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Constructional morphology of some Upper Cretaceous rudists of the Ajlun (Jordan)

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Abstract

The rudists evolved their characteristics during Aptian/Albian time. Their basic morphological patterns appeared rapidly. By Cenomanian and Turonian time typical species lived in the shallow sea at what is the Ajlun today. Up to the end of the Cretaceous rudists dominated the shallow marine environment in tropical settings. Here the requienids like *Apricardia* continued to live in the tradition of their megalodontid ancestors attaching themselves to the substrate by the left valve. The vase-like rudists of the radiolitids and hippuritids, in contrast, cemented their right conical valve to the substrate. Two discussed species of radiolitids with massive walls of cellular construction in mixed structural composition had interior rooms in their valves that remained open to almost the base. They grew singly or formed colonies in which individuals are attached to each other in several levels of growth. Their opercular valve had a flexible and translucent margin and opened to a narrow gape. The hippuritids, in contrast, adopted the strategy of rapid growth with the small soft body moving upward in a solidly calcified shell closed by a series of septa at its base. Individuals attached to each other forming reef-like thickets. Mantle tissue was extended into the surface layer of the opercular valve that had a free margin. This valve was pushed up in total when the animal was active. The caprinid represented in the Ajlun fauna grew singly with irregularly horn-shaped valves of equal dimensions interlinked to each other by massive hinge-teeth. Valves opened only to a narrow gape. Tissue extended into the walls of the valves in numerous pores and canals. A constructional morphological analysis based on the rudists from Jordan and enriched with data from rudists of other occurrences is presented. According to it, symbiontic algae lived in the mantle tissue of the bivalves. This tissue was placed into the porous inner walls and below the transparent outer walls in the caprinids, into the canals and pores of the upper valve in active hippuritids and held below the transparent margin of the opercular valves and on the surface of the thick shell margin of the conical valves in radiolitids.

Introduction:

Between the castle of Rabad and the village of Istafena north of the town Ajlun in northern Jordan deposits of an extensive rudist bank are exposed accompanied by lagoonal limestones above. While the rudist bank was deposited during Cenomanian time, the sediments of the lagoon were formed during Turonian time. Some of the gastropods living in both environments were described by MUSTAFA & BANDEL (1992), while a regular sea urchin from the Rudist bank had been published by BANDEL & GEYS (1984).

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Species belonging to the Radiolitidae and Caprinidae represent the main frame producing elements of the rudist bank (Rabad-rudist member of MUSTAFA & BANDEL, 1992).

While species of the first represent coral-like elevators that grew singly or attached to each other in thickets, the caprinid species consist of recumbent individuals that are never attached to each other or to the substrate. Among actaeonellid shell debris in the shallow lagoon lived a requienid species that retained the ancient constructional morphology of earlier ancestors of the rudists. Within the same environment hipporitids formed thickets attached to beachrock formed at lagoonal shores and to cemented shoal debris.

An attempt to reconstruct the soft-part anatomy of the rudists from the Ajlun area is made since they provide an oportunity to analyse individuals preserved as fossils in an unusual way. Here growth geometry as well as growth ecology and shell-soft part relation can be analysed and reconstructed. Members of four rudists families, the Requieniidae, Caprinidae, Radiolitidae and Hippuritidae are present with 5 species preserved quite well. Among these only the individuals of the genus *Apricardia* are small with shell size below 2,5 cm while the others are large growing to 20 cm and more. According to SKELTON (1991) representatives of the rudists can be grouped into the elevators in which the entire growth margin of the attached valve was deployed in upward growth, like *Sauvagesia* and *Hippurites,* clingers where parts of the growth margin of the attached valve overgrew the substrate, like *Apricardia,* and recumbents that were unattached with valve margins lying flush against the substratum, like *Caprinula.*

1. A traditional rudist of the megalodont type.

Family Requieniidae DOUVILLÉ, 1919 (? 1914)

In lagoonal limestones about 15 m above the Rabad-rudist bank a species of the Requieniidae is found together with a slender rudist and a thick walled *Durania* type rudist, both of which are not described here. The requienid represents a spirogyrally coiled encruster with characters defined by DECHASEAUX & COOGAN (1969, p. N 779).

