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Limits to opportunism in the evolution of the Arcoida (Bivalvia)

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The evolution of the arcoid bivalves is a consequence of the interaction of three distinct, complementary groups of factors which determine organic form. Arcoid diversity has resulted from the opportunistic realization of possible forms, within a range set by the limitations of ancestral morphology, by characteristic growth patterns, and by the requirements of survival in available environments. Historical, phylogenetic constraints include the evolutionary heritage common to all bivalves, the filibranch gill, a shell microstructure suited to form sturdy hinge teeth, and the initial acquistion of a hinge and a ligament both based on the serial repetition of simple elements. Constructional, morphogenetic constraints include the geometrical limitations of the spiral exoskeleton, the unsuitability of the necessarily weak ligament for either epifaunal or infaunal specialization, and hinge teeth that must remain numerous and similar in form. The principal ecological determinant of arcoid form is that individual taxa be functionally adapted to live as shallow burrowers or as endobyssate or epibyssate nestlers, frequently on physically unstable substrates. This requirement is reflected in the close relationship between the overall proportions of arcoid shells and their habitats, in contrast with the conservatism of their soft-part anatomies. Analysis of the interaction between phylogeny, growth and adaptation provides sufficient explanations for individual arcoid forms, while collectively these determinants of form define the adaptive range of the Arcoida. It also yields insight into patterns of evolution. For instance, the repeated occurrence of close evolutionary convergence between arcoid taxa is as much a function of the limited range of solutions to problems of shell growth as it is of common adaptation to a single environment.

Introduction

The divine wisdom of the Author of nature provided Linnaeus with a complete causal explanation of the forms, the diversity, and the origin of the creation he set out to catalogue. In contrast with this deterministic, teleological view of life, the Darwinian account of evolution by natural selection emphasizes the rôle of chance, in the source of variation and in the circumstances of speciation. Emphasis on this opportunism seems often to imply that the process of natural selection is not only an efficient but also a sufficient cause of the patterns of evolution. In fact, selection acts in an existing context, which sets limits on immediate and even ultimate opportunities.

Two dimensions of this context are seen in the comparison of organic forms by analogy and homology, in terms of adaptive function and historical phylogenetic relationship. In addition, D'Arcy Thompson (1942) recognized that the intrinsic possibilities and limitations of growth processes themselves play a major part in the determination of form. Seilacher (1970) has urged that the rôles of phylogenetic, adaptive and 'constructional' factors should be assessed together in the analysis of the skeletal parts of living and fossil organisms (figure 1). In another paper (Thomas 1978a) I have presented an analysis of the evolution and diversity of the arcoid bivalves in this context. Here, I will focus on the rôles of the individual factors and the interactions between them as they have determined the range and limits of arcoid form.

Living arcoids are unspecialized bivalves, exhibiting a small range of variation in their soft-part anatomies (see Heath 1941; Purchon 1957; Lim 1966). Their shell forms, on the other hand, vary over a wide range, reflecting adaptations to epifaunal, endobyssate and shallow-burrowing modes of life. Both in form and in their range of habitats, they are intermediate between typical members of the Pterioida and the Veneroida. Like the burrowing veneroids, most arcoids are equivalve and more or less isomyarian. The sturdy, aragonitic shell, with outer
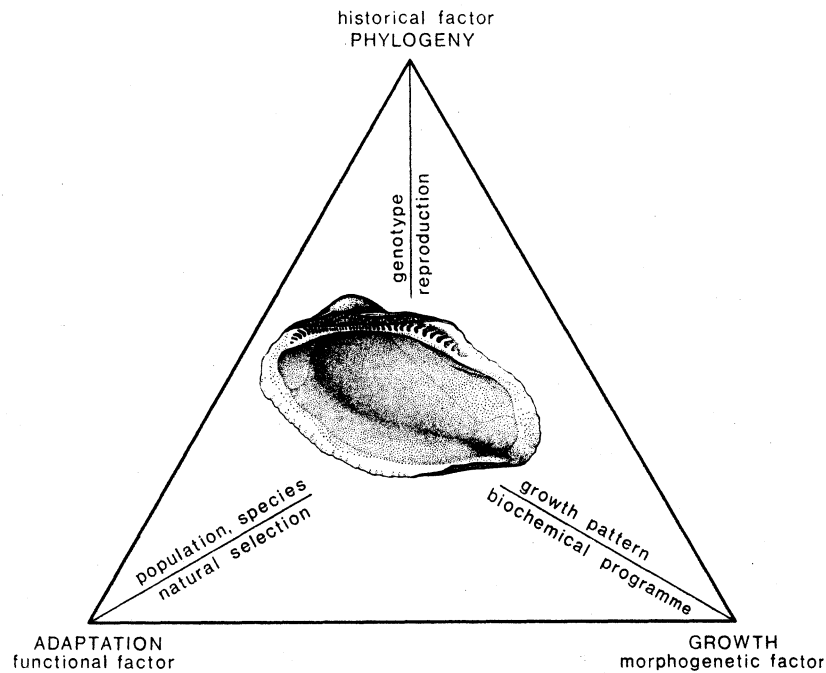

