# Fossils explained 60

## Rudists

Hippuritaceans, colloquially known as rudists, are an extinct group that encompasses some of the most specialized and successful bivalved molluscs that have ever lived. These were sessile marine organisms that dominated tropical shallow waters during the Cretaceous, becoming the most important reef builders during the Mesozoic. Rudists are notorious for their varied and extravagant shapes, which allowed them to exploit a wide range of ecological niches during their long-lived history of almost 100 million years.

Probably the most striking feature of rudist bivalves is their bizarre appearance, which for centuries puzzled renowned scholars of the calibre of Lamarck and Cuvier; as a matter of fact, Lamarck coined the name 'Les Rudistes' to emphasize their rather rugged and aberrant morphology. However, deep inside, rudists are not very different from other bivalved molluscs, although they possess an interesting array of adaptations for their peculiar mode of life.

### External morphology

Rudist valves are usually large and robust in comparison with most other bivalves, and commonly display a remarkable asymmetry in size and shape (Fig. 1). The lower (or adherent) valve is usually the largest and is in direct contact with the substrate by its umbonal (initial site of growth) region. The upper (free) valve is often much smaller in comparison. Although the earliest rudists (e.g. *Diceras*) had almost equally sized and shaped valves, most of the more derived forms are highly asymmetrical, ranging from a moderate-sized upper valve (e.g. *Caprinula*) to the operculate one of more derived representatives (e.g. *Vaccinites*). Another notorious evolutionary trend among rudists is towards the progressive uncoiling of both valves. Primitive representatives usually have tightly coiled valves, but a nigh straight conical lower valve and loosely or non-coiled cap-like upper valve is almost the ground pattern for many of the younger forms. The surface of the valves is commonly adorned with growth lines and ribs comparable to those of other bivalves.

Apart from their unusual looks, one of the reasons that hampered the early recognition of rudists as bivalves is the apparent absence of a ligament.

In bivalve molluscs, the ligament is a proteinaceous tissue that acts as an antagonist to the adductor muscles (i.e. it forces the valves open). Although the attachment site of this structure is relatively easy to identify on normal bivalves, the ligament in rudists is often invaginated within the dorsal part of the shell wall, forming the so called 'ligament groove' (Fig. 1). The exact position of the ligament is easier to trace based on the internal morphology, as the shell wall displays clear evidence of its internalization (ligament chamber) (Fig. 2).

### Internal morphology

Like any other bivalved mollusc, rudists possessed a double-layered calcium carbonate shell wall, which consisted of an internal aragonitic and an external calcitic layer. The aragonite provided strength to the shell and served as the site of attachment for the muscles and other soft tissues, while the calcite was in direct contact with the environment and other individuals. In primitive rudists (e.g. diceratids, requienids, monopleurids), the aragonitic fraction occupied the bulk of the shell wall and lacked any distinctive features, while the calcite was limited to a very thin superficial film (Fig. 2).

In later representatives (e.g. caprinids), the proportions of aragonite/calcite changed little, but the shell wall incorporated a series of longitudinal hollow structures known as 'pallial canals'. The pallial canals allowed rudists to reach greater sizes and attain erect stances in an efficient manner by producing relative-