Genus *Apricardia* GUÉRANGER 1853

The genotype is *Apricardia carinata* GUÉRANGER, 1853 figured by DOUVILLÉ (1886 Pl.28, Fig. 3.) that looks very similar to the Jordanian specimen.

Species *Apricardia* sp.

Only two specimen were found among shell debris forming a bank in the lagoonal limestone in the small quarry on the hill ridge Zuan between castle Rabad and Istafena. *Hippurites requieni* that is well known from many Turonian limestones around the Mediterranean Sea dates these lagoonal limestones.

The coiled valves of *Apricardia* differ from each other in size and shape. The attached left valve is the larger one (maximum diameter about 3 cm) and forms a coil of about half a whorl. The right, free valve forms less than half a whorl and is flatter than the left valve (2 cm maximum diameter). The hinge resembles that of *Diceras.* A single tooth along with a tooth-like thickening behind the posterior socket is present in the left valve and the right valve has two teeth. The hinge plate is massive and projects from the valve margin. The insertion of the posterior muscle lies on a plate that passes below the cardinal platform.

Remarks: BLANKENHORN (1890) described *Diceras noetlingi* from the rudist limestone of Abeih where it occurs together with *Sphaerulites sauvagesi* = *Radiolites syriacus*. *D. noetlingi* is characterized as similar to *Chama* in shape and attached by the larger left valve. According to BLANKENHORN's (1890) description the umbo of both valves points in anterior direction, and valve surface is smooth. The ligamental groove is bordered by a tooth-like ridge. The left valve carries one solid tooth with longitudinal grooves on its hinge as well as a wide groove into which the broad tooth of the lower right valve is fitted. The posterior muscle scar rests on a ridge that is oriented toward the umbo below the hinge. The widest shell measures more than 2 cm in largest diameter. BLANKENHORN (1890) presented no illustration but his description fits to the individuals from Ajlun. In a later publication BLANKENHORN (1934, Pl. 11, Fig. 88a,b) illustrated a *Diceras noetlingi* which demonstrates that the posterior myophore does not extend below the umbo and thus differs from our species.

Diceras had a long and external ligament (SKELTON, 1979, fig. 5A). It migrated posteriorly with growth, so that its anterior end was split and overgrown by shelly material (YONGE, 1967). Reconstruction of the anatomy of early rudists like requienids indicates that the ventral margins of their gills lay close to the ventral parts of the commissure, as in oysters (SKELTON, 1978). According to SKELTON this implies adaptation for a broad inhalent zone and limited fusion of the mantle margins.

Requieniids represent Cretaceous species of an evolutionary lineage that is connected and very similar to species of the Diceratidae of the Upper Jurassic. Both posessed a modified external ligament, an exaggerated backward tangential growth resulting in overgrowth of the old ligament and thus invagination of the ligament. In other rudists such ligament invagination allowed them to grow with uncoiled tubular shell. The Jordanian *Apricardia* lived on a carbonate substrate in a shallow lagoonal environment. Rather similar living conditions within warm carbonate lagoons were also present in the habitat of many members of the megalodontid branch of bivalves. Like Diceratidae and Requieniidae, *Megalodon* and *Cornucardia* grew up in the shallow lagoons near to the reef edge to the open ocean in the Upper Triassic Tethyan environment of the southern Alps (ZARDINI, 1981).

2. Reconstruction of the large reclining *Caprinula*.

Family Caprinidae D'ORBIGNY, 1850

Description: The valves may be straight, horn shaped or coiled. They are of about the same size, or the right valve is the larger one. The ligament is invaginated and forms an internal infold. The right valve may be attached and has one hinge tooth while the left one is always free and has two teeth. The outer shell layer is thin and of largely calcitic structure while the inner layer is thick and of argonitic composition. It usually bears many tubules (pallial canals). In many cases the valve interior is split into a principal cavity and pallial canals along with accessory cavities that accompany the tooth sockets which are present in one or in both valves. All cavities may be tabulate. Individual cavities and tubes have been closed by shell material and septa in different levels (DECHASEAUX & COOGAN; 1969; CHUBB; 1971, SKELTON; 1991). The subfamilies Caprininae D'ORBIGNY, 1850 and Plagioptychinae DOUVILLÉ, 1910 are differentiated. The later hold genera like *Mirocaprina* and *Plagioptycha* and have a horn-shaped opercular left valve with shell tubes while the short conical attached valve has no tubes.