FIGURE 1. The determinants of organic form. For the species as a whole, form depends on the gene pool transmitted by reproduction, on biochemically controlled growth processes, and on the adaptation of populations by natural selection. Individual variation occurs by chance and by physiological adaptation to immediate circumstances. The arcoid is a living noetiid, *Sheldonella lateralis* (Reeve), from the Red Sea.

crossed-lamellar and inner complex crossed-lamellar layers, is very similar in structure and composition to the shells of many veneroids and quite unlike those of the pterioids (Taylor, Kennedy & Hall 1969, 1973; Omori *et al.* 1976). However, the arcoids have typical filibranch gills, like those of most pterioids and quite unlike the eulamellibranch gills of the veneroids. Furthermore, the chevron or duplivincular ligament, which is found only in the arcoids among living bivalves, is shared with the Palaeozoic pterioids, whose surviving descendants have acquired more specialized ligaments (Newell 1937; Truman 1969; Pojeta 1971).

The earliest fossils assigned with certainty to the Arcacea are of Devonian age. However, it has been generally agreed that the later arcoids evolved from the Cyrtodontacea (Douvillé 1913; Newell 1954; Pojeta 1971; Thomas 1978a). The early Ordovician appearance of this group is consistent with the likelihood that the Arcoida originated directly from an ancestral bivalve lineage, close to the initial divergence of the pterioids and the progenitors of the heterodonts, as indicated by Vogel (1962) and Pojeta (1971). Both the cyrtodontaceans and later fossil arcoids exhibit a range of shell forms and inferred modes of life comparable with those of living arcoids (Pojeta 1971; Stanley 1972). The later Palaeozoic arcoids are poorly known, but a major diversification took place during the Mesozoic, with the appearance of most of the modern families and sub-families during the Jurassic and Cretaceous.

Determinant factors in arcoid evolution

Phylogenetic, adaptive and morphogenetic factors are necessarily all involved in the genesis of any organic structure, but the individual factors have different kinds of consequences for form. Any circumstance or process that affects the morphology of a group of organisms makes a certain range of forms possible, but it also sets limits to that range. In the following discussion, limitations placed on arcoid evolution by various determinants of form will be emphasized. These limitations constitute boundary conditions under which the otherwise opportunistic diversification of the arcoids has taken place.
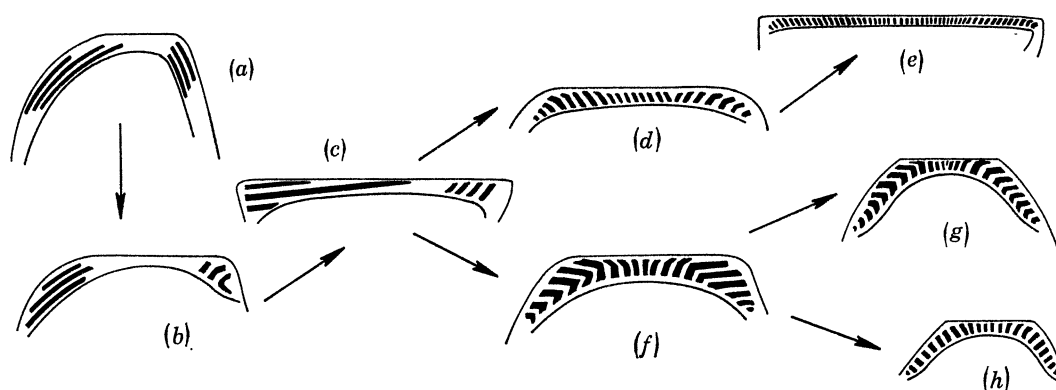