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**Fig 1.** Rudist disparity and external morphology. Representatives of the major families: **a.** *Caprinula* (Caprinidae), **b.** *Diceras* (Diceratidae), **c.** *Toucasia* (Requieniidae), **d.** *Monopleura* (Monopleuridae), **e.** *Ichthyosarcolites* (Ichthyosarcolitidae), **f.** *Durania* (Radiolitidae), **g.** *Vaccinites* (Hippuritidae) (modified from Dechaseux *et al.* 1969 and other sources). Right valves are shaded in grey.
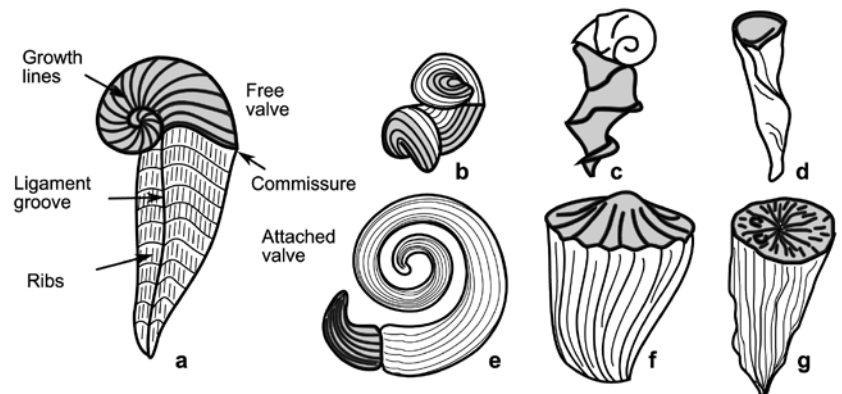
ly lightweight but strong shells with little additional metabolic input. However, in the largest rudists (e.g. radiolitids, hippuritids) the mineral proportions of the shell wall are reversed, with the aragonite occupying a relatively small area near the body cavity, and a large and complex network of calcite forming most of the shell wall. In the case of hippuritids, the shell wall also features distinctive columnar structures called 'pillars', which define and separate the inhalant and exhalant siphonal apertures to allow water intake into the body cavity.

On its dorsal region, the shell wall bears the hinge mechanism, which consists of one tooth on the right valve, two teeth on the left valve, and their matching sockets. As with other bivalves, the hinge provided leverage to open and close the valves according to their necessities. Another important modification of the inner shell wall is the thickening of the anterior and posterior edges into myophores, which provided sites for the attachment of the adductor muscles. These muscles controlled the voluntary aperture of the valves; when contracted the adductor muscles close the valves, in an opposing action to the ligament. Finally, most of the inner volume of the valves is occupied by the mantle or body cavity, which is the site were the visceral mass, gills and all other organs were located. The mantle cavity is normally much larger on the adherent valve, were most of the body mass was concentrated.

## Distribution and mode of life

During the Cretaceous an important proportion of lowlands were submerged due to the elevated sea level which then covered 85 per cent of Earth's surface. At the same time, global temperatures increased due to the accumulation of atmospheric $CO_2$, leading to the formation of a massive body of warm and shallow waters known as the Tethys Domain in the intertropical regions. Rudists thrived under these conditions, forming enormous carbonate platforms around the circum-equatorial belt all over the world, most notably the UK, the Caribbean region, west of China, the Mediterranean, Mexico, the Middle East, south of USA and Saudi Arabia among others.

