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The evolution of functional design in rudists (Hippuritacea) and its taxonomic implications

BY P. W. SKELTON†

*Department of Geology, University of Liverpool,
Brownlow Street, P.O. Box 147, Liverpool L69 3BX, U.K.*

[Plate 1]

Poor understanding of rudist growth geometry and anatomy has hampered systematic studies of the superfamily. A flexible model that simulates the growth of rudist shells is therefore presented so that evolutionary trends in the group may be consistently analysed; this model is constructed by rotational or irrotational stacking of inclined gnomons around a contained axis. Functional analysis of shell geometry and reconstructed anatomy provides a more solid foundation for rudist systematics. The first rudists (Diceratidae) employed one or other of the spirogyrate umbones, inherited from megalodontid ancestors, as a facultatively elevating encrustation stem. Invagination of the ligament in the Caprotinidae permitted uncoiling of the shell, though this also entailed reduced gaping and therefore externalization of food entrapment, with increasing involvement of the mantle margins. Caprotinid functional design was preadapted to several new adaptive zones, which were exploited by various advanced descendant groups. Some of these groups show homeomorphic evolution and have often been assembled by earlier workers into polyphyletic ‘families’ (e.g. Caprinidae). An attempt is therefore made to establish a skeletal classification of rudists on the basis of true clades, as distinguished by careful functional analysis.

INTRODUCTION

Present rudist systematics are unsatisfactory for two main reasons. First, there has been little analysis of their growth geometry. This had led to inconsistent orientation of compared specimens, and therefore spurious notions on evolutionary and developmental trends. Secondly, little attempt has been made to reconstruct the soft-part anatomy of rudists, such that ignorance of the functional and structural significance of many features has prevailed, and false homologies have thus been proposed.

The purpose of this paper is therefore to outline the evolution of functional design in rudists. To this end, shell growth geometry and its significance are analysed in terms of a flexible model, and soft part anatomy is reconstructed on the evidence of muscle and other scars, shell microstructures, analogy and homology. Such insights provide a surer platform for phylogenetic systematics. A modified classification of rudist families, each hopefully representing a true clade is therefore proposed (p. 315).

A MODEL TO SIMULATE THE GROWTH GEOMETRY OF RUDIST SHELLS

Primitive rudists possessed a modified parivincular ligament comparable to that of *Chama* (figure 1, plate 1); continuous backward expansion of the ligament was coupled with rupturing and shelly overgrowth of its anterior parts (Yonge 1967). Successive valve increments therefore

† Present address: Department of Paleobiology, National Museum of Natural History, Smithsonian Institution Washington, D.C. 20560, U.S.A.

appear rotated with respect to one another, such that the umbones spiral outwards from the commissural plane. Following this backward migration of the active ligamentary site, all points on the valve rim traced helicospiral growth loci of one sense, with the terminations of those on opposite sides of the commissure pointing in contrary directions (the 'tangential component of growth' of Yonge (1967)). Hence the axis of incremental rotation is contained within the valve rim, passing obliquely through the commissural plane (figure 2, plate 1). Growth was essentially gnomonic (ignoring early xenomorphic distortion).

A model consisting of inclined, wedge-like gnomonic increments rotationally stacked about a contained axis thus simulates the turbinate valve growth of primitive rudists (figure 10*a*). This represents a special case of the univalve shell coiling model described by Thompson (1917).

Outward growth of the umbones was more efficient in most later rudists (figure 3, plate 1). In these the ligament was progressively invaginated (figures 7–9, plate 1). Incrementation around the dorsal valve margin therefore kept more or less abreast of that at the ventral margin; so umbonal separation became simply and directly achieved, without continuous backward migration of the ligament. Contrary to the opinion of Yonge (1967), the 'tangential component of growth' was not increased in such forms, but secondarily reduced. Successive tube-like increments are therefore barely rotated with respect to one another, if at all, and the former coiling axis becomes instead a focal axis of radial growth.

The growth of such uncoiled forms may be simulated by a modification of the coiling model, wherein expanding (though not exactly gnomonic) increments are stacked with decreasing rotation, or even without rotation, along a contained axis (figure 10*b*). The progressive loss of whorling in such forms renders Raup's (1966) parameters of whorl expansion rate and translation rate unusable, since these are expressed as rates per whorl. Indeed, it is difficult to devise measurable parameters for the model presented here, given its scope for uncoiling. Its main

DESCRIPTION OF PLATE 1

Horizontal white bars are 1 cm scales.

FIGURE 1. Ligamentary area and umbo of left valve of *Epidiceras sinistrum* (Deshayes), from the Upper Oxfordian of northeastern France. For explanation, see figure 12*b*.

FIGURE 2. Whole specimen of figure 1, orientated to show sense of rotational growth around coiling axis (vertical white bar).

FIGURE 3. Right valve of small individual of *Monopleura pinguiscula* White, from the Albian of Texas (W. J. Kennedy Collection), showing progressive uncoiling around curved axis (vertical white bar).

FIGURE 4. Dorsal aspect of internal mould of *Eodiceras perversum* (G. B. Sowerby), from the Upper Oxfordian of northwestern France. The mould of the left (attached) valve is uppermost. The mould of the hinge has broken off. The smooth triangle of the left valve is clearly visible to the right of the gastropod mould, the area adumbonal to it being radially striated.