Subfamily Caprininae D'ORBIGNY, 1850
Genus *Caprinula* D'ORBIGNY, 1847

Description: Accessory cavities may be present in both valves and pallial canals fall into smaller outer polygonal and innner larger pyriform series. The diameter of the canals decreases from interior of the valves outward. A single tooth of quadrilateral cross section is present in the right valve, and two teeth are found in the left valve, of which the anterior is the larger. The genotype is *Caprina boissyi* D'ORBIGNY, 1850 from the Corbières in southern France.

Species *Caprinula boissyi* D'ORBIGNY, 1847
Plate 1, Figures 1–4; Plate 2, Figures 1–4; Plate 3, Figures 1–6

Description: Both cylindro-conical valves reach a depth of 25 cm and marginal width of 8 cm. The dorsal side of the valves can be recognized by the ligament groove visible on the outside and the hinge on the inside. Valves are of about equal size but of variable shape. Horn shaped valves with about one or a bit more than one whorl are planispirally, others dextral- or sinistral-helically coiled. The spiral twist may go in one shell into the same direction or, in another individual, into opposite directions. Some have one straight valve and the other coiled, and rarely both valves are straight or almost straight. Valve section is circular with somewhat flattened ligamental side.

The exterior ligament groove and low longitudinal ribs which increase in width relative to the growing valve sculpture the outer shell surface. This shell surface is preserved as print on the sediment cast. The originally predominantly calcareous layer has commonly been bored by sponges that used the shell as substrate. The following layer is also thin, smooth and has fine growth lines. This second mineral layer has been of calcitic composition. In the originally aragonitic third layer tubes of various sizes and shapes are present, which became filled with fine sediment during deposition. The tubes lie within a solid and continuous originally aragonitic mineral layer that has totally disappeared during diagenesis. The outermost tubes form a continuous layer with tubes close to each other. They measure only 0.5–1 mm in width. (Pl. 2, Figs. 3, 4; Pl. 3, Figs. 1–3). In large individuals with 7 to 8 cm wide valves the outer tubes have been open for 1 to 2 cm of shell length and were closed further back by shell material. On the dorsal side of valves this layer is thin consisting of only one layer of fine tubes. On the ventral side the inner aragonitic layer may be considerably thicker, and several layers of tubes are found. Tube diameter usually increases further toward shell interior. Individuals differ strongly regarding size, dimension and number of layers of canals present in valves.

The inner shell cavity has a variety of shapes among individuals of this species. (Pl. 1, Figs. 1–2; Pl. 3, Figs. 1–4). Most of the valves interior remains open up to the umbonal area. At a valve of 20 cm length only the 2.5 cm long final umbonal portion has been closed by shell material. A 15 cm long and 6 cm wide valve has a continuous cavity that is 14 cm long with only the last one cm of shell interior filled by shell material. In young individuals the end of the cavity of the valve is usually pointed and may in its morphology reflect the regular gyroconical shape of the umbo. (Pl. 1, Figs. 3–4). During subsequent growth a pointed shape may be retained in some individuals while in others a large variety of shapes can be found. The valve cavity may have broad and sack-like shape but may also be subdivided by vertical septa into a smaller or larger number of accessory cavities. Often the larger ones of these accessory cavities fuse with the main cavity or they may join each other somewhere in the interior of the valve.

Here dividing walls (vertical septa) end before reaching the valve's margin. Most accessory cavities are continuous though to the valve's margin. Still a continuous gradation from body cavity to accessory cavities and pallial canals is found in the valves of this rudist.

