT-FIG. 4. Evolution of a wide range of adaptational strategies in soft-bottom oysters was facilitated by a sequence of ecological steps:

(a) The 'derailing' of morphogenetic programmes in fully cemented rock-dwelling oysters.

(b) The progenetic miniaturization in soft-bottom pioneers that used dead shells as stepping stones into the new habitat.

(c) True soft-bottom dwellers use shell substrates only in their early growth stages and become stabilized by size increase, shell thickening, or mud sticking as adults.

*Arctostrea* sp. (Lower Cretaceous, East Africa; GPIT 1604/1). Horseshoe-shaped elongation stabilizes the shell with the inhaling convex flank facing upcurrent. It is on this anterior side that the zigzag commissure is most pronounced. Since the left valve is excessively thickened and bears lateral outrigger spines in another species (*A. colubrina ricordeana*; see Carter 1968) this was probably the preferred resting surface.

*Lopha marshi* (Middle Bajocian, Aalen, southern Germany; GPIT 1604/2). After a relatively long encrusting stage that bears the xenomorphic sculpture of pelecypod or ammonite substrates, the shell became fan-shaped, plicate, and very thick, particularly after cessation of radial growth. Epizoans indicate that the species could recline on either valve.

*Crassostrea* sp. (Upper Eocene, Oriz, Vic Basin, southern Spain; GPIT 1604/3). This large species grew rather irregular throughout life; but the large ligament area, small body cavity, and excessively thick valves as well as a dense shell structure indicate that shell growth had the main purpose of making the animal heavier and continued long after the soft parts had reached their ultimate size.

*Exogyra* sp. (Upper Cretaceous, Kansas; GPIT 1604/4). Prosogyrous spiral growth was established already in miniaturized epizoic species of the Lower Toarcian. In later reclining species it allowed the umbo of the left valve to become a heavy bottom weight, while the right valve formed a thinner lid. Stabilization was also improved by a gradual evolutionary increase in adult size.

*Gryphaea arcuata* (Lower Sinemurian, southern Germany; GPIT 1604/5). The almost planispiral growth of this genus is also derived from the way in which epizoic ancestors and juveniles lift off the substrate. It allowed the lower left valve to become even heavier compared to the upper. Narrow species such as this one may also have been passively righted by the principle shown in text-fig. 12.

*Saccostrea* sp.; East Africa (GPIT 1604/6; reconstructed after specimen courtesy of Dr. D. Nations, Flagstaff). Cone-shaped growth of the lower valve, convergent to rudists and richthofeniid brachiopods, might appear the simplest way to transform a cemented bivalve into a mud sticker, but it creates problems in forms that maintain a functional break ligament with very unequal attachment areas.

*Platygena asiatica* (Upper Eocene, U.S.S.R.). In this genus a mud-sticking mode of life with the umbones down is documented by field evidence (section of colony, from Hecker 1956). Its valves are relatively thin and very flat. Most characteristic is the internal view (from *Treatise Inv. Pal.* N 1147) with lateral areas of regressive growth lines. They transform the umbonal part of the body cavity into a narrow handle and may have assisted the ligament to open the valves and keep the sediment from entering, if they were provided with flexible brims.

*Konbostrea konbo* (Upper Cretaceous, Japan; after Chinzei 1982, and in prep. and GPIT 1604/7). Early ontogenetic replacement of the ligament function by the elastic bending of the flat and thin right valve allowed this species to develop a stick-shaped shell, in which the body cavity is restricted to the uppermost part. The rest of the gutter-like left valve is filled with chalky layers, whose upper end forms the fulcrum for the flexible left valve (compare *Lithotis* in text-fig. 5).

All scales = 1 cm.

contrast to the previous types, however, there is no preference for lying on either the right or left valve. This is indicated by equivalve shell thickness and can be tested by the statistical distribution of epizoans.

Zigzag folding of the commissure, exemplified by reclining species of *Lopha*, corresponds particularly well to his mode of life. As shown by Rudwick (1964) for brachiopods, it reduces the danger of sediment intake. On the other hand it guarantees that in either position one side of the folded commissure is well above the sediment level. Also it eventually results in the anchoring ribs.

Less sculptured flat oysters may also belong to this type (*Deltoideum delta* in the Upper Jurassic), but their attribution is less certain, because spoon-shaped mud stickers may have similar shapes. Therefore additional evidence (epizoan distribution and slope orientation; observation of life positions in the field) is desirable in these cases.

*Convergences.* This adaptational strategy is found in Tertiary species of *Plicatula*, an originally cemented recliner, but also in byssal stocks such as many pectinids, the limid *Ctenostreon*, and the anomids *Placuna*, *Carolia*, and *Huyella*.

#### *Outriggered recliners*

In this case a large resting surface is acquired by deviation from the rounded outline. This can be done by wing-like expansion of the hinge, by finger-like extension of radial ribs, or by elongation of the whole shell into a curved, crescentic outline. The oysters have made use of all three possibilities. *Rastellum* forms a long auricle on the posterior side (much like reclining *Isognomon isognomum*, text-fig. 5). *Lopha quadriplicata* lacks auricles, but in the adult stage it produces strong outriggered ribs by local expansions of the commissure, very much like in the isognomid genus *Mulletia* (text-fig. 5). More common is the third solution (*Arctostrea*, text-fig. 4), combined with a zigzag commissure line. Its curved outline also improves the separation of the inhaling and exhaling currents because the convex inhaling side faces up-current in the hydrodynamically stable position. As in the previous type it makes no difference for outriggered recliners which valve is up; but in *Arctostrea* from the Chalk additional outrigger spines are developed only in the left valve, which must have been down in life position (Carter 1968).

*Convergences.* Because of the broader range of possibilities, outriggered recliners are more common in some byssate groups (see below), but also among brachiopods.

#### *Cone-shaped 'mud stickers'*

The morphogenetic strategy in which the attached valve grows up into a slender cone while the other forms a lid, is well known from rudists as well as richthofeniid brachiopods and seems to be the simplest answer to a rising sediment level. A *Saccostrea* from the East African coast (text-fig. 4) resembles rudists not only in shape, but also by the thin-vaulted septa that obstruct the lower part of the cone as the soft parts move up. But its 'mud-sticking' mode of life is only inferred and needs to be verified by field observations.

In bivalves, however, this mode of growth poses a major problem. In a break ligament the two ligament areas should be of corresponding dimensions, because a break in the middle invalidates equal areas on both valves. Thus the extreme disproportion of ligament attachment on the two valves of *Saccostrea* (text-fig. 4) required a drastic rearrangement in ligament structure, which would deserve a detailed study. In rudists this problem was bypassed by reduction of the ligament and its probable functional replacement by a diductor.

*Convergences.* Although cone-shaped rudists are commonly referred to as reef-builders (which they may secondarily have become in some cases), their morphology suggests that they originated as 'mud stickers'. This seems also to be the case with the brachiopod *Richthofenia* and other 'coralliform' species, such as the gastropods *Rothpletzia*, in which the operculum, and *Vermicularia*, in which the shell has become tube-like. All these had at some time been cemented to hard substrates. To what extent cone-shaped corals and sponges conform to this model remains to be studied.

Sponges obviously can be 'mud sticking' only with a defunct basal portion, so that the living parts remain washed by water from all sides.

It is probably no coincidence that no cone-shaped forms seem to have evolved from non-cemented bivalves, because they would have no reason to grow up from the substrate by elongation of only one valve.

#### *Spoon-shaped 'mud stickers'*

In this type the ligament remains submerged in the sediment. It thus acts against sediment pressure and needs either to be very strong or supplemented in its action by other elastic structures, such as uncalcified shell margins that also keep the sediment from laterally entering the mantle cavity in the open position. The modern *Crassostrea virginica* represents this mode of life, approaching stick- or club-shaped 'mud stickers' with its elongate outline. More characteristic is the Tertiary *Platygena* (text-fig. 4), in which the umbonal part of the body cavity becomes secondarily narrowed to a handle-shaped apsis flanked by broad areas of regressive growth lines. Field evidence (Hecker 1956) shows that they stuck in the sediment as colonies that opened like the pages of a book. Corresponding shell shape suggests a similar mode of life for the extremely flat Upper Jurassic oyster *Deltoideum delta*, although this species has not yet been recorded in life position.

*Convergences.* So far only the Jurassic genus *Lithioperna* can be quoted as a direct analogue (text-fig. 5). It is quite variable in shape, ranging from inequivalve, cup-shaped recliners with thick shells to flat, equivalve forms. In the Calcarei Grigi of northern Italy, some beds consist almost solely of these flat forms, whose imbrication superficially resembles current-induced post-mortem accumulations. But since in these beds all specimens are double-valved, have their umbones pointing downwards, and are unusually elongated, they must be considered as dense beds of 'mud stickers'.

A slightly different version seems to be represented by stacks of the anomiid *Carolia* that T. Aigner found in the Eocene of Egypt. In these stacks, only the first individual closes the byssal notch during ontogeny in the usual fashion. The other ones attach with exactly the same orientation to the convex left valve of their neighbour and secrete on it a calcareous plug that upon retraction of the byssus snugly fits into the persisting byssal notch. These stacks, consisting of up to six individuals, were found in various positions in the rock. They are likely to have been reworked as an aggregate and buried alive during catastrophic events such as storms, while they originally lived in an inclined position similar to *Lithioperna*, with the weight of the byssal plugs adding to keep the umbonal side lowermost.