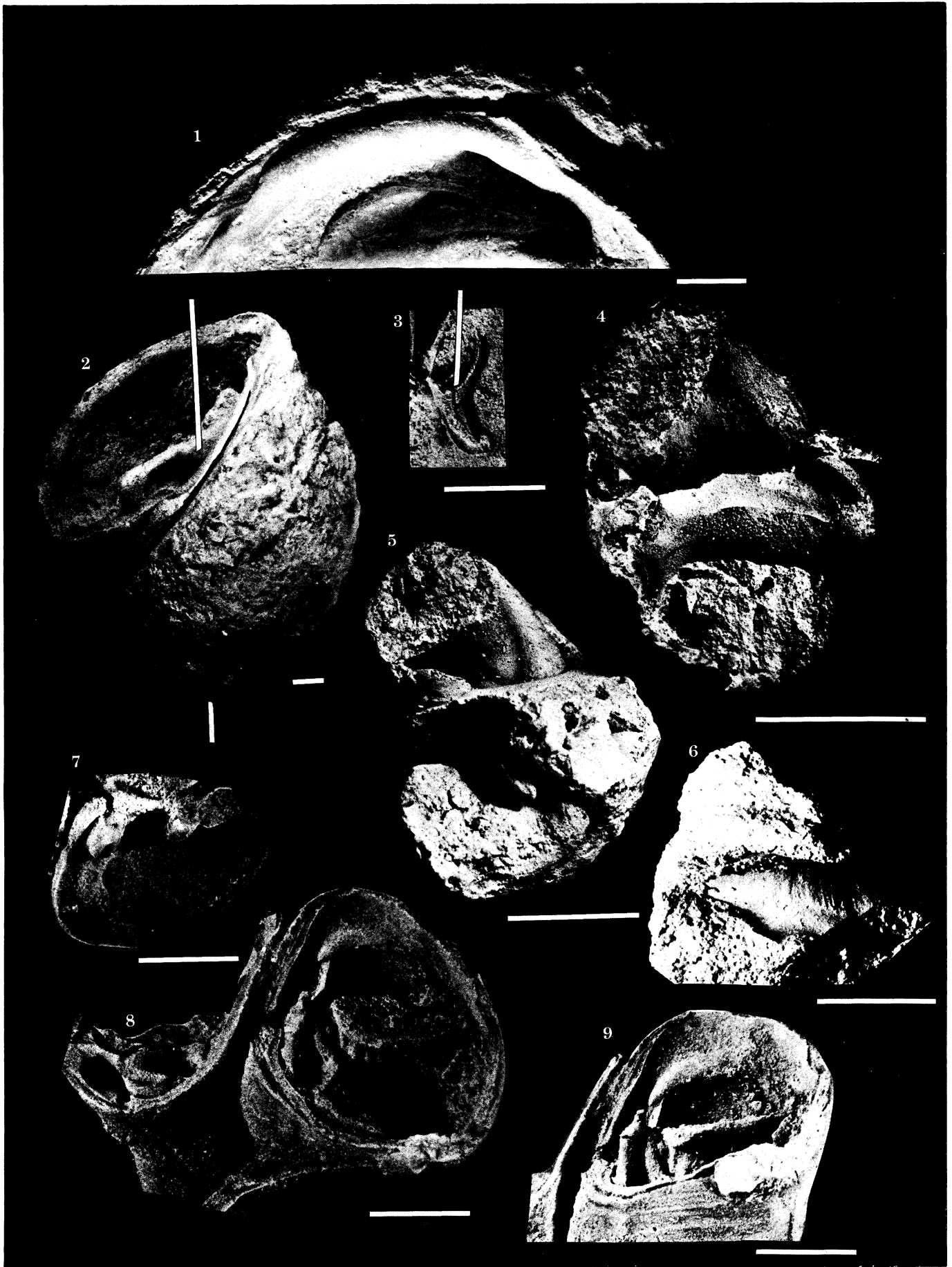
FIGURE 5. Another specimen as in figure 4, in antero-dorsal aspect. The mould of the hinge is here complete. The anterior part of the smooth triangle of the left valve (uppermost) can be seen joining the anterior adductor scar at right. Note the lack of any distinct pedal muscle scars.

FIGURE 6. Internal mould of left valve of *E. perversum* from the Upper Oxfordian of northeastern France, in dorsal aspect. The line of ridges (on the mould), delineating the crest of the smooth triangle, is clearly visible.

FIGURE 7. Left valve of *Monopleura pinguiscula* (as in figure 3), in dorsal aspect, showing site of invaginated ligament adjacent to posterior tooth.

FIGURE 8. Two joined right valves of *M. pinguiscula* (as in figure 3), in commissural aspect, showing invagination of ligament. For explanation see figure 14*a* (detail).

FIGURE 9. Specimen to the right in figure 8, tilted to show up reduced bourrelet.



FIGURES 1-9. For description see opposite.

(Facing p. 306)

value is as a pictorial analogue, for analysing trends in the evolution of internal shell features such as hinge teeth, etc., which are closely controlled by overall shell geometry.

In the following account of the evolution of functional design in rudists, examples are therefore figured in aspects corresponding to those of the growth models in figure 10, for graphic comparison of growth geometries. Other orientations are also depicted in order to portray internal features, life position, etc. For purpose of systematic orientation, the ligamentary site is treated as the dorsal reference datum.

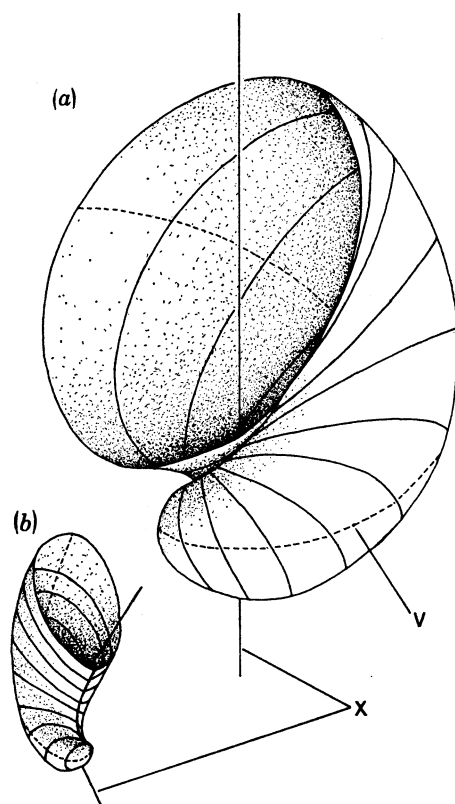


FIGURE 10. (a) Model of shell growth in primitive rudist. (b) Model of shell growth in uncoiled rudist. For explanation, see text. v, growth locus of mid-ventral point on rim; x, coiling axis.

EVOLUTION OF FUNCTIONAL DESIGN IN RUDISTS

The ancestors of the rudists were probably megalodontids (Böhm 1882), of which the Devonian *Megalodon cucullatus* J. de C. Sowerby (figure 11) is a relatively unspecialized example. The valves of this form are inflated and spirogyrate, because of the modified parivincular ligament. The originally aragonitic shell wall is thick, particularly in the umbones, and the hinge plates massive (figure 11 a, b). Most of the mass of the shell is therefore concentrated in these antero-dorsally situated elements. In life position (figure 11 e; see Fischer (1964) who described similar Triassic forms), the umbones, and hinge plates within them, projected downwards into the sediment, so that the lighter, blade-like postero-ventral part of the shell projected upwards. The former parts of the shell thus acted as ballast, stabilizing the elevation of the latter. It is worth noting that the aptly sited hinge plates, despite their size, grew very

economically. Figure 11*c* shows that their forward migration brought each near the lowest part of the generating curve (commissure) of its valve, in close proximity to the coiling axis. The hinge plates thus traced minimized volumetric growth loci.