An important factor that led to the dominance of rudists in the shallow waters across the Tethys was their morphological plasticity, which allowed them to cope with the shortcomings of this environment and occupy novel ecological niches within it. Like most bivalves, rudists were filter-feeding organisms that obtained particle-sized nutrients from the sea currents. This strategy, coupled with the fact that they were sessile (i.e. unable to move), meant that their basic requirements were to be able to firmly anchor themselves and to filter water effectively. In environments with hard substrates one of the valves
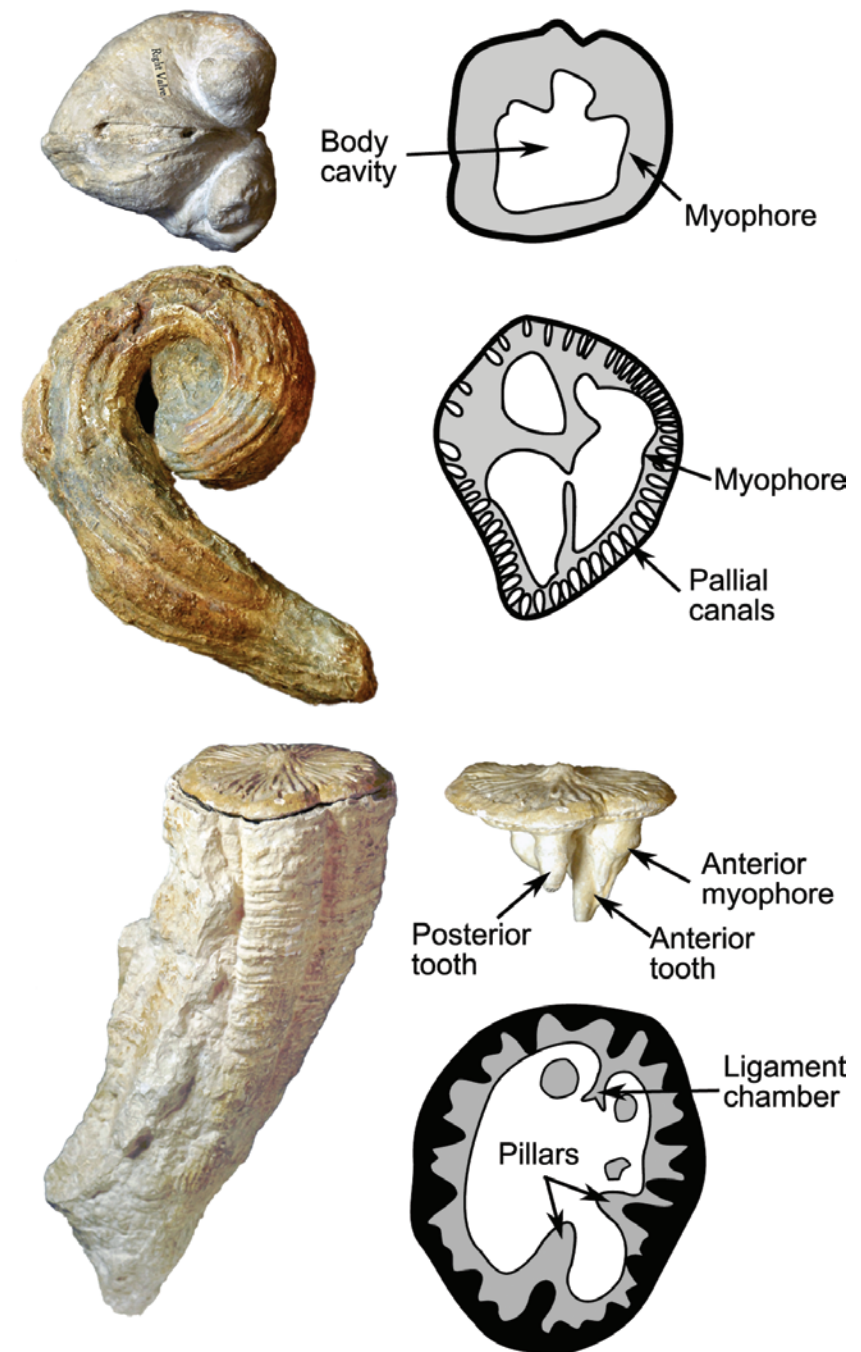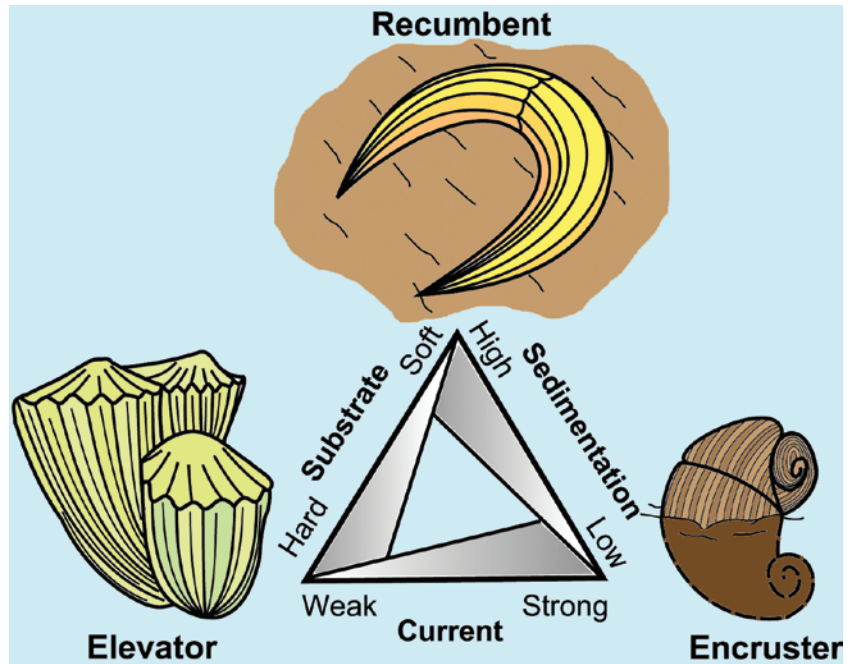
could be easily cemented to provide a steady support to carry on the filtering process. However, areas with soft sediments represented an adverse environment for the first rudists, as their tightly coiled valves were unable to elevate the commissure enough from the substrate to prevent contamination of the gills and the mantle cavity. Likewise, local environments with high sedimentation rates threatened the lives of primitive forms for the same reason, which meant that most rudists at this stage lived in moderate to high energy environments with low sedimentation