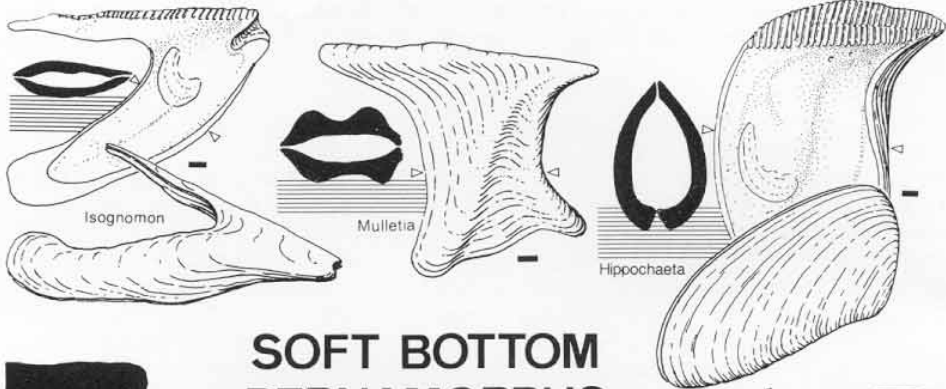
#### *Club-shaped 'mud stickers'*

*Konbostrea konbo* (Chinzei 1982) from Upper Cretaceous mud-flats (text-fig. 4) represents the most extreme deviation from the oyster bauplan. Its elongation, combined with a documented 'mud-sticking' mode of life, was made possible through the early ontogenetic replacement of the ligament function by elastic bending of the right valve, which accordingly remained very thin and completely flat. The left valve, attached only in the juvenile stage, grew in a gutter-like fashion; but its cavity became successively filled by chalky shell material as an alternative to light-weight obstruction by septae, which is possible only in cone-shaped valves. In this way the body and the shifting 'hinge' zone with its fulcrum could move up like an elevator to compensate for the accumulation of mud between the individuals of a colony.

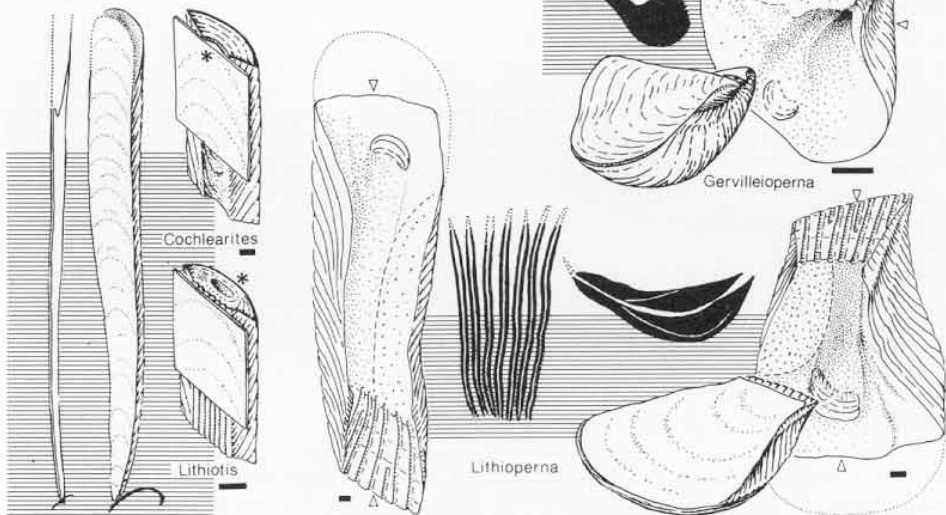
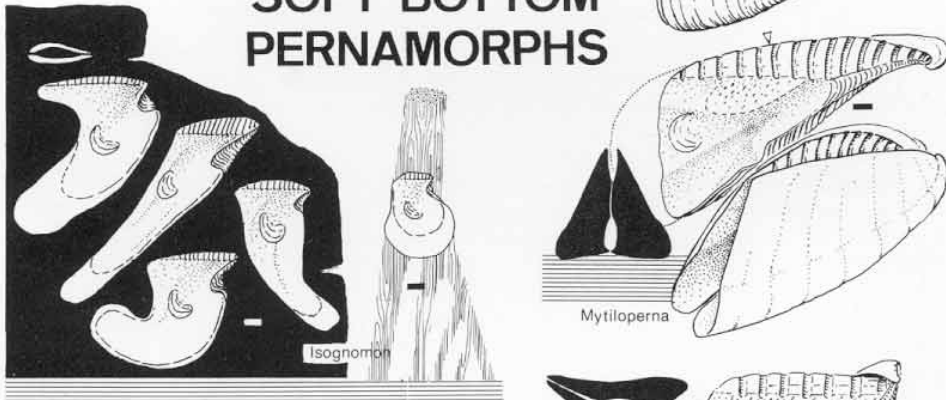
*Convergences.* The genus *Lithiotis* (text-fig. 5), characterizing a shallow-marine limestone facies in the Lower Jurassic Tethyan realm (Geyer 1977) was convincingly shown to have grown and functioned in an analogous way (Chinzei 1982). This is also true for the associated genus *Cochlearites*, in which it is not the right, but the left valve that provided the fulcrum. Also the fulcral area has a different structure (text-fig. 5). Therefore, Chinzei concluded that the two genera evolved independently, but probably from related stocks. Their taxonomic relationship is still uncertain. Most probably they belong to the bakevelliid stock (*Mytiloperna*, *Gervilleioperna*, *Lithioperna*; text-fig. 5), which shows an unusual radiation in the *Lithiotis* facies. These genera are characterized by a broad-tooth plate

outriggered recliners

edgewise recliners



SOFT BOTTOM  
PERNAMORPHS



stick shaped  
mud stickers

spoon shaped

cup shaped  
recliners

(broken lines in text-fig. 5) that could have evolved into fulcral areas in the elongated forms. Both genera, however, seem to have been cemented to shelly substrates during early ontogenetic stages, *Lithotis* with the right and *Cochlearites* with the left valve (Chinzei 1982), in contrast to the byssal attachment of other bakevelliids. In fact, cementation might have been necessary to induce their extreme inequivalvedness.

#### BYSSATE STOCKS AND THEIR SOFT-BOTTOM DERIVATIVES

The adaptational history of byssate bivalves has been treated extensively by Stanley (1972). While I agree with most of his interpretations in terms of functional morphology, I am not so certain about his assumption that most epibyssate forms have evolved, without habitat change, in soft-bottom environments and with the endobyssate stage as an initial step. Stratigraphical evidence does not always support such a sequence (for instance are the first representatives of the bakevelliids and

TEXT-FIG. 5. Secondary soft-bottom dwellers derived from byssate stocks are commonly edgewise recliners that maintain weak byssal attachment in addition to stabilization by shape and weight. Other strategies resemble those in cemented stocks (text-fig. 4); but it should be noted that no cone or stick-shaped mud stickers have evolved from non-cemented rock dwellers.

Modern rock-dwelling isognomonids (*Isognomon (Isogonum)* sp.; Langun, Malaysia; GPIT 1604/8) are much more firmly attached than mangrove species (*I. (I.) ephippium*, Philippines; GPIT 1604/9). Therefore they show extreme variability ('morphogenetic derailing') that helped them to evolve extravagant shapes in soft-bottom descendants.

*I. (I.) isognomum* (Philippines; GPIT 1604/9) is a V-shaped recliner lying either on the right or left valve. It further develops the ventral elongation of rock-dwelling ancestors plus long posterior auricles as outriggers. Increased shell thickness and size also improve stabilization.

*Mulletia mulletii* (Lower Cretaceous, England, from *Treatise Inv. Pal.* N 325) outriggers by toe-like expansions of the commissure.

*Hippochaeta sandbergeri* (Oligocene, Weinheim, Germany; GPIT 1604/10) could have been either a flat or an edgewise recliner; but similar forms from the Jurassic (Fürsich 1980) have been found in edgewise life position (see text-fig. 8).

*Mytiloperna* sp. (Calcarei Grigi, Lower Jurassic; Vajo dell'Anguilla, Verona, northern Italy; GPIT 1604/11). Like the following forms, it has a broad tooth plate (broken outline) that indicates affiliation with the Bakevelliidae rather than the Isognomonidae. Triangular cross-section and extreme shell thickening as well as reduced height (compare *Tanchintongia*, text-fig. 8) are typical for edgewise recliners. The posterior gape, the marginal position of the posterior adductor, and the lack of marked growth lines indicate that the shell was originally covered by a less calcified outer layer that formed a flexible flap on the posterior side, much like in the following forms. Note that this is the only edgewise recliner in the bakevelliids. This indicates evolution via mud stickers.

*Gervilleoperna* sp. (Calcarei Grigi, Lower Jurassic; locality as before; GPIT 1604/12) represents the gryphaeid type of cup-shaped recliners.