The pedal scars (figure 11*a, b*) indicate original presence of a foot, which might have allowed at least initial byssate attachment. The ballasting of the shell described above would nevertheless have rendered this mode of stabilization redundant in adults; besides, megalodontids tended

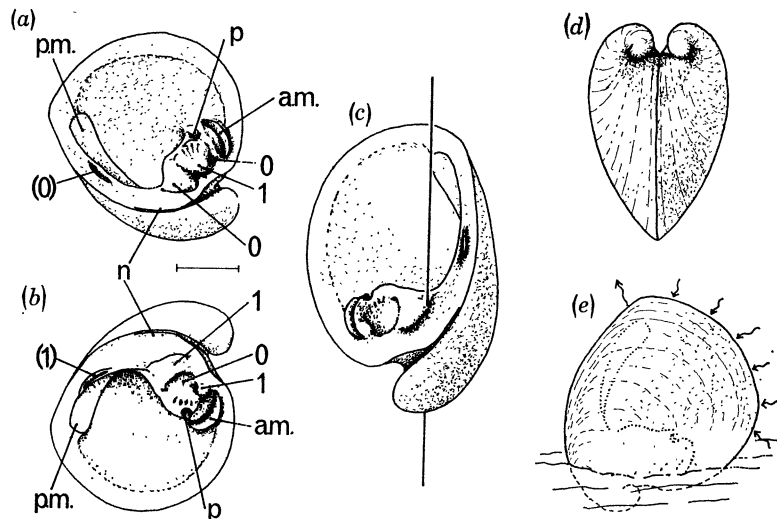


FIGURE 11. *Megalodon cucullatus* J. de C. Sowerby. (a), (b) Internal features of right (a), and left (b) valves. 1, tooth; 0, socket; a.m., anterior adductor scar; n, nymph; p, pedal muscle scar; p.m., posterior adductor scar. Horizontal black bar is a 1 cm scale. (c) Left valve showing growth around coiling axis. (d) Anterio-ventral aspect of whole shell. (e) Shell in semi-infaunal life position, seen from left side. Dotted lines show up positions of hinge plates and adductor scar sites within. Arrows indicate inhalent and exhalent currents.

to cluster together in calm, 'ultra back reef' environments (Müller-Jungbluth 1968). One feature nevertheless still suggests at least early pedal dominance in stabilization: the pedal muscle scars are sited near the ventral margins of the anterior adductor scars, which have themselves been engulfed by the forwardly shifted hinge plates. It seems that the anterior adductor was not able to escape ventrally (in contrast to that of the diceratids, discussed on p. 310); it must literally have been trapped in its mid-anterior position. Unobstructed anterior protrusion of the foot must therefore have been essential to the animal at some stage in its life. Since these were not burrowing forms, a phase of byssate attachment is the most likely explanation.

The first rudists belong to the family Diceratidae, and are exemplified here by *Diceras arietinum* Lamarck (figure 12). They make an abrupt appearance in the Upper Oxfordian of a broad area stretching from France to the Crimea (Pchelintsev 1959). The umbones show even greater extension than those of *Megalodon*, though their form is under the same ligamentary control (figures 1 and 2, plate 1). One or other umbo served as a spiralling encrustation platform, or stalk, according to surrounding sedimentary accretion (figure 12*e*). The valve of attachment appears to be fixed for each species (Bayle 1873; Douvillé 1935). The shell is more or less inequivalve, the attached valve generally being larger (figure 12*d*). A simple reduction in the rate of valve expansion, coupled with the introduction of valve asymmetry, thus permitted the diceratids to replace the ancestral byssate/ballasted mode of stabilization by that of umbonal

encrustation. This new potential for growth elevation allowed the diceratids to exploit substrata, which though normally stabilized, experienced episodes of spasmodic sedimentation. The sediments exploited by diceratids comprised variously stabilized, shelly to peloidal lime sands, with or without interstitial lime mud or marl, commonly neighbouring shallow patch, or knoll reefs (Skelton 1976*b*).

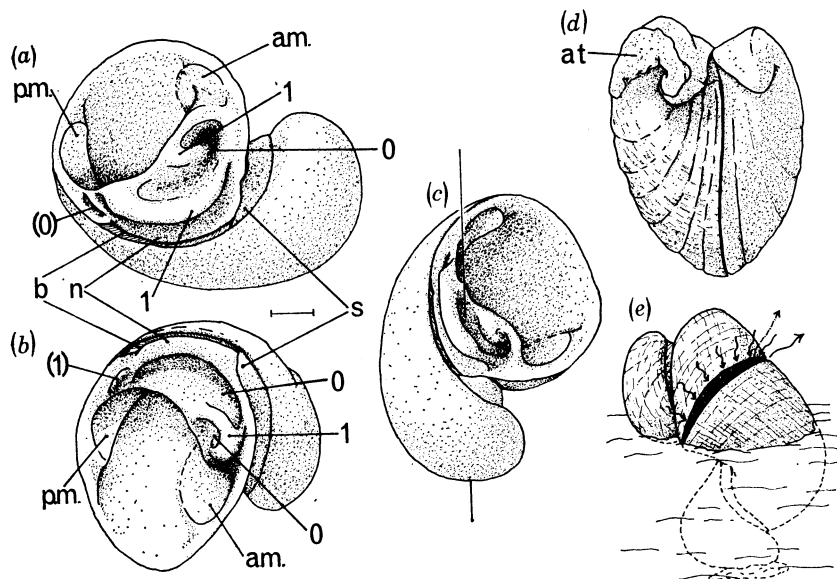


FIGURE 12. *Diceras arietinum* Lamarck. (a), (b) Internal features of right (a), and left (b) valves. 1, tooth; 0, socket; a.m., anterior adductor scar; b, bourrelet; n, nymph; p.m., posterior adductor scar; s, calcareous overgrowth on split ligament. Horizontal black bar is a 1 cm scale. (c) Right (attached) valve, showing growth around coiling axis. (d) Anterio-ventral aspect of whole shell; at, attachment site. (e) Shell in life position, overgrowing sediment surface with anterior face of right valve. The ventral margins of the ctenidia are shown just within the valve margins. Full arrows indicate inhalent and exhalent currents. Broken line arrow represents supposed site of pseudofaecal ejection.

Another adaptive innovation of the diceratids was the acquisition of an outer shell layer of fibrillar prismatic calcite. It was to remain an important feature of all rudists. This layer is radially ribbed externally (figure 12*d*). The ribbing is markedly coarser in the attached (left) valve than in the free (right) valve in the large *Epidiceras sinistrum* (Deshayes). It therefore seems probable that this ornament assisted the frictional stability of the attached valve on the sediment surface, in this form at least. The calcitic layer probably also afforded some protection against algal boring.

The massive hinge plates project anteriorly (figure 12*a, b*), as in *Megalodon*, entailing the same economy of growth (figure 12*c*). There are three prominent teeth: two in the right valve and one in the left, though there is also an additional small tooth in the left valve, lying immediately posterior to the ligamentary site (figure 12*b*). The strongly tangential component of growth accretion has given the teeth a 'streaked out' aspect, exactly as described by Owen (1953) in the case of *Glossus humanus*. Tooth form is thus closely linked to growth geometry. Yet, differences in tooth form have been used for the erection of new diceratid genera; since these may merely reflect small changes in shell form, itself heavily influenced by ecological factors, I believe such splitting to be unjustified.