**Fig 2.** Rudist internal morphology. Aragonite (grey) and calcite (black) ratios on (top to bottom) the shell wall of requieniids (*Epidiceras*), caprinids (*Caprinula*) and hippuritids (*Hippurites*) monopleurids, caprinids and hippuritids (modified from Dechaseux *et al.* 1969 and other sources).

rates, as encrusters (Fig. 3). However, the internalization of the ligament and subsequent uncoiling of the lower valve allowed many genera to acquire a semi-recumbent or elevator stance, effectively keeping the commissure well above the sediment–water interface and enhancing food consumption and growth. The elevator mode of life became the staple of several of the most successful rudist families as it prevented the entombment by sediment through vertical growth and increased stability by the accumulation of sediment around the conical lower valve. This type of development also enabled some rudists to shift from solitary to a gregarious behaviour by enhancing the utilization of space due to the small surface required for the initial attachment, allowing numerous individuals to occupy relatively small areas and forming structures known as 'biostromes' (Fig. 3). Although many rudists living in low to moderate energy environments with high sedimentation and hard substrates possessed an elevator stance, others managed to exploit very high energy areas by acquiring a recumbent position. Recumbent rudists include some of the largest representatives (e.g. *Titanosarcolites*, up to 2 m in length) and are characterized by having both valves in contact with the substrate. This morphology was ideally suited for areas were the substrate was too soft and the currents too strong for the settlement of elevators or encrusters (Fig. 3).

As sessile inhabitants of shallow tropical waters, rudists have been compared with corals in terms of their ecology and adaptations to their environment. Recent and fossil hermatypic corals are characterized for their symbiotic relationship with zooxanthellae (microscopic algae), which allows them to grow rapidly in regions where the water is clear enough to enable photosynthesis by absorbing sunlight. A similar mechanism has been proposed to account for the massive growth of radiolitid and hippuritid rudists during the late Cretaceous. Some of the evidence that has been gathered in favour of this theory includes the widespread occurrence of rudists within the photic zone, the presence of very thin and somewhat translucent upper valves, and observations suggesting that the mantle was partially exposed during life. Furthermore, comparison with living bivalved molluscs that possess photosynthetic zooxanthellae in their mantle tissue (*Tridacna* and *Corculum*) demonstrates that such symbiosis is possible and that this relationship can be recognized in the fossil record based on morphological adaptations (e.g. translucent shells).