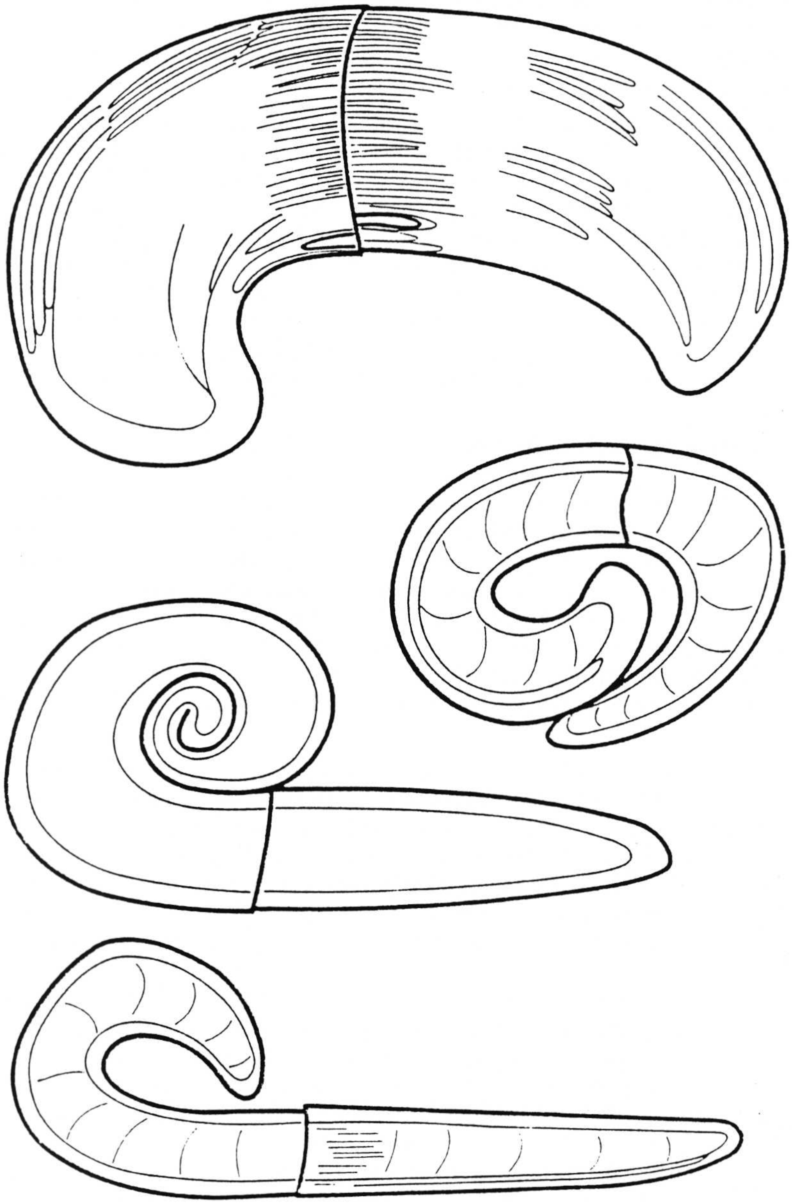
Narrow canals have in general been closed by shell material after a shorter distance than wider canals. Only the open canals became filled with sediment after death of the bivalve and have thus become preserved during the special diagenesis that dissolved most of the original shell, but preserved the sediment filling in all its holes, even the very fine ones. The fossil caprinid in different portions of its shell therefore has a different appearence when viewed in transversal sections. The shell in those parts of valves where accessory canals and narrow tubes have been filled by mantle secretions consisted of solid calcareous material as is documented by bore holes within them. This massive substrate was utilized by sponges and other boring organisms to excavate their tunnels and caverns.

The tooth of the right valve lies anterior to the ligamental groove and is of rounded conical shape. It may measure up to 1.5 cm in length. The individual two teeth of the left valve differ in size. The posterior one lies just behind the ligament groove, and its shape and size is similar to that of the tooth of the right valve. The other tooth of the left valve is broader and of wider diameter and shows a grooved surface. In fully grown individuals it extends into the socket of the right valve for some centimeters. (Pl. 1, Figs. 1–2; Pl. 2, Figs. 1–2; Pl. 3, Figs. 4-6). The grooved anterior tooth of the right valve is the longest that projects deeply into the grooved socket. Teeth were hollow and open toward the valves interior. They have thus after death of the bivalve been filled with sediment.