The anterior adductor of diceratids, unlike that of *Megalodon* (p. 308) escaped ventrally from the encroaching hinge plates. This suggests that there was no longer a protrusible foot; indeed no pedal muscle scars like those seen in *Megalodon* are visible (figures 4–6, plate 1), implying complete atrophy of the organ. The posterior adductor was sited posteriodorsally, between prominent ledge-like myophores similar to those in *Megalodon*.

The large adductor scars indicate powerful adductor muscles, which complemented the strong, elongate ligament (figure 12*a, b*). The diceratids would therefore have been fully capable of valve-clapping for the expulsion of pseudofaeces (Skelton 1976*b*): an important feature for cemented bivalves in particular (Yonge 1967).

Beneath each hinge plate is a small arc of muscle-scar-like pits. These are plainly visible on the finely preserved internal moulds of *Eodiceras* shown in figures 4–6 (plate 1). Each arc separates an adumbonal, smooth triangular area from an adumbonal zone of fine radial striae, which represent the growth traces of the pits. In recent heterodonts, such as *Arctica* and *Glossus*, similar scars represent the dorso-lateral limits of attachment of the visceral mass to the inside of the shell; the smooth triangles thus effectively delineate the dorsal surface of the body. The anterior part of each arc also corresponds to the anterior limit of each inner demibranch, where the latter joins the food groove passing between the labial palps. This correlation between the antero-dorsal limits of the body and the crests of the ctenidial axes appears to be maintained even in forms with extended umbonal cavities, such as the chamids (see figures 19 and 20 of Yonge 1967). Diceratid anatomy is therefore here shown reconstructed with the position of the body and gills based upon the smooth triangles observed in *Eodiceras* (figure 13). This reconstruction is in contrast to that of Yonge (1967, figure 27), in which the ctenidia are supposed to have extended to the very apices of the umbonal cavities. Loss of the foot, and the relatively ventral situation of the anterior adductor and mouth suggest, rather, that the ventral margins of the ctenidia may have taken up broadly commarginal positions. They would there have been well placed to receive inhalent currents from around a broad ventral zone, held up in life above the sediment surface (figures 12*e* and 13). It is therefore assumed (as with the megalodontids) that the mantle margins were generally unfused. Analogy with oysters is thus presented. Exhalent currents are supposed to have left near the posterior adductor, in conventional fashion (figure 12*e*).

The diceratids would thus appear to have become moderately efficient encrusters (see Skelton 1979), as their rapid spread through the shallow shelf seas of Tethys during the late Jurassic testifies.

The Requienniidae, first represented in the Tithonian (Joukowsky & Favre 1913), essentially retained the growth geometry of diceratids, though becoming even more strongly inequivalved (see Dechaseaux, Coogan, Cox & Perkins 1969). These too were mainly encrusters, with the left valve being attached.

The next big modification in rudist functional design came with *Monopleura* and its allies. This family (Caprotinidae, as defined herein; p. 315) is first represented in the Kimmeridgian of southeastern France (Favre & Richard 1927). *Monopleura pinguiscula* White is here figured as an example (figure 14). The right valve was attached, the left usually becoming small and lid-like. Invagination of the ligament (figures 7–9, plate 1) permitted uncoiled growth (figure 14*c*), as explained on p. 306. Umbonal extension of the attached valve was thus economically achieved, without the need for spiralling growth. This in turn allowed the adoption of an erectly encrusting habit (figure 14*e*), and hence direct elevation of the commissure by growth from small

attachment sites such as shell fragments, etc. Uncoiling also permitted closely packed aggregation of individuals (figure 14e).

The hinge plates again bear a simple relation to growth geometry. Douvillé (1896) showed that the apparently 'inverse' dentition of *Monopleura* and its relatives – two major teeth in the left valve and one in the right – arose by atrophy of the former anterior tooth in the right valve of diceratids, and by development of the minor tooth behind the ligament in the left valve (compare figure 12a, b with figure 14a, b). The functional explanation for this changeover may again relate to economy of growth. Figure 14c shows that invagination of the ligament and

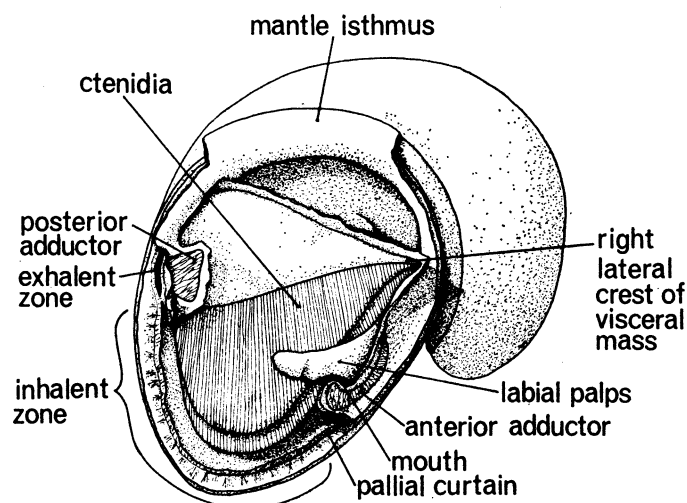


FIGURE 13. Reconstructed anatomy of a diceratid. The right valve and mantle lobe have been removed to show the body and left mantle lobe in the left valve.

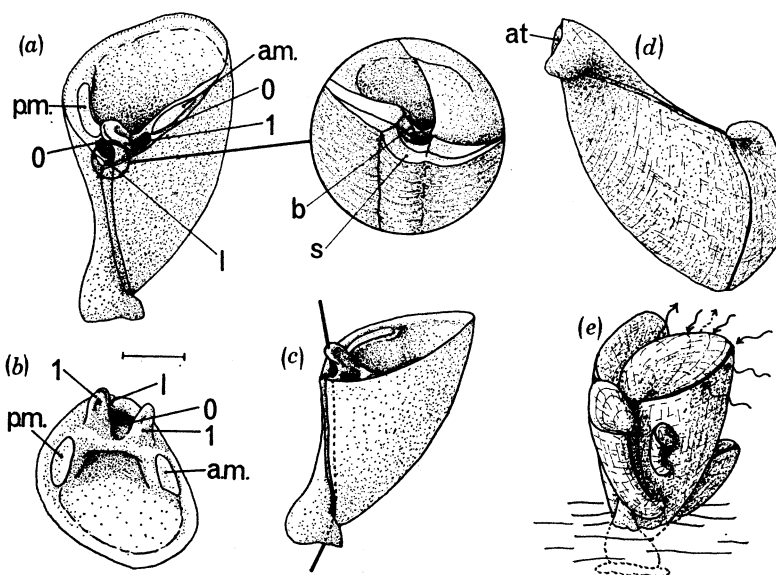


FIGURE 14. *Monopleura pinguiscula* White. (a), (b) Internal features of right (a), and left (b) valves. 1, tooth; 0, socket; a.m., anterior adductor scar; l, ligamentary site (detail in (a): b, bourrelet; s, overgrowth on split ligament, incorporating atrophied nymph); p.m., posterior adductor scar. (c) Right (attached) valve showing uncoiled growth along axis. (d) Anterior aspect of whole shell. at, attachment site. (e) Small bouquet of specimens in life position, projecting from sediment. Full arrows represent inhalent and exhalent currents. Broken line arrow represents supposed site of pseudofaecal ejection (probably only under ciliary control).