FIGURE 2. Evolution of arcoid hinge plates. A hypothesized actinodont ancestor (a) gave rise to Ordovician cyrtodontids (b), believed to be the forebears of Devonian and later parallelodontids (c). In the Mesozoic, these gave rise to the arcids (d, e) and cucullaeids (f), from which both glycymerids (g) and limopsids (h) were derived.

Phylogenetic, historical constraints

The possible forms of a group of organisms are limited by the potential for modification of ancestral forms, from which they must be derived by way of viable intermediate states (Stanley 1975). As molluscs, the arcoids have inherited a spirally coiled, calcareous exoskeleton, gills adaptable for respiration and feeding, and a muscular, hydrostatic foot, suitable for either crawling or burrowing. As bivalves, they have inherited bilateral symmetry, an elastic ligament linking the two valves, anterior and posterior adductor muscles, and a byssus adaptable for both juvenile and adult attachment. Finally, to their common ancestor, the arcoids owe their characteristic shell micro-architecture, the duplivincular ligament, the so-called taxodont hinge, and their notably unspecialized soft-part anatomy.

This inheritance has had specific evolutionary consequences, the more general of which are implicit in the classification of the arcoids as bivalve molluscs. Beyond this, at the time of their origin from a primitive bivalve ancestor, it appears that the arcoids opportunistically adopted the simplest means of increasing shell size and complexity. Both the taxodont hinge and the duplivincular ligament are based on the serial repetition of simple structures, comparable with the hinge teeth of the early Ordovician heteroconch *Actinodonta* (Vogel 1962) and the primary ligament postulated by Owen, Trueman & Yonge (1953), now inferred to have been present in the Cambrian bivalve *Fordilla* (Pojeta, Runnegar & Kříž 1973). This advance made possible the Middle Ordovician radiation of the diverse cyrtodontids (Pojeta 1971) but it also established growth patterns that largely determined the evolutionary course of the later arcoids (figures 2 and 3) as will be shown below.

Quite apart from their growth pattern, the very presence of sturdy hinge teeth, and hence of the capacity for burrowing, is a consequence of the shell microstructure inherited in common by all members of the Arcoida. Well developed bivalve hinge teeth are almost invariably composed of nacreous, crossed-lamellar or homogeneous aragonite (data of Taylor *et al.* 1969, 1973). The hinge teeth of living arcoids, and of those fossils where it has been determined, are all composed of crossed-lamellar aragonite of the outer shell layer (Flajs 1972; Omori *et al.* 1976). On the basis both of homology and common function, it seems likely that the similarly sturdy hinge teeth of the cyrtodontids and perhaps even those of an actinodontoid ancestor common to the arcoids and veneroids (figure 2*a*, *b*) were of a like composition (Thomas 1978*a*).

The arcoids are both morphologically and physiologically unspecialized. The burrowing forms lack siphons and have heavy, inflated shells. The epibyssate and endobyssate forms exhibit little anterior reduction of the shell, remaining almost isomyarian and retaining the massive foot. Several of these characteristics are consequences of morphogenetic constraints, as will be shown below. However, the filibranch gill and inefficient circulatory system, in which blood flowing into a given filament must flow all the way along it and then back to the efferent blood vessel in the gill axis, are simply part of the arcoid inheritance. The widespread occurrence of haemoglobin in the blood of arcoids is surely related to the limitations of their circulatory system, notwithstanding the fact that its occurrence is variable among closely related species (Thomas, 1976). Furthermore, the presumed limitations of the filibranch gill as a circulatory pump (Stanley 1968) may well be responsible for the fact that no arcoids have developed siphons, eliminating the possibility that any members of this group could have become deeper burrowers. With the exception of the aberrant Poromyacea and the rock-boring *Lithophaga*, all the siphonate bivalves are eulamellibranch, as pointed out by Stanley (1968).