*Lithioperna* (Calcarei Grigi, Lower Jurassic; same locality) occurs in two morphotypes. As isolated recliner, it is found in flat position, with a roundish outline and commonly with very thick and cup-shaped cross-section (GPIT 1604/13). In crowded, book-like colonies, the shells remain flat and thinner-shelled and grow much longer (left specimen, from Accrosi-Benini 1978). If the ventral flexible flange extended to the anterior and posterior sides, it could have prevented lateral penetration of the surrounding sediment when the valves were open (compare similar regressive growth line areas in *Platygena*, text-fig. 4).

*Lithotis* and *Cochlearites* (after Chinzei 1982) are perfect homeomorphs of *Konbostrea* (text-fig. 4), though they are certainly not oysters. They are here tentatively affiliated with the bakevelliids, with which they are associated in the Calcarei Grigi, but from which they differ by being monomyarian and cemented as juveniles. Note also that the thin and flat flexible valve is not the same in the two Liassic genera, indicating parallel evolution (asterisk = right valve).

All scales = 1 cm.

inoceramids not modiomorph endobysates?). One should also bear in mind that by their higher fossilization potential 'mud stickers' tend to be well represented compared to rock-dwelling forms, which I would prefer as the initial stage. The main difficulty, however, is the reduction of the foot, which in soft sediments would not have become redundant by the maintenance of byssal attachment throughout life. Certainly, evolutionary pathways between endo- and epibysate forms may have been passable in either direction and one should study each case separately. Still I prefer to consider the majority of byssate 'mud stickers' and recliners as secondary soft-bottom dwellers in the strict sense, i.e. as the result of an evolutionary habitat change from soft to hard bottoms and back again.

As a reference group for byssate bivalves we select here the forms with a multivincular ligament, because they have evolved a great diversity of soft-bottom dwellers both in the Mesozoic and the Recent. In current taxonomy they are grouped under the families of Bakevelliidae and Isognomonidae, which differ in shell structure and in the form of the hinge.

While the mechanical principles of stabilization are the same in cemented and byssate stocks, some general differences should be noted. First, byssate recliners need not be as morphologically stable and thick-shelled as cemented ones, because the byssus may provide an additional means of stabilization throughout life. Secondly, byssate stocks had no access to pathways such as cone-shaped 'mud stickers', but commonly evolved into edgewise recliners, which are conspicuously absent in byssate stocks.

#### *Outriggered recliners*

Compared to cemented stocks, outrigger production differs significantly in byssate forms, because their long hinge lends itself to prolongation into a narrow auricle, which may have had a stabilizing function already in rock-dwelling ancestors (Stanley 1972). In truly multivincular species (*Isognomon*, *Mulletia*; text-fig. 5), an auricle forms only on the anterior side, assisted by elongation of the ventral margin at an acute angle.

*Convergences.* *Malleus*, closely related to *Isognomon* in spite of its alivincular ligament, is the prototype of an outriggered recliner (text-fig. 6); but since it evolved an anterior auricle in addition to the posterior one, elongation of the ventral shell margin proceeds at a right angle to the hinge. Secondary shell thickening separates the auricles in later growth stages of *M. albus* (text-fig. 6), so that only the ventral margin can proceed to grow. This also allows the zigzag undulation of the commissure to develop in a more regular fashion with an overlap of the margins at the bends, which keeps the shell from gaping more widely at these points. Epizoan overgrowth shows that *Malleus* reclines ambivalently on the right or left valve (Seilacher 1982*b*) and is no 'mud sticker' as commonly

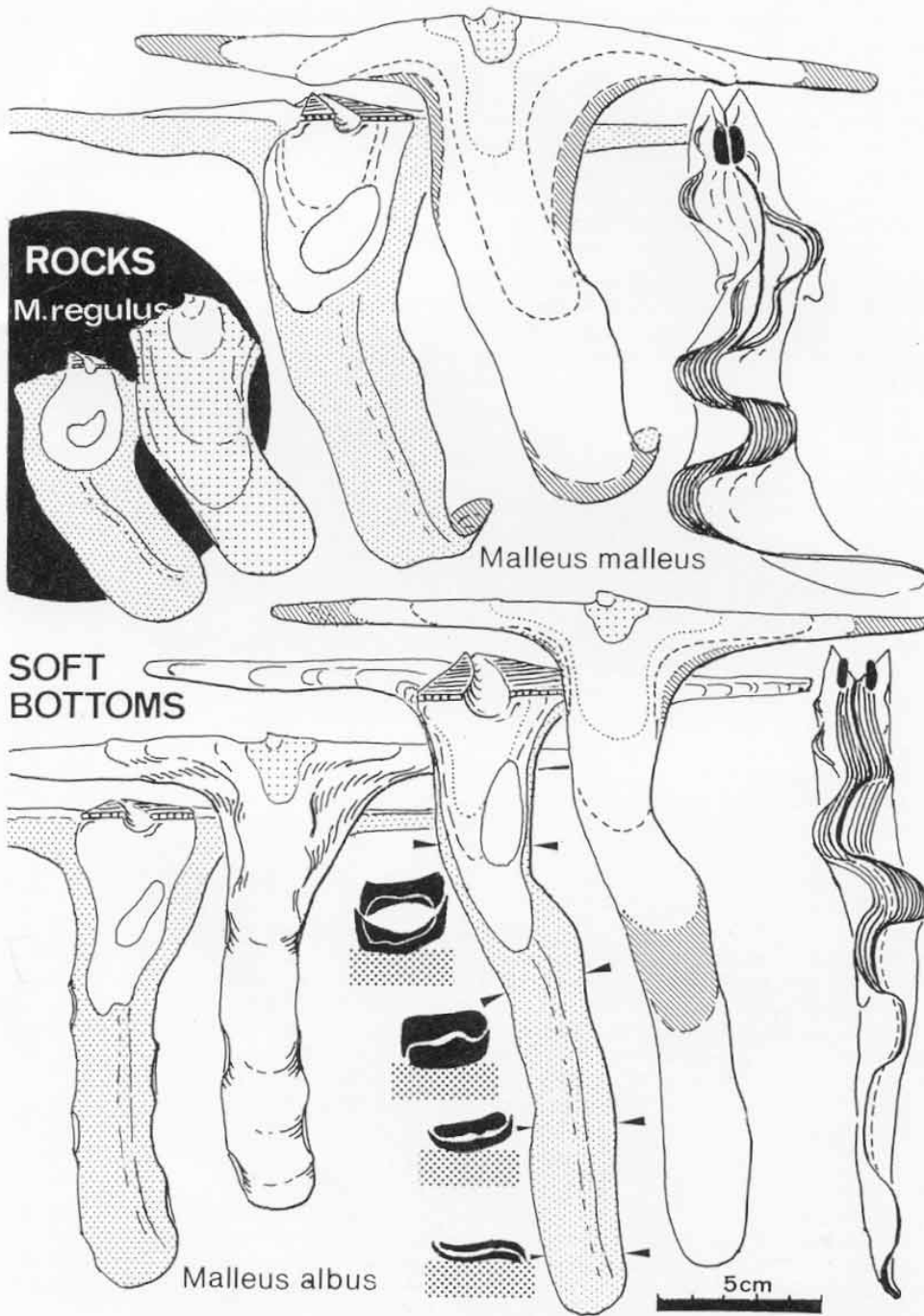
TEXT-FIG. 6. Although being closely related, the Malleids differ from the isognomonids (top part of text-fig. 5) by having an alivincular ligament and by being byssally attached at the umbo rather than at the anterior flank of the shell. Accordingly they were able to evolve outriggered recliners (not mud stickers, as commonly believed) by developing long auricles on the posterior as well as on the anterior sides of the elongate shell.

The ancestral situation is illustrated by *Malleus regulus* (Cebu, Philippines; GPIT 1604/14) that lives firmly attached to rocks and is relatively small, thin shelled, and highly variable in shape.

Similar stages, first with round outline and then with orimantal auricles are also found in the two reclining species; but they are very much reduced in size, indicating that evolution went through a miniaturized stepping stone adaptation. Only in an ontogenetically following outrigger stage does the shell grow hammer shaped, thick, and very large. It also develops a zigzag commissure, in which the absence of secondary shell broadening allows the flanges to overlap and thus to equalize shell gape.

Note also that in comparison to *M. malleus* (Cebu, Philippines; GPIT 1604/15), *M. albus* (Cebu, Philippines; GPIT 1604/16-17) is the more advanced species. It inhabits deeper and finer mud bottoms, is more regular in shape, and has a fourth growth stage, in which only the ventral edge of the shell continues to grow. This is because in this stage the right and left valve auricles become separated and the mantle recedes from them (recessive growth lines on inside of auricles!) in order to allow secondary shell thickening (all specimens drawn to same scale, with the anterior side to the left; from Seilacher 1982*b*).





believed (Yonge 1968). The Pteriacea have probably evolved many pleurothetic recliners, some with pronounced outriggers (*Oxytoma*), but few except the pearl oyster (*Meleagrina*) show extensive shell thickening and excessive sizes.