uncoiling caused the dorsal side of the commissure (where increments are still at their narrowest to represent the lowest part of the generating curve. This zone also lies closest to the coiling axis. A tooth and socket pair lying close to the ligament therefore entails smaller volumetric growth loci than one more anteriorly situated. The expansion of the former and demise of the latter, as seen in *Monopleura*, can therefore be interpreted as representing growth economy. Dental reorganization also permitted a more dorsal location for both of the adductor myophores, which had by now become ventral extensions of the cardinal platforms (figure 14*a, b*).

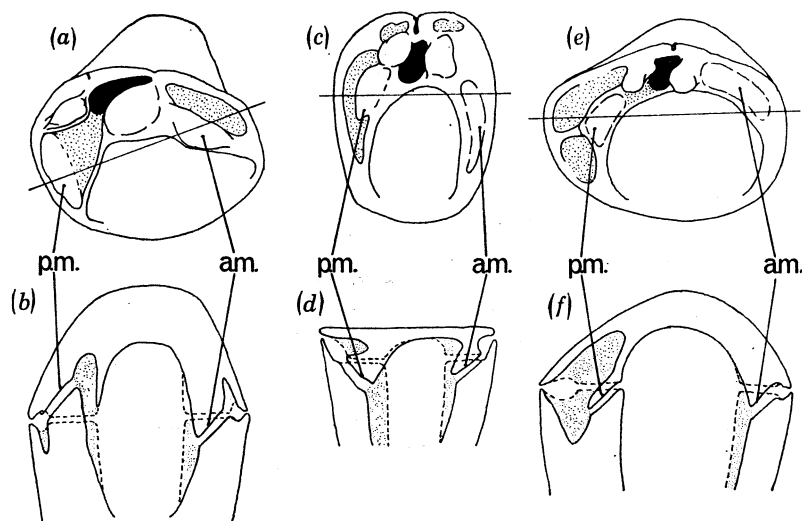


FIGURE 15. (a), (b) *Pachytraga* (based on Paquier 1905). (c), (d) *Polyconites* (based on Douvillé 1889; Dechaseaux *et al.* 1969). (e), (f) *Caprotina* (based on Dechaseaux *et al.* 1969). (a), (c), (e) are left valve interiors. (b), (d), (f) are diagrammatic radial sections along lines shown in (a), (c), and (e), showing left valves overlying right valves. a.m., anterior adductor scar (and myophore); p.m., posterior adductor scar (and myophore). For explanation, see text.

Uncoiling permitted considerable umbonal extension in later inverse rudists. Large amounts of shell material thus became employed in the maintenance by growth of the myophoral buttresses. Again, strictures of economy appear therefore to have brought about radical changes in the orientation of these. Figure 15, based on information given in Dechaseaux *et al.* (1969), Douvillé (1889), and Paquier (1905), shows that rotation of muscle scar sites in a variety of forms has reduced the amount of shell material required for myophoral construction. The dotted lines in the lower diagrammatic sections (figure 15*b, d, f*) circumscribe the amounts of material that would have had to have been used, had the muscle scars remained parallel with the commissural plane. Rotation of the scar planes towards the directions of maximum accretion (upwards in the tubular lower valves) has resulted in their tracing narrower growth loci, although the scars themselves are not reduced in size. The modes of rotation differ in the various forms, but have in all of them given rise to accessory cavities beyond or beneath the myophores (these cavities are represented by coarse stippling in figure 15*a, c, e*). The fine stippling in the lower series of diagrams (figure 15*b, d, f*) shows how much shell material has thus been saved by myophoral rotation and accessory cavity development. Such forms are certainly convergent, but seem unlikely to represent a monophyletic assemblage, since the accessory cavities have arisen in different ways. Nevertheless, the rudist family Caprotinidae Gray, 1848, as described by Dechaseaux *et al.* (1969), is essentially characterized merely by

possession of accessory cavities. I therefore propose to combine the families Caprotinidae and the ancestral Monopleuridae, as described by Dechaseaux *et al.* (1969), thus to treat them as a single, enlarged family (p. 315).

Another important concomitant of uncoiling was loss of ligamentary size and efficiency (figure 14*a*, detail). This seems not to have mattered, though, since caprotinids had evidently become well adapted to circulating feeding and respiratory currents with minimal gaping; the adductors, mounted upon the myocardial platforms, were extremely short – of the order of 1 or 2 mm in most forms – and could not therefore, have been stretched beyond a few millimetres.

Muscle scar evidence for the position of the body in caprotinids is not currently available. Some adjustment to the highly inequivalved nature of the shell must nevertheless have taken place. The positions of the adductor muscle scars (figure 14*a, b*), and evidence that the body in two descendant groups, the radiolitids and hippuritids, was largely suspended from within the left valve (Skelton 1974, 1976*a*), suggests that that too was the case in caprotinids. The ctenidia can then be supposed to have taken up commarginal positions around it, following the trend indicated in the diceratids (p. 310). They would thus have lain in close proximity to a broad inhalent zone extending most of the way around the ventral part of the commissure (figure 14*e*), compensating for the narrowness of the latter's gape.

Reduction of active gaping in such epifaunal forms presumably assisted in the exclusion of predators and other undesired objects, as well as assisting rapid closure during fluxes of muddy water.

A universal trend indicated in later inverse rudists is expansion, by a variety of means, of the valve, and therefore mantle margins. I have elsewhere attributed this trend in the Hippuritidae, in particular, to the evolution of mantle marginal food entrapment (Skelton 1976*a*). Given the restriction of their gaping, however, it is indeed possible that *Monopleura* and related forms had themselves already evolved some degree of mantle marginal food entrapment, supplementing the ctenidia. The closely opposed mantle margins would already have been furnished with cilia and mucus glands; these could have taken on the new rôle via one of entrapment and mere rejection of unwanted particles. The subsequent evolution of inverse rudists might then be taken to reflect the increasing importance of this feeding mode. Such externalization of the food capturing process would have allowed almost direct processing of surrounding water, with minimal gaping. The bulk of the soft parts within the shell would have been almost completely shielded from fouling and predation. Although such a feeding style accords well with hippuritid form, it is unclear as yet precisely how the feeding currents might have been organized in the other forms, and what part (if any) was subsequently played by the functionally dispossessed ctenidia.