Morphogenetic, constructional constraints

The constraints on form set by phylogeny are purely configurational, depending only on the historical continuity that exists between ancestor and descendant. In contrast, the limits set by growth patterns arise from the immanent, geometrical properties of form (Thomas 1978*b*).

The pattern of spiral, accretionary growth of the exoskeleton constitutes a fundamental constraint on the range of possible arcoid shells. A continuous, exoskeletal structure can increase in size without changing in shape only by logarithmic spiral growth. Moreover, Raup (1966) has shown that, of all possible spiral cones, only a narrow range is geometrically suited to be articulated in pairs about bilaterally symmetrical animals. These morphogenetic constraints on form are common to nearly all bivalves (Kauffman 1969; Vermeij 1970).

Both Stasek (1963) and Raup (1966) have observed that bivalve shells cannot be simple, spiral cones, since if they were, their umbones would intersect. The dorsal margins of the valves must grow along spiral paths, displacing the hinge axis ventrally, in order to separate the umbones and stretch the passive, elastic outer ligament between the expanding valves. This process does not require allometric growth; separation of the umbones can be maintained by a proportional retardation of growth along the spirals which generate the dorsal margin, relative to those described by the ventral shell margin (Raup 1966), or by growth along curves with different logarithmic spiral angles around the commissure. The inflated, nearly orthogyrate shells of many arcoids, with their amphidetic external ligaments, necessarily exhibit the most striking inter-umbonal growth of this type among the bivalves.

The duplivincular ligament of typical arcoids consists of alternating tanned lamellar and partially calcified fibrous layers of proteinaceous material (figure 3). The lamellar ligament, which is elastic under tensional stress (Newell 1937), is stretched between the diverging ligamental attachment areas in consequence of the inter-umbonal growth discussed above. It thereby exerts a continuous force which tends to open the shell. The fibrous ligament is elastic only under compressional stress, acting passively as the hinge axis about which the valves rotate. I have argued in detail elsewhere (Thomas 1976) that this ligament is poorly designed for its purpose, compared with those of many more advanced bivalves, in that the lamellar and fibrous portions of the ligament are not set apart in positions where they could best perform their respective functions.
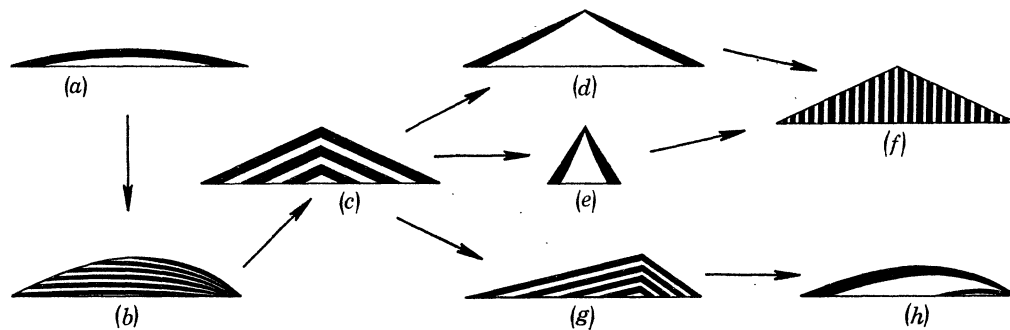

FIGURE 3. Evolution of arcoid ligaments. Lamellar layers are shown in black. (a) Hypothetical primary ligament. (b) Fine horizontal sheets: cyrtodontids. (c) Typical chevrons: parallelodontids, cucullaeids, glycymerids. (d) Outer chevrons only: some anadarinids. (e) Central resilium, limopsids. (f) Vertical strips: noetiids. (g, h) Anterior sheets reduced or lost: many arcids, *Anadara campechensis* (Gmelin). For a discussion of these derivations, see Thomas (1978).