#### *Edgewise recliners*

In equivalved, but thick-shelled species of a generalized outline, such as *Hippochaeta* (text-fig. 5), one might argue whether a pleurothetic or an orthothetic attitude would be most stable—depending on whether or not a byssus was maintained as an additional anchor. In this case, we must rely on field observations, which in the case of Jurassic *Isognomon* species have corroborated an orthothetic life position (Fürsich 1980). Life position is less ambiguous in *Mytiloperna*, whose extremely thickened shell and triangular cross-section provides a stable base on the anteroventral side (text-fig. 5).

*Convergences.* (a) *Ambonychiacea* (text-fig. 7). Analogous forms have evolved among the Palaeozoic Myalinidae. *Orthomyalina* from the Pennsylvanian, comparable to *Hippochaeta* (text-fig. 5) in outline and shell thickening, may be used to illustrate the difficulties of palaeoecological reasoning. Shell geometry and weighting clearly correspond to a mytiliform edgewise recliner resting on the broad and byssus-bearing anterior surface. On the other hand, a significant inequivalved form with respect to external sculpture and to the inclination of the ligamental area suggests that they were pleurothetic recliners with the more coarsely sculptured left valve facing the sediment (Newell 1942). Field observations clearly support the orthothetic model, but introduce another problem: it is not the byssus-down, but the mechanically less stable hinge-down edgewise position that clearly predominates. A similar dilemma has been recorded by Fürsich (1980) in homeomorph species of *Isognomon* from the Jurassic. He concluded that the morphological evidence is misleading and reconstructed a 'mud sticker' in an apex-down position. As an alternative I suggest that the 'life positions' record a response of the animals when being smothered. By the pull of the byssus they would rotate the shell into an unnatural dying position most likely to be preserved.

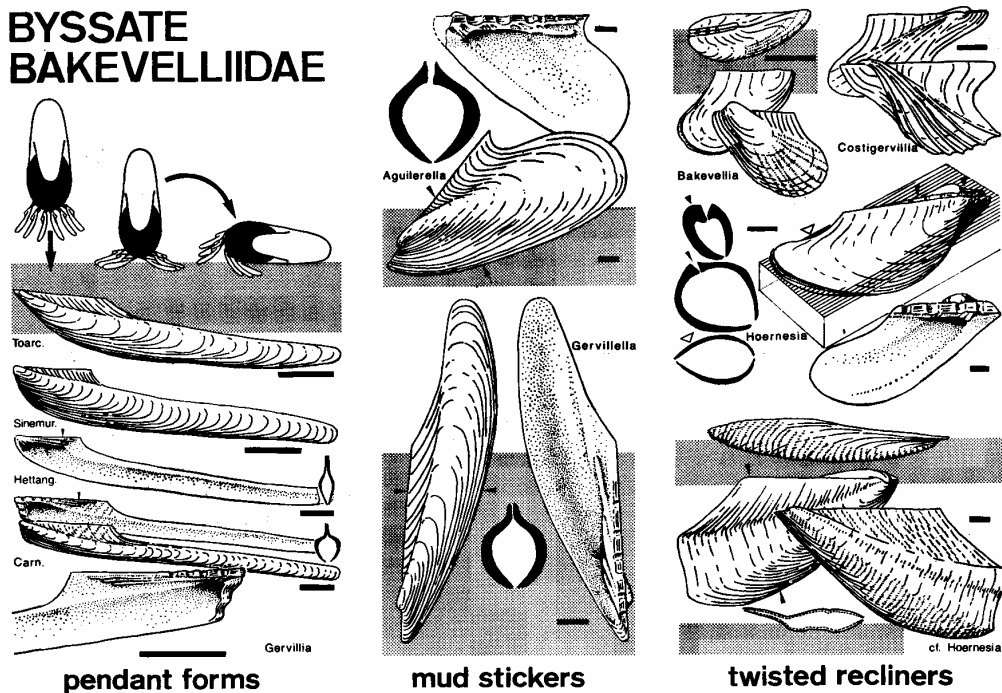
The less ambiguous *Mytiloperna* type is represented in the Ambonychiacea by the giant and thick-shelled *Tanchintongia* that according to Yancey and Boyd (1983) has a myalinid ligament. This genus and other alaticonchiids thrived during the Permian in a facies and climatic zone that seems to correspond to the Lithiotis facies in the Jurassic and the rudist facies in the Cretaceous.

(b) *Mytilacea*. *Congerina*, a thick-shelled relative of the epibyssate fresh-water mussle *Dreissenia*, is broader than *Hippochaeta*, but not as elongate as *Mytiloperna*, with shell-weighting on the recessed anteroventral side. Similar shell thickening is observed in the Jurassic species '*Mytilus mirabilis*' (text-fig. 9) that occurs together with bakevelliid recliners of the Lithiotis facies (text-fig. 5).

All orthothetic recliners discussed so far have probably evolved directly from epibyssate ancestors. The upper Jurassic large- and thick-shelled genera *Trichites* and *Stegoconcha*, however, are derived from endobyssate 'mud stickers' like *Pinna* (text-fig. 9). This derivation is indicated by the fibrous shell structure in both genera and the retention, in *Stegoconcha*, of a keel corresponding to the functional pseudoligament in mud-sticking ancestors (Chinzei *et al.* 1982). The necessity for a thick-shelled pinnid to transform the folding into a breaking ligament may explain why this adaptational pathway has not been used more often in the long history of the pinnids. Derivation from endobyssate ancestors is also indicated for Jurassic Mytilids, in which a square triangular cross-section (*Falcimylus*, *Arcomylus*; text-fig. 8) is combined with a rudimentary anterior extension, like in *Modiolus*. A similar cross-section is also found in a Rhaetic species of *Modiolus* (Seilacher 1972, fig. 5B), which was a deep mud sticker with an extremely elongated shell and divaricate, but non-ratcheted rib pattern. Available specimens unfortunately come from rocks in which only the thin calcitic outer layer is preserved, so that the original amount of shell thickening remains uncertain.

Edgewise recliners are also ambiguous because similar forms, even with an extreme triangular cross-section, may have evolved directly from burrowing ancestors and would thus not be secondary soft-bottom dwellers in an evolutionary sense. Examples are the modern cardiid genus *Corculum*, whose shell acts as a light collector for photosymbiotic algae as well as the Jurassic astartiid *Opisoma* (Accorsi Benini 1981) and the Triassic veneroid genus *Dicerocardium*, for which a similar mode of life has been suggested.

## BYSSATE BAKEVELLIIDAE

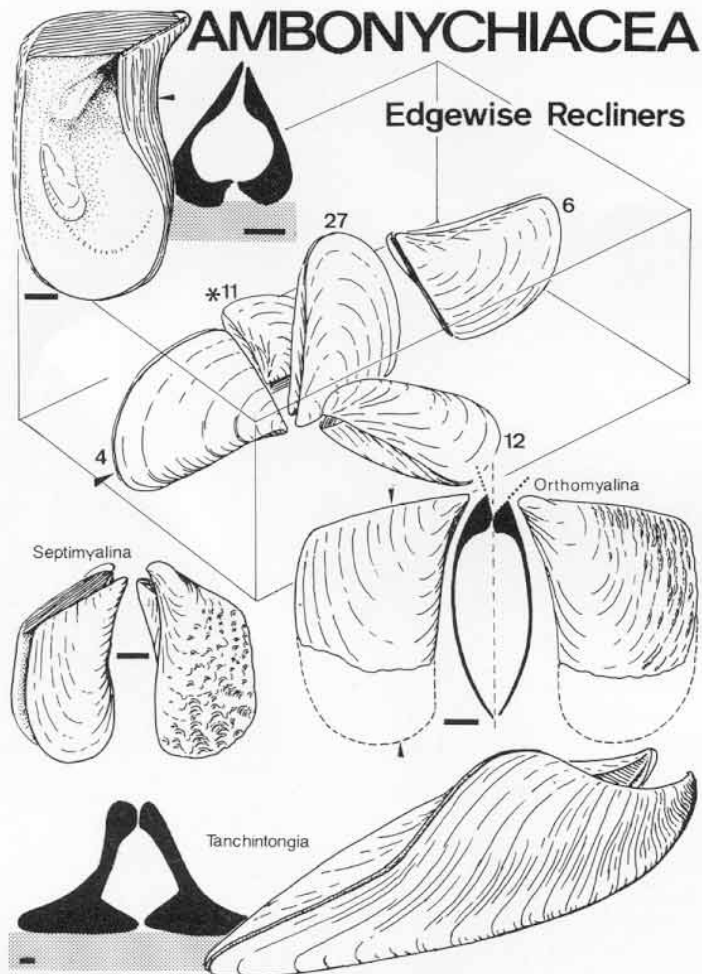


TEXT-FIG. 7. Compared to their more heteromorph derivatives (text-fig. 5), standard bakevelliid genera appear relatively thin-shelled, even if they are not diagenetically reduced to the calcitic outer layer. This indicates that byssal attachment remained an important factor in the stabilization of members living in soft-bottom habitats. Posterior elongation is a general tendency in the group. Because of the possibility of parallel and iterative evolution within the group, no evolutionary pathways can as yet be suggested. Note that mytiliform recliners are not represented except in *Mytiloperna* (text-fig. 5). This and the common occurrence of inequivalvedness indicates pleurothetically attached hard substrate epibyssates as the ancestral stock.