Two new adaptive zones became available with the advent of uncoiling: first, direct growth elevation of the commissure from a small attachment site, in calm, occasionally turbid water environments ('elevators'), and secondly, broadly recumbent growth upon lime sands often subjected to traction currents ('recumbents'). Inverse rudists diversified into both of these adaptive zones, though some remained as, or secondarily became, 'encrusters' on broad, stabilized surfaces (figure 16). These adaptive zones are described in greater detail in Skelton (1979). The hippuritids became the most specialized of the elevators, whilst certain of the large 'caprinid' rudists, such as *Titanosarcolites*, were among the foremost recumbents (see Kauffman & Sohl 1974). Radiolitids encompassed the whole range.

Both elevators and recumbents required considerable umbonal extension in one or both valves, necessitating economical space-filling and support of the cavities within. All the advanced forms evolved tabulae for this purpose, although these were supplemented by canaliculate shell fabrics in many groups. The latter type of structure is usually considered to consist of inwardly migrated 'pallial canals' (see Dechaseaux *et al.* 1969), although in most forms these are only associated with widening of the valve margins. There are, however, several different kinds of

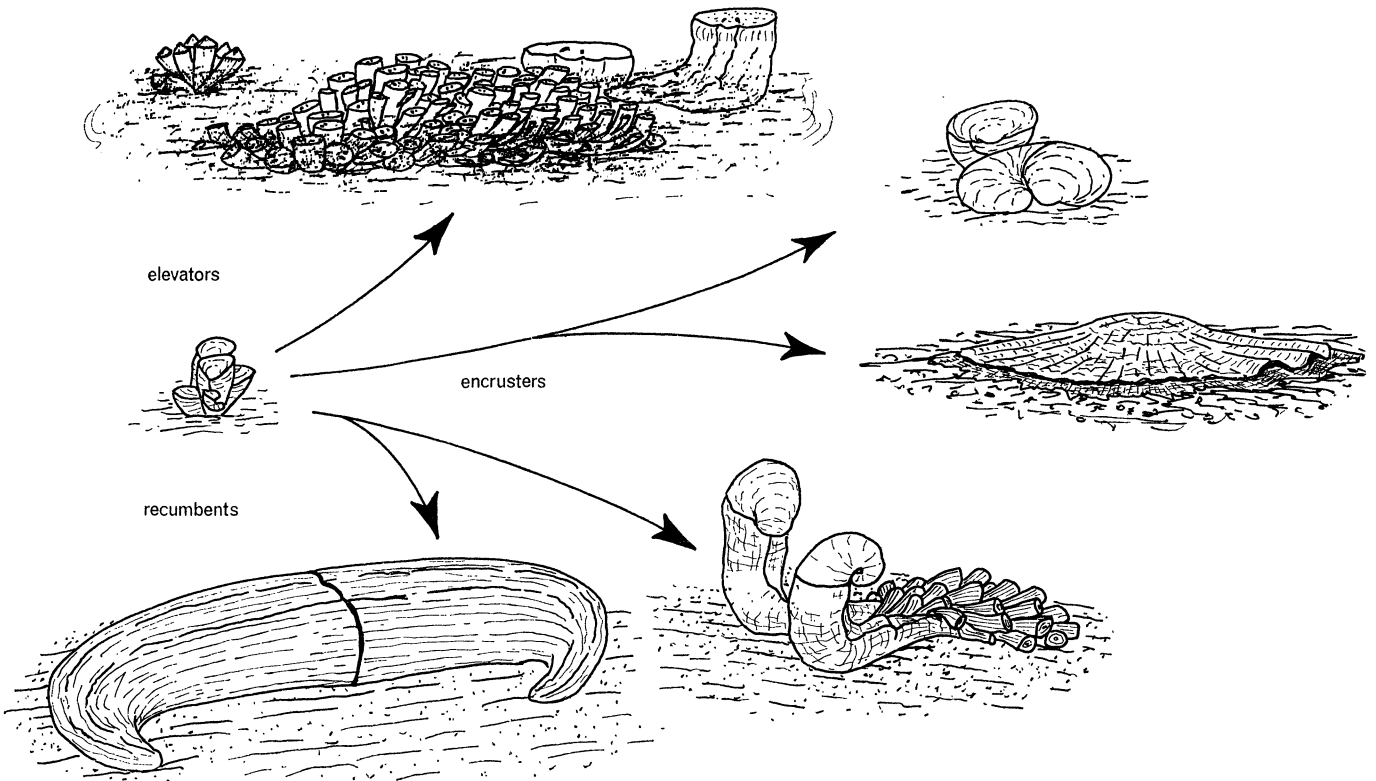


FIGURE 16. Adaptive radiation of inverse rudists. Elevators, e.g. hippuritids and radiolitids; encrusters, e.g. plagioptychids and radiolitids; recumbents, e.g. antillocaprinids (*Titanosarcolites*), caprinids and radiolitids. Ancestral form (e.g. *Monopleura*) is an erect encruster to elevator.

canal, and they are also known to have evolved independently in a variety of different clades (Douvillé 1888, 1904; MacGillavry 1937). The family Caprinidae d'Orbigny, 1850, which is at present just a repository for nearly all rudists with such canals (see Dechaseaux *et al.* 1969) is demonstrably polyphyletic, and should therefore be split into different families based on true clades (p. 316).

Pallial canals have given rise to numerous taxonomic errors. A good example, mentioned by MacGillavry (1937, p. 150), is that of '*Sabinia*' *klingshardti* Böhm; despite Böhm's ascription of this species to a 'caprinid' genus, it is clearly a sauvagesiine radiolitid, as the distinctive cellular outer shell layer of the right valve, and its myocardinal form testify.

The Hippuritidae and Radiolitidae do seem, however, to represent true clades (p. 317).

CONCLUSIONS

I therefore propose the following modified familial classification of rudists, based on detectable clades. Their probable relations to one another are depicted in figure 17. This is essentially a revision of the classification given by Dechaseaux *et al.* (1969). The division of the caprinids (*sensu lato*) into four separate families follows the leads of Douvillé (1887, 1888, 1904), and MacGillavry (1937). I also include general features of functional design, drawn largely from Skelton (1976*b*), and outlined above.