In most arcoids, especially those of large size, the ligament and its attachment areas grow much more rapidly than the rest of the shell (figure 4). This allometric growth is an inevitable consequence of the growth pattern of the ligament. As the umbones diverge during ontogeny, the earlier formed lamellar ligament is stretched more and more. At first, the tension developed in this way serves to open the valves, but later the ligament splits dorsally. Without allometric growth, it can be shown that the strength of the unbroken portion of the ligament would increase less rapidly with size than the mass of the animal. Direct measurements have shown that a linear relation between ligament strength and animal mass is maintained by means of this allometry (Thomas 1976). However, the allometric growth of the ligament has undesirable side effects: ventral displacement of the hinge axis leads to interference with the function of the hinge teeth, which in many species are resorbed along the base of the ligament (Thomas 1975; Omori *et al.* 1976). The length of the lever arm between the hinge axis and the adductor muscles, and hence the closing moment they can exert, is reduced. Furthermore, the rapid growth of the ligament itself involves more divergence of the umbones, more dorsal breakage of the ligament and a need for yet more allometry.

Given its irregular dorsal breakage and the lack of segregation of lamellar and fibrous materials, it is not surprising that the ligaments of living arcoids are weak, as shown by comparative experiments (Trueman 1964; Thomas 1976). This weak ligament has played a major part in directing the course of evolution of the arcoids. The exploitation of fully infaunal habitats has been limited by the fact that the ligament is unable to brace the shell firmly against the substrate during the probing phase of burrowing; arcoids are slow, inefficient

burrowers (Ansell & Trueman 1967). Specialization for an epifaunal mode of life is usually accompanied by substantial reduction in the anterior adductor and shell (Yonge 1953; Stanley 1972); the arcoid ligament is too weak to accommodate the tangential stress developed by anterior and posterior adductors exerting substantially different closing moments about the hinge axis. Moreover, the large foot must be retained in epifaunal arcoids such as *Arca* and presumably some species of *Parallelodon* to aid in opening the shell. Thus, the weak ligament has both limited the specialization of the arcoids and facilitated the repeated changes in the direction of their evolution, between shallow burrowing and byssally attached modes of life, outlined by Stanley (1972).
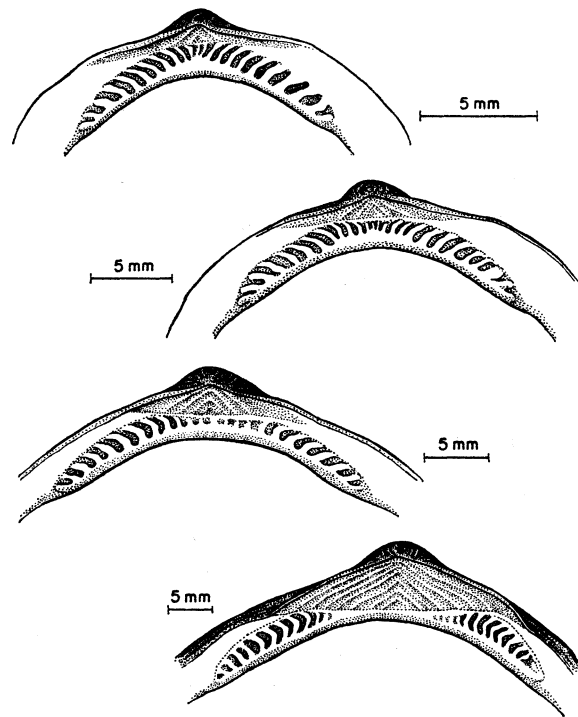

FIGURE 4. Ontogeny of *Glycymeris subovata* (Say), showing strongly allometric growth of the ligamental area and its effect on the distribution of teeth on the hinge plate. Left valves of Pliocene fossils from the Yorktown Formation, Chowan River, North Carolina. M.C.Z. (Harvard) specimens 18034–18037.