Remarks: *Caprinula* sections illustrated by DOUVILLÉ (1886, Fig. 10 and 11) are very similar to what may be seen in *C. boissy*. But DOUVILLÉ (1886) interpreted the right valve to be fixed to the substratum while only the left is free. In the Jordanian species both valves were free. According to DECHASEAUX (1943) *Caprinula cedrorum* (BLANKENHORN 1890) from the Cenomanian of the Lebanon was of somewhat more simple construction than is found in *Caprinula boissy* from the Ajlun. But the Lebanese specimen could have represented a juvenile individual of *Caprinula boissy* and thus *C. cedrorum* could be conspecific to the species from Ajlun. Shell morphology externally and internally is quite varible in *Caprinula boissy*. Perhaps *Schiosia linguis* of BÖHM (1927) characterized as inequivalve could represent *C.* sp. with one valve actually not smaller but twisted off in an unexpected way. *Schiosia nicolinae* MAINELLI, 1983 and *S. paolae* MAINELLI, 1983 from the Middle Cretaceous of Italy exhibit a similar pattern of canals as is found in *Caprinula boissyi,* but contrasts to the later by being attached and having tabulae in the attached valve. These Italian species with similar shell structure thus had a different mode of life compared to the recumbent Jordanian species.

Caprinula Strategy

Hinge: The ligament lies at the end of the infolded outer shell layer between the teeth of the hinge. It consists of a massive elastic ribbon that pushes both valves to a narrow gape when the musculature relaxes. The hollow teeth fit into large grooves. Two teeth extend into the right valve, and one tooth projects into the left valve. Teeth fit tightly into their sockets allowing only little movement of the valves against each other and thus enabling only a minute gape of the margins of the valves.



Text figure 1: Different growth forms of *Caprinula boissyi*.

Shell musculature: Two muscle bundles marginal of the hinge attach both valves to each other and are fixed to shell septa.

Shell: Valves are similar to each other in size and shell construction. The translucent outer layer has a longitudinally striated surface and a thin inner solid calcitic layer. The thick, inner, aragonitic shell layer is pierced by tubes which open on the wide shell edge of the aperture. Outer, narrower tubes are open for only a short distance and have been closed by septa and solid aragonitic shell further down in the valve. Tubes lying further inward reach deeper down, and the large tubes near the inner shell wall remain open to almost the umbonal end of the valves throughout life of a large individual that grows up to about 40 cm length.

Mantle edge: Numerous tentacle-like protrusions of the mantle edge are placed into the inner aragonitic layer of the shell. This mantle contains symbiontic algae in its tissue which is illuminated through the thin outer shell layer when the sun shines. A further function of these tentacles of the mantle, that reaches back to almost the umbo, consists in keeping off boring organisms and preventing them from penetrating deeply into the shell. Borers infest only the solid outer layers and the filled umbonal valve portions as long as the bivalve is alife.

Mantle cavity: Ingestion and egestion of water into the pallial cavity is carried out opposite to the hinge along the narrow gape of the valves.

Morphology of the soft body: The large soft body is compartimented regarding the mantle edge as well as the visceral mass. Septa are quite individually formed and differ in valves of the same individual as well as between different individuals having about the same size. Thus mantle surface is increased and a large number of symbiontic algae can dwell here.

Ecology: Shallow, clear, warm, well illuminated sea water in a current swept area just below and within the lower portion of the tidal area.

General remarks to the ecology and evolution of the Caprinidae:

Development of abundant pallial canals in caprinids produced a thick spongy porous shell. According to DOUVILLÉ (1886), PERKINS (1969) and SKELTON (1978) this layer may have been rapidly deposited and contained a minimum amount of calcium carbonate for its strength. The main shell cavity was interpreted as to have contained the visceropedal mass and gills while the accessory cavities where thought to contain only a lining of mantle tissue (PERKINS 1969). Besides economical thickening of the valve walls as the principle function of the canals, SKELTON (1991) suggested an additional biomechanical effect that could have been increasingly resistant to bending stresses.