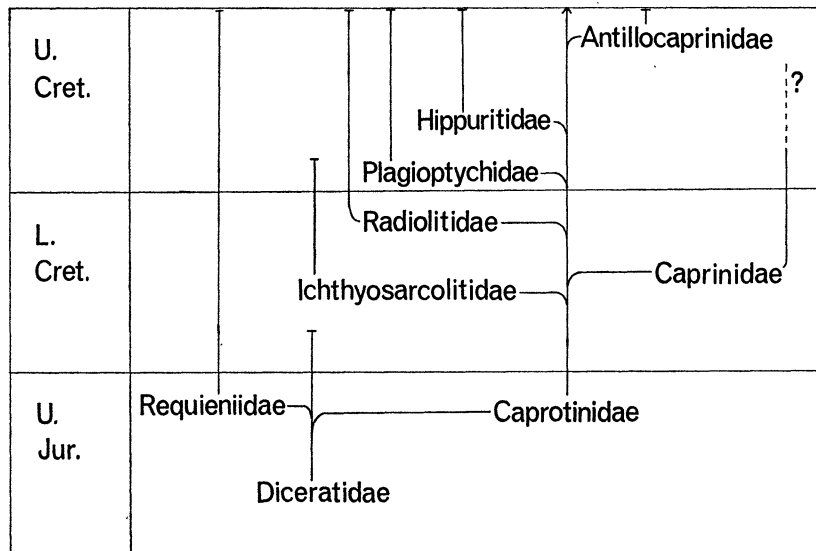


FIGURE 17. Phylogeny of rudist families.

Class Bivalvia Linné, 1758

Subclass Heterodonta Neumayr, 1884

Order Hippuritoida Newell, 1965

Superfamily Hippuritacea Gray, 1848

(Diagnosis as in Dechaseaux *et al.* (1969, p. N749)).

Family Diceratidae Dall, 1895

Spirogyrally coiled encrusters. Otherwise, characters as defined in Dechaseaux *et al.* (1969, p. N776).

Comment. The subfamilies described in the *Treatise* do not stand up to scrutiny, and need revision.

Family Requieniidae Douvillé, 1919

Spirogyrally coiled encrusters. Otherwise, characters as defined in Dechaseaux *et al.* (1969, p. N779).

Family Caprotinidae Gray, 1848

Shell inequivalve and more or less uncoiled, with right valve umbonally extended, and left valve cap-like to operculiform. Ligament short and in most species invaginated. Encrusters (low to erect) and elevators, with attachment by the right valve. Thin to thick outer shell layer of fibrillar prismatic calcite, with growth rugae and radial ribs or fine striae. Inner shell layers aragonitic. Two major teeth in left valve, and one intervening tooth in the right. Adductor

muscle scars on extensions of hinge plates, though reorientation of either adductor may cause expansion of one myophoral support at the expense of its counterpart in the other valve. Such displacements may involve the production of accessory cavities.

Comments. As defined by Dechaseaux *et al.* (1969, p. N784) the Caprotinidae is a small and polyphyletic assemblage of monopleurid descendants, merely characterized by possession of accessory cavities. It is therefore best to combine these forms with their monopleurid ancestors, to form one large (single clade) family. This must take the name of Caprotinidae, which has priority over Monopleuridae Munier-Chalmas, 1873. *Rousselia*, an obscure form with pallial canals, is also allocated to this family; it probably evolved from *Monopleura* (Douvillé 1904).

Family Ichthyosarcolitidae Douvillé, 1887

nom. transl. Skelton, herein (*ex* Ichthyosarcolitinae Douvillé, 1887)

Shell large, inequivalved, and uncoiled, though secondarily curved in open planispiral fashion. Right valve larger than left valve. No ligament. Recumbent. Outer calcitic shell layer reputedly wanting (MacGillavry 1937). Shell therefore of aragonite, with ubiquitous non-tabulate, radially aligned canals of rounded section in both valves. Tabulae present in umbonal cavities of both valves. Two teeth in left valve, fused with projecting adductor myophores, forming radiolitid-like myocardial arc, which fits into set of corresponding notches in right valve shell wall.

Comments. *Ichthyosarcolites* presently seems to be the only member of this enigmatic family. The origin and function of the canals is obscure. The lack of a ligament means that the family cannot be ancestral to the Caprinidae. Conversely, the non-tabulate canals are quite unlike those of contemporaneous caprinids, as is also the dentition, suggesting quite independent origins.

Family Caprinidae d'Orbigny, 1850 (*sensu stricto*)

Shell inequivalved and uncoiled, though the left valve may be secondarily enrolled and the right valve curved to irregular. Right valve usually, but not invariably, larger than left valve, though both are umbonally extended. Ligament present, though well invaginated. Basically recumbent, with initial attachment of right valve, though the commissure is commonly projected upwards in some forms. Thin outer shell layer of fibrillar prismatic calcite. Inner shell of aragonite, with tabulate, radially aligned canals in pallial regions of both valves, or, in a few forms, only in left valve. The canals are primitively pyriform in cross section, to polygonal or rounded in more advanced forms. Tabulae may be present in umbonal cavities. Two knob-like teeth in left valve, straddling prominent tooth in right valve. Anterior adductor scars variably rotated out of commissural plane. Posterior adductor scars rotated into left valve, so that that of right valve sits on myophoral plate, facing out onto low buttress on posterior wall of left valve. Residual ventral myocardial edge of left valve projects as salient plate to inside of posterior myophoral plate of right valve, thereby separating off a large accessory cavity in the left valve as posterior-ventral extension of central tooth socket (*cf.* figure 15*a, b*). Other accessory cavities generally also present.

Comments. This family comprises the forms closely associated with *Caprina* itself. MacGillavry (1937) detected three lineages in the group, which he referred to as the 'Caprininae': *Amphitricolus*, *Planocaprina*, *Coalcomana*, *Caprinuloidea* and *Sabinia kugleri* in the New World, and *Praeacaprina*, *Caprina*, *Orthoptychus*, *Sphaerucaprina* and *Offneria*, *Caprinula* and ? some species of *Sabinia* in the Old World. The pallial canals of these forms arose by the repeated subdivision of

marginal accessory cavities by radial and later, tangential septal laminae (Douvillé 1887, MacGillavry 1937). Economical thickening of the valve walls, and therefore mantle margins, appears to be the principal rôle of the canals in this family.

Family Plagioptychidae Douvillé, 1888

nom. transl. Skelton, herein (*ex* Plagioptychinae Douvillé, 1888)

Shell inequivalve, and weakly to moderately uncoiled, with the left valve cap-like, and the generally larger, attached right valve more or less spirally conical. Ligament only weakly invaginated, particularly in early forms, though secondarily lost in some later genera. Flat (spiralling) to erect encrusters, though later forms also became elevators and recumbents. Outer shell layer of fibrillar prismatic calcite, thin in left valve, but thick in right valve, such that the right valve margin extends out beyond that of the left valve. A pair of radial bands, wherein the growth lines are deflected, is visible on the posterior outer surface of the right valve. Inner shell of aragonite, with radially aligned, tabulate canals, of pyriform cross section, in the crossed-lamellar middle shell layer of the left valve only. Other tabulate canals, of polygonal to rounded cross section, may also occur in the inner shell layers of both valves in later forms. These latter canals are considered to be of separate origin (MacGillavry 1937). Dentition and myophores as in the Caprinidae, though the rotation of the adductor scars is only slight.