Pendant epibyssate attachment to hard substrates is documented in the saber-shaped *Gervillia lanceolata* of the Lower Toarcian Posidonia Shales (*a*: from Seilacher 1982*a*). This species lived attached to live ammonites and became characteristically oriented when their host died, sank to the bottom, and tipped over in a stagnant basin. By analogy, a similar (but not necessarily pseudoplanktonic) mode of life is assumed for other saber-shaped species (*G. olifex* Quenstedt, Sinemurian oil shales, Dusslingen, GPIT 1604/18; *G. angulati* Quenstedt, Upper Hettangian sandstone, Göppingen, GPIT 1604/19; *G. sp.*, Carnian, Lower Luning Farm, Pilot Mountains, Nevada, GPIT 1604/20).

Endobyssate mud stickers may be either modioloid in shape (*Agulerella pernoides*, Lower Aalenian dark shales, Sondelfingen; GPIT 1604/21–22; compare text-fig. 9) or lance-shaped (*Gervillella aviculoides*, Kimmeridgian limestones, Malagoszcz, Poland; GPIT 1604/23). Note, however, that the hinge is much longer than in similarly elongated epibyssate forms, because the ligament must act against the sediment pressure.

Flatly reclining forms are recognized by various degrees of inequivalvedness and twisting of the commissural plane. All figured species rested on the left valve, which is always more convex and bears stronger sculpture to increase adhesion to the sediment (*Bakevella subcostata*, Trigonodus Dolomite, Middle Triassic, Schwieberdingen, GPIT 1604/24; *Costigervillia crassica*, Bathonian, England, from *Treatise Inv. Pal. N* 307). More elongated forms (*Hoernesia tortuosa*, Aalenian, Gundershofen; internal view from Aalen; GPIT 1604/25–26) have the possibility to grow in a twisted manner, thereby keeping the anterior end in an almost vertical position for endobyssate attachment, while the posterior part reclines flatly on the sediment (see series of cross-sections). A very large undescribed form (*H. sp.*, Sinemurian Limestones, Cerritos Bayos, Chile; GPIT 1604/27) combines twisting by about 30° with divaricate adhesion ribs on the lower valve.



TEXT-FIG. 8. The Ambonychiacea, differing from the isognomonids and the bakeveliids mainly by their ligament pattern, have evolved similar forms of recliners, but seemingly with a narrower range of strategies (no pleurothetic recliners).

In the Permian genus *Tanchitongia* (from Yancey and Boyd, 1983) an edgewise reclining stage is clearly indicated by broad triangular cross-section, extreme shell thickening, and giant size (compare *Mytiloperna*, text-fig. 5).

In *Orthomyalina slocomi* (Upper Pennsylvanian Vinland Shales, Atchinson Co., Kansas) the evidence is more conflicting. Its marked inequivalency with respect to sculpture (even more pronounced in *Septimyalina*; GPIT 1604/29) and to the dip of the ligament areas (outside views and cross-section in posterior view; GPIT 1604/28) would suggest reclining on the more strongly sculptured left valve (asterisk position). Field measurements (with the kind help of Ron West, Manhattan, Kansas) of isolated bivalved specimens, however, clearly speak for an edgewise attitude—but with the ligament rather than with the byssus side down, as the shell outline and cross-section (GPIT 1604/30) would suggest (arrowed position). The dilemma is solved if we assume that upon irritation the byssus could pull the shell partly into the sediment and rotate it to what would become the preferred burial position.

*Cup-shaped recliners*

While it is the attached valve that develops into the cup in recliners derived from oysters and other cemented groups (*Spondylus*, *Chama*, *Hinnites*), the relationship is reversed in pleurothetic epibyssates. Here the valve originally facing the hard substrate remains flat and the stronger curvature of the exposed valve (usually the left one) determines the cup of the recliners. If this succession applies also to ontogeny an inversion of the life position is needed. Excessive thickening of the cup-shaped valve, as observed in *Gervilleoperna* (text-fig. 5), may facilitate this change. It is also interesting that *Lithioperna*, which is mostly found as a thin and elongated 'mud sticker', occurs occasionally in a cup-shaped and much thicker shelled ecophenotype (text-fig. 5).

*Convergences.* *Gervilleoperna* and *Lithioperna*, as well as truly isognomonid recliners, maintain the deep recess on the anterior side, in which the byssus was originally located. In malleids, in contrast, the byssus leaves the shell in an umbonal direction through a notch on the anterior side of the ligament area. It was probably this detail, plus the alivincular ligament, that allowed them not only to develop an anterior auricle (*Malleus*; text-fig. 6), but also rather symmetrical gryphaeid shapes without an anterior recess (*Gryphaeligmus*; Lewy 1982). Cup-shaped forms, but without excessive shell thickening and with a long hinge, have evolved in a number of other pteriomorph epibyssate families (*Cassianella*, *Rhaetavicula*).

*Twisted recliners*

Shell torsion is another deviation from the standard bivalve bauplan that has received considerable attention recently (McGhee 1978a, b; Savazzi 1981a, 1982a, b, and in press a, b). It is restricted to groups that are endobyssate in principle and twist the plane of the commissure in the emerging posterior part of the shell in such a way that is more or less parallel to the sediment surface. The twist is counter-clockwise (i.e. in a right-hand screw) in the arcid genus *Trisidos* (McGhee 1978a) and clockwise, but less extensive, in species of *Barbatia* (Savazzi 1981a). Similarly backvevelliid species (text-fig. 7) may twist either clockwise (*Hoernesia socialis*; *H. tortuosa*; McGhee 1978a, b) or counter-clockwise (*Pseudoptera*; Savazzi, in press b), while twisting of the present-day mytilid *Modiolus americanus* is ecophenotypically determined and may go in either direction (Savazzi, in press a).

All twisted bivalves have in common that they are relatively thin-shelled (particularly if only the calcitic outer layer is preserved), have two adductors, and that the byssus leaves the shell in a ventral or anteroventral direction. Most show also a slight marginal overlap of their more convex valve, which facilitates the development of radial or divaricate ribs in this valve that are suppressed in the other. Since the more convex valve is usually the one that through the twist comes to face the sediment, its inequivalve sculpture may help to stabilize the shell on the mud (text-fig. 7).

*Endobyssate 'mud stickers'*

'Mud stickers' are much more common in byssate than in cemented stocks of secondary soft-bottom dwellers, probably because a byssal anchor can also be used to pull the shell deeper into the substrate if growth proceeds faster than sedimentation and if the animal is irritated. I prefer to see the endobyssate state in most cases as a secondary step, following epibyssate adaptation to rocky substrates. This view is also supported by the fact that the forms sticking more deeply in the sediment usually show more derived features than shallower endobyssates.

The most striking example is the genus *Pinna*. Its mode of life is commonly modelled after the sand-living Mediterranean species *P. nobilis*, in which only the anterior third of the shell is buried. The vast majority of tropical *Pinna* and *Atrina* species, however, live in mud with the truncated posterior margin level to the sediment surface (text-fig. 9). In this situation, opening of the shell becomes a major problem. It has been solved by making the outer shell layer flexible through a high organic content (therefore it has commonly disappeared during fossilization) and by retarding its enforcement with a nacreous inner layer. The elasticity of this shell aids the ligament in opening the valves in such a way that gaping is restricted to the exposed posterior margin, while the buried ventral

part of the commissure remains closed. Such a shell can be closed by the strong posterior adductor through elastic deformation.

The genus *Pinna*, which appears in the lower Carboniferous, has gone one step further. Here the valves become actively broken along a line that then forms a median carina at some distance from the growing edge. This carina heals on the inside by an elastic shell layer and is not covered by the more rigid nacreous layer except near the umbones. Thus it can act as a pseudoligament that in conjunction with the ligament restores the squarish cross-section after it has been deformed into a rhomb by the adductor (text-fig. 9).