This diversity of shape and function led rudists to create a whole new environment of their own, establishing vast populations composed of hundreds of individuals growing on top of each other and creating a myriad of microhabitats for other benthic organisms. Although Jurassic rudists were part of the associated fauna in coral reefs, in the lower Cretaceous they had



**Fig 3.** Palaeoecology of the main rudist morphotypes exemplified by (clockwise from top) *Titanosarcolites* (Antillocaprinidae), *Requienia* (Requieniidae) and *Durania* (Radiolitidae).

already started producing considerable aggregations and by the middle-upper Cretaceous they had almost completely displaced corals as the major reef builders in the Tethys.

## Origin, diversification and extinction

The evolutionary history of rudists can be broadly divided into three diversification-extinction episodes that span from the Late Jurassic (160 Ma) to the end of the Cretaceous (65 Ma) (Fig. 4). The first rudists originated in the Oxfordian (Late Jurassic), having evolved from megalodontid bivalves, which are characterized by their massive shells and robust hinge teeth. Although the majority of rudist species were attached to the substrate by their right valve, the first representatives (family Diceratidae) had no particular preference and could attach themselves by either valve. They had compact and sturdy shells mainly composed of aragonite and just a superficial layer of calcite, much like those of their megalodontid ancestors, and specialized in an encrusting mode of life. Shortly after their appearance, rudists diversified into two main groups: those that only attached themselves with the left valve (family Requienidae) and those that attached with the right valve (all other groups); however, in the Valangianian (Early Cretaceous), a sudden global cooling event led to the extinction of diceratids.

The second phase commenced with the origin and diversification of caprinid rudists (family Caprinidae), most of which acquired recumbent or semi-erect modes of life by means of an elongated right valve. Caprinids retained the primitive condition of a mainly
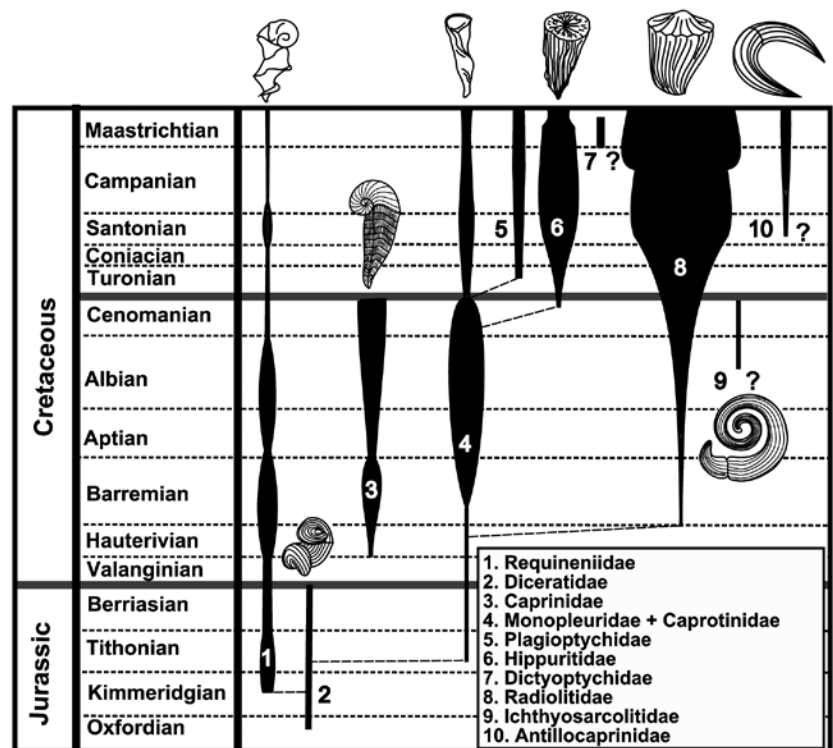
aragonitic shell with a thin outer layer of calcite, but managed to attain larger sizes due to the novelty of hollow pallial canals within the shell walls. Other lesser groups diversified and also attained similar dimensions (e.g. families Monopleuridae, Caprotinidae and Polyconitidae) by incorporating greater amounts of aragonite into the shell, thus making them very sturdy and heavy. In the Aptian (120 Ma), rudists experienced yet another global drop of the sea temperature that, while not as drastic as the previous one, lasted for a longer period of time. Although this phenomenon did not instantly eradicate most of the families, it had a marked effect on requeniids and caprinids.