The evolution from Albian to Cenomanian *Caprinula* to Maastrichtian *Antillocaprina* and *Titanosarcolites* includs the tendency to increase the number of canals and the number of accessory cavities in the valve interior. This tendency is also noted to occur during the ontogeny of the shell of *Caprinula* sp. While canals in young individuals are simple, in older specimens of *Caprinula* they are rather complex. *Antillocaprina* TRECHMANN, 1924 and *Titanosarcolites* TRECHMANN, 1924 differ from *Caprinula* by tubular structures that have invaded the myophores and hinge teeth and by the absence of an external ligament groove (CHUBB, 1971). In the large *Titanosarcolites* canals fill most of the valve interior (CHUBB; 1971). *Titanosacrolites giganteus* with up to 2 m in shell length and 30 cm in shell width represents the extreme of this development.

From the view of functional morphology *Titanosarculites* represents the exteme specialist in the caprinid evolution, by having evolved a body that consisted largely of more or less slender and more or less delicate tentacles of the mantle stuck into the thick large shell, while the actual visceral mass is small and slender taking the medium part of the large shell. Not only most of the thick inner aragonitic shell layer consists of tubes that open at the shell margin, but also the hinge teeth are riddled with them.

The evolutionary derivation of the pallial canals from the accessory cavities separating the myophores from the valve walls has been demonstrated by PAQUIER (1905). DOUVILLÉ (1886), MACGILLAVRY (1937) and PERKINS (1969) thought that pallial canals characterize the genera and groupings within the Caprinidae. In transverse section early caprinid genera have simple undivided or bifurcating radial plates that make a pattern of marginal pyriform canals. Later several rows of marginal canals appear in the periphery of the shell. Approximately quadrangular canals are considered characteristic for *Amphitricoelus* (HARRIS & HOBSON, 1922), regularly oval or pyriform canals are represented in *Coalcomana* and *Caprinula,* and irregular polygonal ones are found in *Coralliochama.* Longitudinal canals are thus derived from caprotinid type accessory cavities as found in *Pachytraga* PAQUIER, 1900. CHUBB (1971) noted that in advanced forms the whole circuit of the shell consists of fine tubes. MACGILLAVRY (1937) had suggested that *Titanosarcolites* has been derived via *Antillocaprina* from some genera like *Caprinula.*

The generic diagnosis of *Caprinuloidea* PALMER, 1928 as phrased by CHUBB (1971) can also be applied to *Caprinula boissyi.* Differences between *Caprinuloidea* from the Western Hemisphere to *Caprinula* in the Eastern Hemisphere are difficult to find. Sections of *Caprinula* also closely resemble sections of *Sphaerocaprina seafieldensis* as illustrated by CHUBB (1971) who considered *Sphaerocaprina* closely related to the American *Coalcomana* as well as to European *Schiosia,* differing from both only by details of canal shape and size of the body cavity. SKELTON (1991) in contrast considered the bean-shaped outline of the posterior accessory cavity plus socket in the right valve in *Coalcomana* to represent a synapomorphy for the Coalcomaninae COOGAN, 1973 suggesting independant lineages in New- and Old-World caprinids. According to his ideas *Amphitricoelus* would be a good model for an ancestor of the New-World genera while Old World *Caprinula* and *Schiosia* are considered to be an evolutionary endpoint coming from *Caprina*-like ancestors.

3. Radiolitidae GRAY 1848

Description: The attached (right) valve of the Radiolitidae is of conical shape, while the free (left) valve is operculiform. In its outer surface the attached valve bears two shallow longitudinal grooves (siphonal band) that lie opposite to the hinge. These grooves are differently ornamented from the rest of the shell. The texture of the thick outer wall of the attached valve is cellular with prismatic, calcitic walls, while the thin inner wall is massive and of aragonitic structure (SKELTON 1974, 1979). The hinge bears one tooth and two sockets in the conical valve and there are two teeth of the free valve. A ligamental ridge is present (Radiolitinae, Sauvagesiinae DOUVILLÉ, 1908) or absent (Biradiolininae DOUVILLÉ, 1902, and Lapeirousiinae KÜHN, 1932). It is accompanied by accessory cavities in small or large numbers within the inner shell layer. Muscles are attached to the wall of accessory cavities in the conical valve and to myophores in the operculiform valve. Descriptions are based largely on data presented by DOUVILLÉ (1910), CHUBB (1971), DECHASEAUX & COOGAN (1969), and SKELTON (1979).