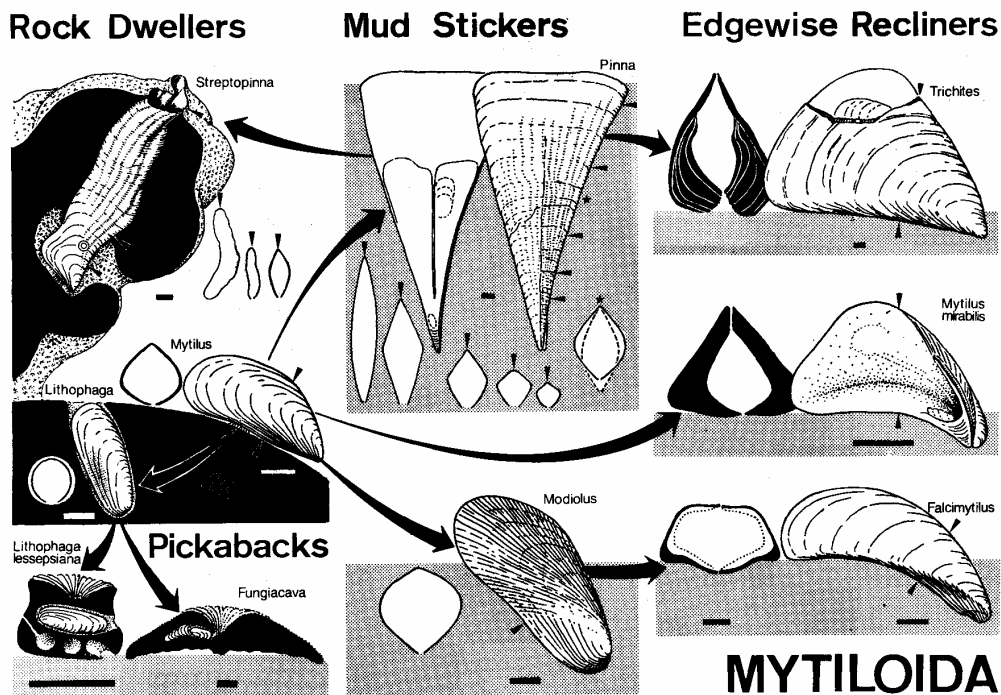
*Convergences.* While the functional adaptation of *Pinna* seems to have been unique, similarly elongated 'mud stickers' with a near-terminal umbo have evolved in several byssate groups such as the bakevelliids (text-fig. 7). In these cases, however, the shell was only half buried and equipped with a relatively long ligament strong enough to open the valves.

Among the mytilids, a very elongate *Modiolus* from Rhaetian mudstones of the northern Alps (Seilacher 1972, fig. 5B) bears a dense pattern of divaricate ribs that are not ratcheted. This sculpture is similar to that of the borer *Lithophaga* (text-fig. 9) and suggests that this derived species was sticking more deeply in the mud than the *Modiolus* stock.

#### Swimming bivalves

Although we will not go into the details of bivalve swimming in this context (Thayer 1972) it should be remembered that this secondary mode of mobility has evolved independently in two groups of living bivalves. Both are monomyarian and have an alivincular hinge and both are primarily epibyssate, but with different orientations.

The limids attach to hard substrates in an orthothetic attitude, which they also maintain while



swimming with the umbo ahead. The pectinids, in contrast, are pleurothetically attached and swim accordingly, but in the direction of the ventral margin. Nevertheless the ability to swim is not universal in either group, nor is it unequivocally expressed in shell morphology.

*Limidae*. *Plagiostoma lineata* from the Lower Muschelkalk is much more highly vaulted than limid swimmers today and has a broad anterior base for reclining. This shape, the common slope-oriented overgrowth by other organisms (Seilacher 1954), the nestling of juveniles in the byssal recess of adults (Jefferies 1960) as well as the common preservation in life position suggest that it was essentially an edgewise recliner. Similarly, the Lower Jurassic *Plagiostoma gigantea* is much too big and thick-shelled to have been an effective swimmer in spite of its flatter shape and smooth surface. Still it can not be excluded that these species were able to swim. An immobile mode of life can be safely assumed, however, for forms like the Middle Jurassic *Ctenostreon*, whose thick shell and anchoring spines suggest a heavy and possibly pleurothetic recliner.

*Pectinidae*. Similar difficulties arise with the interpretation of fossil scallops. *Pleuronectites laevigatus* from the Upper Muschelkalk was probably not a swimmer. Its left valve is more convex and more commonly overgrown than the right one. Thus the geometry is the opposite of what we find in

TEXT-FIG. 9. The origin of the Mytiloida is here placed in a rocky habitat in order to explain the loss of a burrowing foot. From forms like *Mytilus edulis* they evolved—either directly or via mud stickers—into the niche of edgewise recliners, but also back into the growing rocky substrate of reef corals. Another interesting lineage leads to rock borers and from there to commensalism with corals that had themselves become secondary soft-bottom dwellers.

'*Mytilus*' *mirabilis* (Calcari Grigi, Lower Jurassic, Vajo dell Anguilla, northern Italy; GPIT 1604/31) occurs in association with the recliners *Mytiloperna* and *Gervilleioperna* (text-fig. 5). It became stabilized by differential shell thickening and triangular cross-section.

*Modiolus americanus* (New Jersey; GPIT 1604/32) represents the adaptation of the mytilid shell shape to mud sticking.

*Falcomytilus* (Upper Jurassic; from *Treatise Inv. Pal. N 277*; cross-section from *Arcomytilus pectinatus*; GPIT 1604/33) is stabilized mainly by its square cross-section, with some shell thickening in the lower parts of the calcitic outer layer that is only preserved. A vestigial anterior lobe indicates derivation from modiolid ancestors.

*Pinna diversicolor* (Mindoro, Philippines; modified from Chinzei *et al.* 1982; GPIT 1604/34) is a perfect mud sticker. The opening function of its long and curved ligament is supplemented by the elasticity of the shell, in particular by the pseudoligament (Chinzei *et al.* 1982). This forms on the inside the median carina, where the shell becomes actively broken and is not covered by the internal shell layer. While the series of arrowed cross-sections was made from a plaster cast to show the secondary deformation, the one with a star is drawn from a saw cut through a fresh shell, whose pre-stressing deformed the posterior (broken line) and the anterior side of the cut in the opposite sense.

*Trichites giganteus* (Upper Jurassic, Schnaitheim, southern Germany; GPIT 1604/35) is one of the rare pinnids that have become edgewise recliners stabilized by triangular cross-section, extreme shell thickening, and giant size.

*Streptopinna saccata* (Okinawa; GPIT 1604/36) starts its life as a byssate nestler in the crevices of living coral colonies. It then becomes inevitably enclosed by the coral and continues to grow atop of the host. In this stage the two valves become united into a flat tube that can no more be closed. Accordingly, the posterior adductor remains in its juvenile (circle) position to where the soft parts are retracted in defence. On the other hand the loss of bivalvedness allows the tube to grow in a tortuous manner.

*Lithophaga lithophaga* (Adriatic; GPIT 1604/37) penetrates into calcareous rocks as a chemical borer. This is expressed by the elongate and almost cylindrical shell and fine divaricate ribbing.

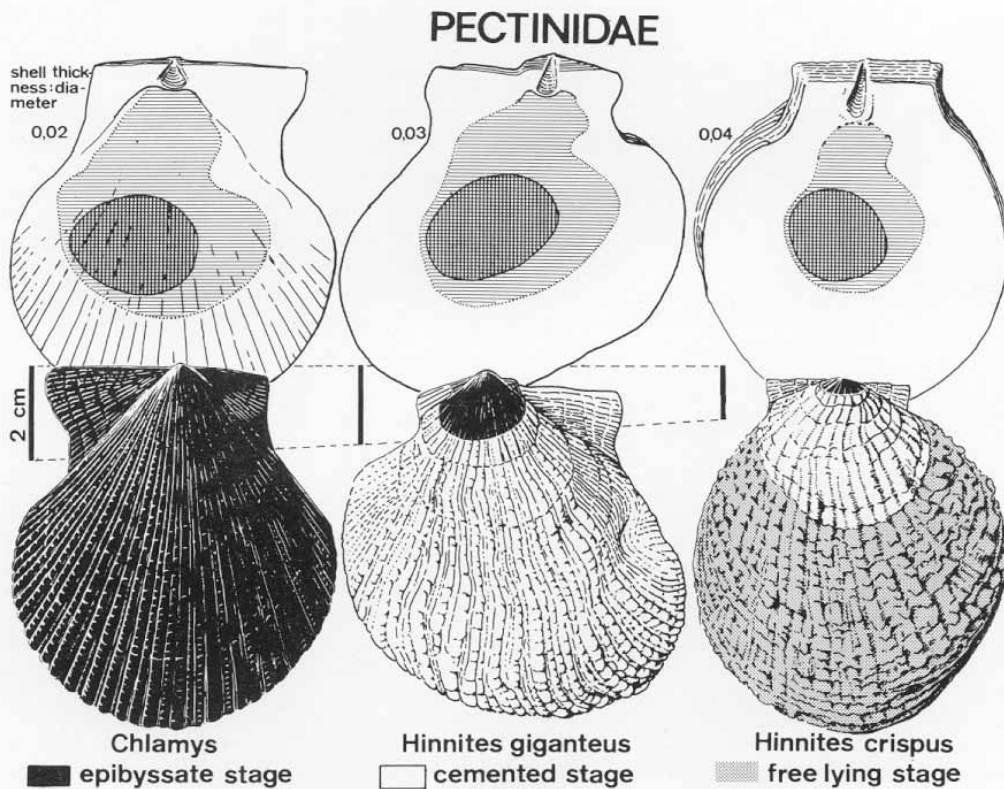
*L. lessepsiana* and *Fungiacava eilatensis* (from Savazzi 1982*d*) transfer this habit to live corals. These have themselves become secondary soft-bottom dwellers, either pickabacking with a sipunculid worm (left) or as disk-shaped recliners (right).

All scales = 1 cm.

modern *Pecten jacobaeus*, where the right valve is convex to allow easy take-off and sinking back in the right orientation, while the left valve is flat or slightly concave. Still an inverse life position in *Pleuronectites* is unlikely, because preserved colour bands are restricted to the left valve, like in many modern *Pecten* and *Chlamys* species.