In the ontogeny of most arcoids, the number of hinge teeth first increases with size but later decreases, especially in very large shells (Brower 1973). This pattern is the product of interaction between two processes (figure 4). New teeth are added at the anterior and posterior extremities of the hinge plate, especially earlier in ontogeny. The growing ligamental area continually overlaps the hinge plates of earlier growth stages, often with some resorption of the hinge teeth, but almost invariably with the elimination of the smallest, earliest formed teeth at the centre of the hinge plate. This second process is accentuated in the later stages of ontogeny, as the ligament grows allometrically. The growth pattern of the hinge plate places significant constraints on the forms of the hinge teeth. Since the same teeth first occupy more distal and later more central positions, they cannot become very much differentiated around the hinge plate. Secondly, since the hinge plate must be overgrown by the ligamental area, the hinge teeth and sockets cannot be very deep, especially near the hinge axis. In consequence, the burrowing arcoids must retain a long, arched plate of teeth to ensure that the valves interlock securely,

whereas the heterodonts achieve the same end with a few larger and deeper, specialized teeth. Clearly the pattern of growth of the arcoid hinge plate, like that of the ligament, has severely limited potential specialization in the Arcoida.

These constraints do not apply at very small sizes. The epibyssate philobryids, which are tiny, neotenous arcoids (Tevesz 1977), have a few simple hinge teeth, or none at all, and simple ligaments comparable with those of the early juveniles of other arcoids. Many philobryids are mytiliform, with the anterior adductor much reduced or even absent. This is quite consistent with the inference that the potential for specialization of the larger, typical arcoids has been limited by the serial ligament and hinge teeth, which evolved to facilitate size increase.

Adaptive, functional constraints

It is self evident that organic form is adaptive. At any given taxonomic level, a group of related organisms shares a phylogenetic heritage and a more or less narrowly defined set of growth patterns. Within the bounds of these constraints, the group may diversify opportunistically. However, a further constraint on the variety of possible forms is implicit in the concept of 'opportunity'. The organisms must be mechanically well designed to function effectively in a particular environmental setting. The arcoids have evolved a range of forms by which they are adapted to survive in rather varied marine environments. Modification of the shell in response to the requirements of life on different substrates is by far the predominant feature of arcoid adaptation. Remarkably little adaptive divergence of soft-part anatomy has been reported among the arcoids, although Lim (1966) has demonstrated in several species of *Anadara* a close correspondence between the development of the labial palps and life in more or less turbid environments.

The arcoids share a common pattern of spiral shell growth such that relatively few forms are very strongly prosogyrate or opisthogyrate. However, shells of varied shapes are developed by differential rates of growth around the commissure, which determine its outline, and by growth along spirals of different curvature, which determines the inflation of the shell. My data (Thomas 1978a) confirm Stanley's (1970) observation that in free-living arcoids the shell length:height ratio is less than about 1.35, while byssally attached forms are more elongated. Circular shells, like that of *Glycymeris* are adapted for anterior–posterior rocking locomotion at the sediment surface (Thomas 1975), while posterior truncation such as that of *Cucullaea* and many species of *Anadara* inhibits excavation of shallow burrowers by scour (Stanley 1975). Shells which are elongated and laterally compressed are suited to nestling in crevices, among stones and in branching coral, as in *Barbatia*. In contrast *Arca*, being elongated and dorso-ventrally compressed, is designed to be held closely against rocky surfaces by its massive, flaring byssus (Kauffman 1969).

Ligament dispositions and strengths are also closely related to arcoid modes of life (Thomas 1975, 1978a). Active burrowers such as *Glycymeris* and crawlers such as *Barbatia* have the most compressed shells; their ligaments are consequently less deeply split and relatively strong. In contrast, the most inflated shells of less mobile arcoids, with interumbonal growth like that of *Arca*, have ligaments that are functional only very close to the hinge axis and hence extremely weak. In many nestlers with prosogyrate umbones, the ligament becomes largely or entirely opisthodetic, with limited interumbonal growth and less consequent dorsal splitting. This has been carried to an extreme in the cockle-like shallow burrower *Anadara campechensis* (figure 3h), but here the lamellar ligament splits anteriorly as it does in *Glossus* (Owen 1953) and is very

weak. *Noetia ponderosa* also has a weak ligament (Thomas 1978a), but here the opisthogyrate curvature of the umbones reduces the angle between the anterior portions of the two ligamental attachment areas. This is clearly adaptive, in that the ligament splits less rapidly and is strongest anteriorly, where the animal is typically partially buried in the substrate.