Comments. The earliest form, *Plagioptychus*, is contemporaneous with the latest caprinids, and yet exhibits considerably less ligamentary invagination (MacGillavry 1937). It must therefore be of separate ancestry, from some weakly uncoiled inverse rudist. The recumbent *Dictyoptychus* may belong to this family.

Family Antillocaprinidae MacGillavry, 1937

nom. transl. Skelton, herein (*ex* Antillocaprininae MacGillavry, 1937)

Shell variably inequivalved to secondarily almost equivalved, and completely uncoiled. The attached right valve is stump-like and irregular, and the left valve secondarily enrolled, though in the advanced *Titanosarcolithes*, both valves are gently curved and horn-like. Ligament deeply invaginated or lost. Encrusting to recumbent. Outer shell layer of radially ribbed fibrillar prismatic calcite is very thin. Shell therefore mainly aragonite, with radially aligned canals of polygonal cross section throughout both valves. These canals are tabulate, except possibly for an outer marginal row (MacGillavry 1937). Dentition and myophores (also canaliculate) of simple monopleurid form in *Antillocaprina*, but strongly modified in *Titanosarcolithes* (see MacGillavry 1937, p. 98). No accessory cavities.

Comments. These late Cretaceous forms are restricted to the New World, and are quite dissimilar to contemporaneous rudists with canals. They are probably an independent stock, arising from *Monopleura* or one of its allies (MacGillavry 1937).

Family Radiolitidae Gray, 1848

Encrusters, recumbents and elevators. Otherwise, characters as defined in Dechaseaux *et al.* (1969, p. N803); note, however, that several forms with umbonally extended left valves have pallial canals in that valve.

Comments. This is clearly a true clade, as indicated by the large number of common features possessed by all forms, namely cellular construction of the outer shell layer of the right valve alone, ligament strongly invaginated or even lost, and uncoiling therefore complete, teeth and

myophores of left valve projecting as myocardial arc into dorsal region of right valve, siphonal bands or pseudopillars and/or oscules, and so forth.

Family Hippuritidae Gray, 1848

Elevators. Otherwise, characters as defined in Dechaseaux *et al.* (1969, p. N799).

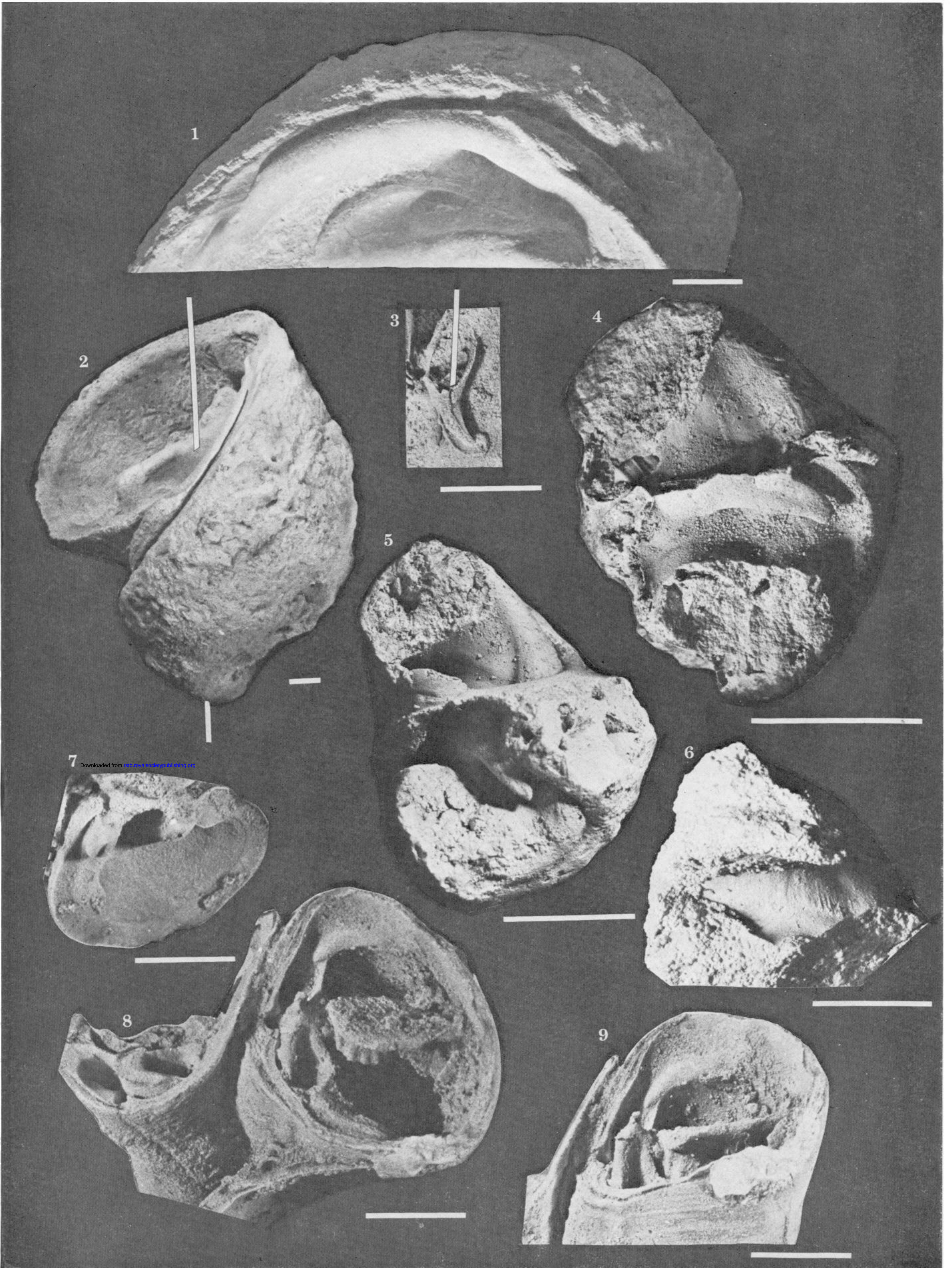
Comments. Again, this family appears to be a true clade, on account of the number of common features possessed by all forms, namely radial canal and pore system in outer shell layer of left valve, ligament strongly invaginated or even lost, and uncoiling therefore complete, all elevators (either solitary or aggregative), teeth and myophores of left valve forming myocardial arc of distinctive form, projecting into right valve, pillars and oscules, and so forth.

A number of genera remain difficult to place, partly because they are not well enough known, and partly because some have become polyphyletic assemblages of species as a result of insufficient systematic comparison of ascribed species. *Sabinia* and *Schiosia* are good examples of the latter, and *Immanitas* is one of the former.

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FIGURES 1-9. For description see opposite.