The Cenomanian (100 Ma) represented an important stage in rudist evolution with the diversification of the families Hippuritidae and Radiolitidae, arguably the two most diverse and abundant groups, not to mention the ones that attained some of the largest sizes. At the end of the Cenomanian, an extinction event completely eliminated caprotinids and heavily mangled most other families. However, the hippuritids and radiolitids survived almost unscathed and carried on to diversify occupying the vacant array of ecological niches, becoming massive elevators or facultative recumbents. This lead to the reinvention of pallial canals in new groups (e.g. family Antillocaprinidae) in order to effectively increase their size and to compete with the giant species. During this final stage, various lesser rudist groups (e.g. families Dictyoptychidae and Plagioptychidae) evolved and occupied the palaeoecological role of accompanying faunas for the main reef builders, alongside the remaining monopleurids and requienids.

However, all rudist families became extinct at the end of the Maastrichtian (65 Ma), just as they reached the pinnacle of their diversity and morphological radiation, in the same event that killed non-avian dinosaurs. Although various independent lines of evidence support a number of explanations to account for this gargantuan extinction (e.g. meteorite impact, extraordinary volcanism, global sea regression), most palaeobiologists agree that it must have been triggered by a massive event on a global scale. It is likely that the strong provincialism of rudists in warm, shallow waters made them vulnerable to drastic climatic changes. A phenomenal regression of the sea level, occasioned by intense tectonic activity, would have left vast areas of shallow reefs exposed to subaerial conditions, effectively leaving rudists and numerous other marine organisms helpless against asphyxiation and dehydration.

## Suggestions for further reading:

Dechaseux, C., Cox, L.R., Coogan, A.H. & Perkins, B.F. 1969. Superfamily Hippuritacea Gray, 1848. In: Moore, R.C. (ed.) *Treatise on Invertebrate Palaentology, Part N, Mollusca 6, Bivalvia, 2.* Geological Society of America, Boulder, CO, and University of Kansas, Lawrence, KS, pp.N749–N817.

Skelton, P.W. 1978. The evolution of functional design in rudists (Hippuritacea) and its taxonomic implications. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, v.284. pp.305-318.

Skelton, P.W. 1991. Morphogenetic versus environmental cues for adaptive radiations. In: Schmidt-Kittler, N. & Vogel, K (eds) *Constructional Morphology and Evolution.* Springer, Berlin, pp.375–388.

Skelton, P.W. & Smith, A.B. 2000. A preliminary phylogeny for rudist bivalves: shifting clades from grades. In: Harper, E.M., Tayor, J.D. & Crame, J.A. (eds) *The Evolutionary Biology of the Bivalvia.* Geological Society of London, Special Publications, v.177. pp.97–127.

Skelton, P.W. 2003. Rudist evolution and extinction—A North African perspective. *In*: Gili, E., Negra, H., Skelton, P.W. (eds) *North African Cretaceous Carbonate Platform Systems.* NATO Science Series IV, Earth and Environmental Sciences, 28. Kluwer Academic Publishers. pp.215–227.

Steuber, T. 2002. Plate tectonic control on the evolution of Cretaceous platform-carbonate production. *Geology*, v.30. pp.259–262.

Vogel, K. 1975. Endosymbiotic algae in rudists? *Palaeogeography, Palaeoclimatology, Palaeoecology*, v.17. pp.327–332.

**Fig 4.** Evolutionary history of rudists (modified from Skelton 2003).