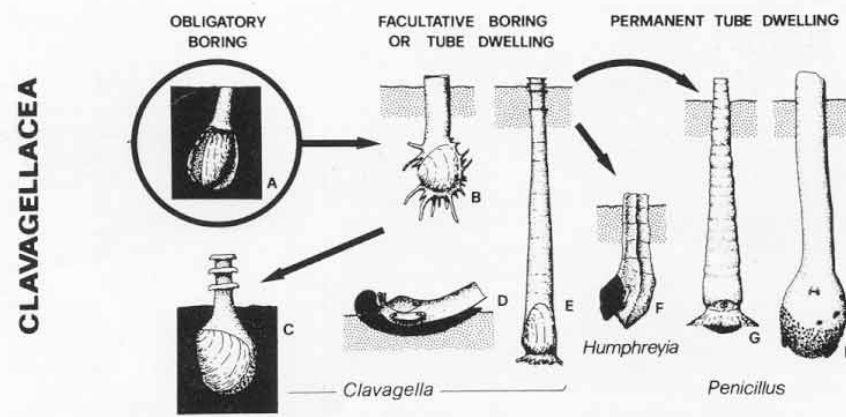
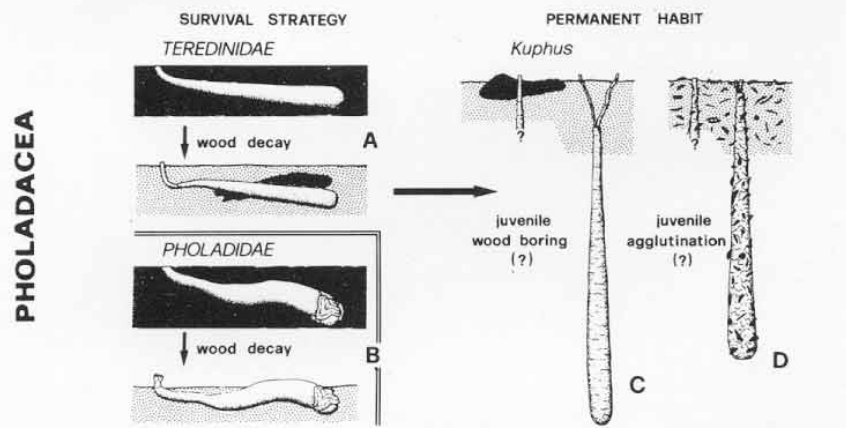
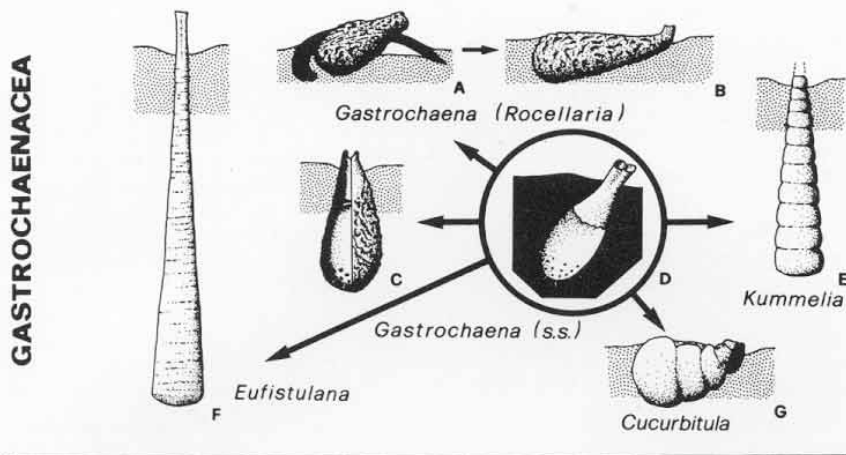
Two pectinid lineages have become sessile again by cementation. The spondylids retain the eyes along the mantle margin (Yonge 1968), while the shell grows thick and irregular as in oysters and allows the introduction of an isodont hinge. Spondylids that became free recliners again in later stages of their ontogeny have already been mentioned as homeomorphs of *Gryphaea*.

More unusual is the life history of *Hinnites giganteus* from the California coast. Here, transition to the cemented state does not occur in early growth stages, but later in ontogeny. Pliocene species went even a step further by becoming soft-bottom dwellers again. Accordingly, their shells record an ontogenetic succession of three adaptational stages (text-fig. 10). The epibyssate and swimming



TEXT-FIG. 10. The double strategy of byssal attachment (with the right valve facing the substrate) and free swimming has enabled the scallops to become very efficient secondary soft-bottom dwellers (*Chlamys* sp., Peru; GPIT 1604/38). The return to a rocky substrate in *Hinnites giganteus* (California; GPIT 1604/39) is marked by the transition, after a juvenile *Chlamys* stage (black), to oyster-like cementation and irregular shell growth. Other species (*H. crispus*, Pliocene, N. Italy; GPIT 1604/40, courtesy of E. Savazzi) have again become recliners by adding a third stage, in which the shell grows very large and thick (shaded part). Note that in this stage growth becomes also more regular and that anchorage in the sediment is provided by a new kind of scaly spines.





TEXT-FIG. 11. Tube dwelling pelecypods. This unique adaptation to secondary soft-bottom dwelling has evolved only in borers, but independently in three groups and in different genera within them. The two valves remain either free within the bag-like cyst (Gastrochaenacea and Teredinidae), or they become incorporated (Pholadidae, Clavagellacea). Through the tubelets at the lower end of Clavagellacean cysts water can be expelled for piston-burrowing (from Savazzi 1982c).

*Chlamys* stage has a regular shape, while growth becomes irregular and xenomorphic in the following oyster stage. In comparison with the modern, rock-dwelling species, these two stages are reduced in size and relatively thin-shelled in the soft-bottom dwellers in order to fit the unstable substrate of available dead shells. Their third growth stage, in contrast, reflects the mode of life of an immobile recliner, i.e. the shell now grows large and thick for increased stabilization. This evolution transition may have occurred more than once, because one of the two studied species (text-fig. 10) is an ambivalent recliner, while the other (from the Pliocene of New Zealand) is consistently inequivalve with the attached right valve becoming thicker-shelled and cup-shaped in the reclining stage. It is also noteworthy that with the return to a more regular growth in this stage the sculpture does not continue in the *Chlamys*-stage fashion, but attains a new character.

#### STOCKS BORING IN HARD SUBSTRATES

The comprehensive studies of Enrico Savazzi (1982c, d) have shown how boring bivalves returned to soft bottoms. In three groups (Pholadacea, Gastrochaenacea, Clavagellacea) we observe the convergent development of calcareous crypts (with or without inclusion of the valves). These become tube-shaped because further growth is restricted to one or both ends of the closed cylinder (text-fig. 11).

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TEXT-FIG. 12. Horn-shaped growth provides secondary soft-bottom dwellers with the possibility to passively become righted-up and replanted in the sediment.

The 'Savazzi effect' (from Savazzi 1982c) implies that a washed-out horn-shaped body comes to rest on the sediment in a lateral position with the convex side facing the current and that it then tips into the erosional depression forming on the upcurrent side. This mechanism may be enhanced by differential weighting of the skeleton on the convex side and near the apex. Complete burial may be avoided by expanding structures that keep the open end at the surface like a snow shoe.

The crypt of *Cucurbitula cymbium* (Malaysia; GPIT 1604/41) lacks differential weighting, but the presence of soft-bodied snow shoe expansions (dotted) is suggested by accessory perforations on the concave side near the siphonal opening.

*Gryphaea arcuata* (Lower Jurassic, southern Germany; GPIT 1604/5), unlike more dilatate species, is most perfectly adapted to the Savazzi effect by its rounded cross-section and weight distribution.

The sessile gastropod *Maoricrypta radiata* (Miocene, Waipara Gorge, New Zealand; GPIT 1604/42; courtesy of D. Mackinnon, Christchurch) resembles *Gryphaea* in shape and excessive shell thickness in the apical part. Still it is doubtful whether it had a similar life position on the soft bottom, because the differential weighting of the apical part is on the concave rather than on the convex side and because soft-bottom species of the related genus *Crepidula* tend to form horn-shaped colonies, to whose stabilization the shell thickening would have also contributed.

In horn-shaped species of *Hippurites* (Gosau, Upper Cretaceous; Reichenhall, *Inst. hist. Geol. Pal.*, Munich; courtesy of R. F. Höfling) the internal pillars of the right valve are situated on the convex side for differential weighting. Tabulate fill structures (shaded, in the studied specimen recrystallized) provide additional weight to the apical part. Horn corals provide many good examples.

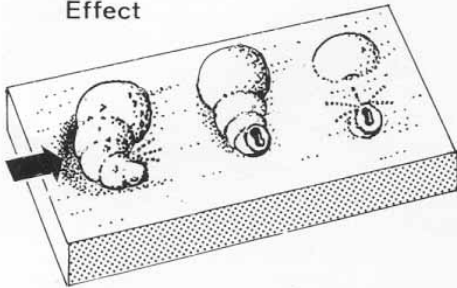
In *Phaulactis* (after Wedekind 1927) differential weighting is obtained by secondary thickening of septa in the apical and convex part of the calyx.