The function of bivalve hinge teeth has been well explained by Dall (1895). They must guide the valves to precise apposition during closure and effectively resist shear in the plane of the commissure once the shell is shut. The widespread occurrence among the arcoids of teeth which parallel the hinge axis, or of chevrons with long horizontal elements (figure 2c, f), is explained by the need to align the valves correctly. Because of the growth pattern of the ligament, the position of the hinge axis is not precisely defined; it is simply near the base of the ligament (Newell 1937; Thomas 1976). As a result, well developed horizontal guides are needed to ensure the apposition of the valves. This is borne out by the fact that in arcoids where the hinge teeth are reduced to vertical elements alone, such as *Arca* and some anadarinids, the hinge axis is well defined by virtue of the fact that only the most ventral part of the ligament is functional at all.

Chevron-shaped hinge teeth, which effectively resist shear in the plane of the commissure (Thomas 1975) are characteristic of active burrowers (figure 2f, g), and especially so among the cucullaeids, which lack interlocking crenulations around the shell margin. Arcoids which have vertical tooth elements alone are either epifaunal, like *Arca* or they have well developed marginal crenulations like those of *Noetia* and *Senilia*.

The external shell sculpture of the arcoids cuts across taxonomic lines and is broadly related to the animals' modes of life (Kauffman 1969). Prominent ribs of some shallow burrowing forms are thought to aid in cutting into the sediment (Stanley 1970), bracing the shell during the probing phase of burrowing (Thomas 1975), or increasing stability and resisting scour (Kauffman 1969; Stanley 1970). At the same time, the smooth shells of other arcoids living in similar habitats evidently create less resistance in burrowing. It is not yet clear under what particular conditions one of these adaptations is favoured over the other. Finer surface patterns are related to the attachment of periostracum to the shell and the stabilization of nestlers in their crevices (Thomas 1978a). Shell thickness itself is adjusted to achieve maximum stability. Shallow burrowers on unstable bottoms have thick shells which increase their inertia. In contrast, *Arca*, which must hold its own mass onto the surface to which it is attached, has an extremely thin shell for an arcoid.

Conclusions

Arcoid bivalves are abundant and varied in modern seas, occurring at all latitudes and at depths ranging from the low water mark to the ocean floors. They have a fossil record extending over 475 Ma, in which the convergent recurrence of similar forms is a characteristic feature. This is a successful group of organisms, evidently well adapted in its particular range of ecological niches. The limitations of arcoid form enumerated in this paper constitute boundary conditions which prescribe what arcoids can and cannot be. The arcoid ligament, hinge and gill may not approach general mechanical paradigms (Rudwick 1964) for a spring, a lock and a combined filter-pump and gas exchanger as closely as the structures of more specialized bivalves. Nevertheless, these structures serve the arcoids effectively under the circumstances in which they are employed.

The majority of arcoids are generalists, shallow burrowers and endobyssate or epibyssate

nestlers, which exhibit only modest modifications of the basic arcoid form. Many of them live on relatively unstable substrates – shifting sand, shell gravels, among stones – where they are likely to be disturbed. These animals employ what I have called a recovery strategy (Thomas 1978a), being adapted to roll about and then crawl in search of new, suitable sites for burrowing or byssal attachment. *Arca* itself accommodates the turbulence of its rock and coral substrates in the opposite way, its stronghold strategy entailing secure attachment to stable substrates. In marked contrast with these typical arcoids, a few forms have evolved specializations, convergent on those of other groups of bivalves, which enable them to avoid or reduce the risk of being dislodged. I have discussed the adaptations of these specialists in some detail elsewhere (Thomas 1978a), showing in each case how they are constrained by the limitations of arcoid form. Competition with more specialized bivalves has evidently not prevented the evolution of these taxa, although most of them have somewhat limited geographic and temporal distributions.

Historical accident is not the only determinant of organic form. Animals are not machines, nor are they simply the expressions of ideal growth processes. Phylogenetic inheritance, patterns of morphogenesis and the requirements of function are all integral in the genesis of form. The explicit simultaneous analysis of these causal factors yields a convincing account of the limitations and possibilities of arcoid form, in the context of which the actual evolution of the Arcoida may be better understood.

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