In Archaeocyathid sponges (after *Treatise*) this explanation is more problematic, because the buried parts of the body would be excluded from active feeding. It should be tested whether the horn shape in some figured species is a regular feature.

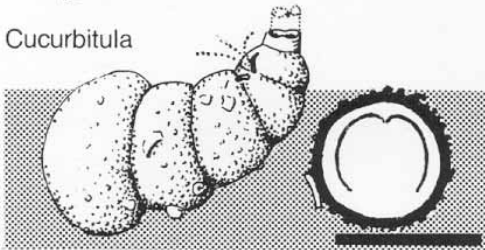
In the lepadomorph barnacle *Euscalpellum zelandicum* (Senonian, Waipara Gorge, New Zealand; reconstruction from Tübingen material) the flexible pedicle is transformed into a solid calcareous body with regular horn shape and root-like scales concentrated on the apical and convex surfaces. The belemnite-like cross-section shows that the central cavity is always excentric, thus providing differential weighting of the convex side.

# HORN SHAPED RECLINERS

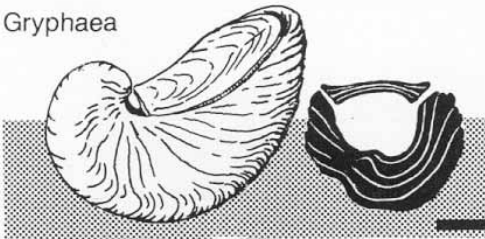
SAVAZZI  
Effect



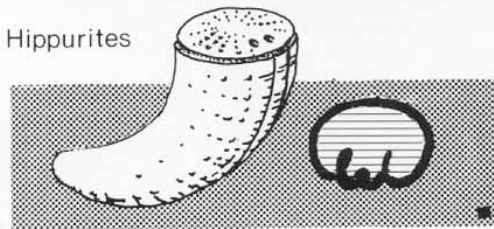
Cucurbitula



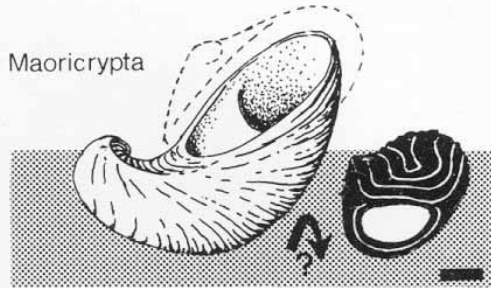
Gryphaea



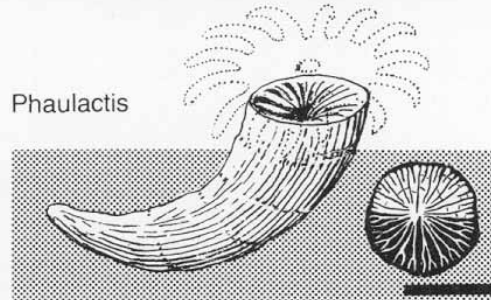
Hippurites



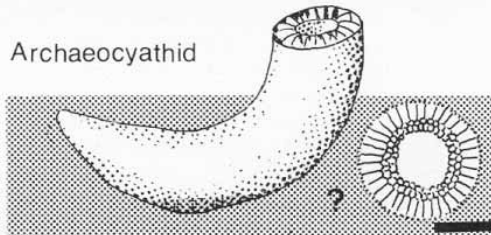
Maoricrypta



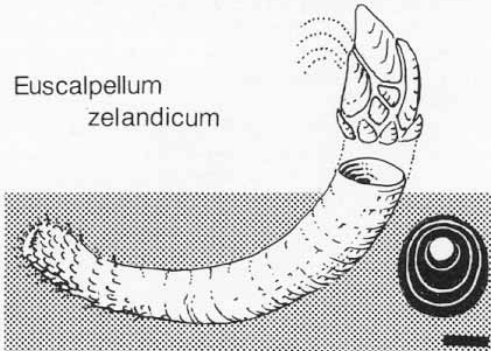
Phaulactis



Archaeocyathid



Euscalpellum  
zelandicum



### *Tube dwellers*

The multiple parallel evolution of crypts between and within the three groups (text-fig. 11) becomes understandable if we consider the evolutionary constraints and options involved. All tube dwellers seem to be derived from ancestors that bored in biogenic materials, such as shell, coral, or wood. Such materials, smaller pieces of which are also available on the soft bottoms of low energy environments, favour the formation of calcareous linings that seal the borehole against a porous substrate and allow repair when this substrate has rotted or broken away. Thus cyst formation can be viewed as an extension of former emergency strategies (Savazzi 1982c).

Such tubes could lie simply at the surface; but some species have evolved special mechanisms that allow them to become planted in the way of 'mud stickers'. The most spectacular adaptation is found in some clavagellids, such as *Penicillus*, whose crypt grows only at the posterior (siphonal) end. This allows the lower part of the crypt to develop into an expanded chamber with an elaborate system of perforations and tubelets, through which water can be expelled into the sediment to produce a piston-boring effect (Savazzi 1982c, fig. 15). The gastrochaenid genus *Cucurbitula*, in contrast, becomes passively buried. Its tubes grow consistently in a curved fashion. Exposed to a current, such a horn-shaped cyst will come to rest on its side and orient itself with the convex side upcurrent. In this position eddies will carve out the sediment in front of it, so that the body automatically tumbles into the depression (Savazzi 1982c, fig. 5). This principle which has so far only been tested in the flume (Savazzi 1982c), can also be applied to fossil horn corals, to *Gryphaea*, to horn-shaped rudists, and to the Cretaceous cirriped *Euscalpellum zelandicum* (Withers 1951), in which the convex side of the horn is additionally weighted to facilitate the planting process (text-fig. 12).

### *Commensals*

Another pathway into the soft-bottom habitat is commensal association. For boring bivalves it is favoured by the tendency of other secondary soft-bottom dwellers to develop massive skeletons. If the hosts are molluscs, no special adaptations are necessary other than the selective settlement of the larvae and an adequate miniaturization of the adults. But in the fossil state it may be difficult to distinguish commensal borings from those made in dead shells, except by callus formation and the avoidance of surfaces that were covered by soft parts while the host was alive. Not so in solitary corals, in most species of which the skeleton is covered by living tissue and can grow on the whole external surface. Their infestation requires the ability to penetrate living tissue and to cope with substrate growth and is therefore likely to be more host-specific. Modern (and some fossil) examples, as reviewed by Savazzi (1982d), all involve mytilid borers. Since the mytilid bauplan does not allow the formation of long siphons, this group was not only excluded from the tube-dwelling strategy discussed in the previous paragraph. In a growing coral skeleton, mytilid borers are also forced to keep in contact with the surface by boring backwards and filling the evacuated anterior part of the bore hole with calcareous deposits or septa recognizable in the fossil state.

Mytilid coral borers, which make their excavations mainly by chemical means, also maintain special attitudes and positions with reference to the host. In their horizontal bore holes they lie with the umbones lowermost, so that the inhaling current keeps clear of the sediment. *Fungiacava eilatensis* (text-fig. 8) always settles in the gastrocoel of large mushroom corals so that it can participate (a parasite rather than a commensal) in the host's meals (Savazzi 1982d, figs. 19–20). *Botula cordata* bores Eocene trochiform corals (Savazzi 1982d, figs. 17, 18) from the outside wall, but the opening of its borehole follows the upward growth of the 'mud sticking' host. *Lithophaga lessepsiana* (text-fig. 8) has a similar position on *Heteropsammia*. In this case the host itself has established a symbiotic relationship with a mobile sipunculid worm (*Aspidosiphon*), for which it builds a shelter and in return is held in an upright position and carried around. 'Pickaback' strategies like the last example are much more common and more highly developed in associations of encrusting sponges, hydrozoans, actinians, corals, and bryozoans with hermit crabs.

## CONCLUSIONS

1. In contrast to one current view that evolution, being a stochastic process, can produce virtually anything, actual lineages are strongly channelled into a limited number of pathways by the constraints derived from inherited bauplans, fabrication principles, and the adaptive landscape. As a result, adaptational histories appear quasi-deterministic, with convergent, iterative, and parallel evolutions being the rule rather than the exception. This sets a limit to the cladistic analysis within bivalve groups.

2. Tempo and degree of evolutionary change depend largely on the ecological circumstances. While shell forms in the large group of burrowing bivalves have remained conservative (apart from the introduction of burrowing sculptures in some species), they show rapid and sometimes bizarre modification in the small group of secondary soft-bottom dwellers.

3. In the latter group, rapid change was necessary to cope with the problem of passive stabilization on a mobile substrate. It was also facilitated by the 'morphogenetic shunting' induced by miniaturizing stepping stones that pave the way for sessile rock dwellers into the soft-bottom habitat and the following trend towards gigantism for autonomous stabilization.

4. Constructional morphology, if applied to larger groups and used in a comparative way, is a valid tool in evolutionary studies, because it leads to an understanding of evolutionary pathways and thus complements the cladistic reconstruction of phylogenetic relationships.

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