Subfamily Sauvagesiinae DOUVILLÉ, 1908

The radiolitinid shell consists of a conical, vase-like, attached right valve capped by an operculiform free left valve. The four subfamilies differ from each other by the arrangement of the cellular calcitic structure of outer wall, which is prismatic in longitudinal section in the Sauvagesiinae. (TOUCAS, 1907).

Genus *Sauvagesia* CHOFFAT, 1886

Description: The conical shell has two broad concave bands opposite to the hinge. The flat opercular valve has a thick median portion that is smaller than the aperture of the attached valve, and has about the dimension of its central opening. The outer surface of the conical shell is ornamented by rounded radial ribs and growth rugae. The outer shell layer consists of fibrillar prismatic calcite, which is cellular in the right valve and solid in the left valve. Accessory cavities accompany the tooth sockets in the aragonitic inner layer of the conical valve. A similar description has been presented among others by DOUVILLÉ (1910), CHUBB (1971), DECHASEAUX & COOGAN (1969) and (SKELTON 1974, 1979).

Sauvagesia sp.

Plate 4, Figures 1-4: Plate 5, Figures 1-5

The operculiform free valve has a flat upper surface and is of round outline. At individuals the conical attached valve is up to 35 cm long and up to 9 cm wide. Individuals commonly join to each other to form bush-like structures. (Pl. 5, Fig. 2). In such autochthonous interlocking growths the free valves of all members are usually still found in place. The grooved teeth of the operculiform valve fitting into the tight sockets of the conical valve as well as the thick internal ligament connecting both valves to each other had successfully prevented the dislodgment of the valves of most individuals even after death.

The free valve is fitted into the slightly concave aperture of the conical valve. Its two teeth slide into two sockets of the attached valve which are open deep down into the shell. Long teeth are inclined into outward direction and are ridged (Pl. 4, Figs. 3–4; Pl. 5, Figs. 3–4). The anterior is the larger one. Teeth become erect and parallel to shell axis of the conical valve when the free valve opens to a narrow gape. Tooth sockets remain open to almost the tip of the valve throughout life and are accompanied by two further (accessory) canals (maximum length 10 cm) which have probably served as attachment grooves to the retractor muscles. The anterior tooth socket lies next to the accessory canal and is a bit smaller than the posterior tooth socket that lies just anterior of the ligament.

Muscle scars on the free valve are longitudinally wrinkled. The posterior one is the bigger and rests on a special plate while the anterior muscle scar is smaller and depressed into the surface. A short tooth extends from the attached valve into the free valve. The posterior tooth of the free valve fits into a socket in the attached valve next to the widened groove holding the interior ligament. Its elastic material connects both valves tightly to each other. The ligament contained in a groove on the shell interior forming a widened tube that extends running from the umbo to the margin and hinge and across it to the free valve (Pl. 4, Figs. 2–4; Pl. 5, Figs. 1–3). It is surrounded by shell. After death the ligament decomposes after burial in the sediment. Thus the room occupied by the organic ligament opens after sediment had filled the other cavities of the shell.

Sculpture of the conical valve consists of numerous longitudinal ribs, crossed by more or less strongly incised growth increments. (Pl. 5, Fig. 2). Two shallow longitudinal grooves feature the outer shell opposite to the hinge. The narrower groove is the posterior one and the wider is the anterior one. The outer shell is composed of a rectangular network of calcitic sheets in concentric arrangement, crossed by radial ones and plates following the inclined upper surface of the margin of the valve. The cells formed by the calcitic material measure about 0.5 mm in diameter and wall thickness may be up to 2 cm. Cells were originally filled with aragonitic shell material that became dissolved during later diagenesis while the calcitic portions were preserved. Crowded individuals have thinner walls as is the case when they have grown all by themselves. The outer cellular shell layer of neighbouring individuals may fuse to each other.

The interior of the attached valve is large and almost as long as the valve is high. Valve space is thus not reduced by septa but extends to almost the narrow umbonal end of the valve. Its inner surface consists of the originally aragonitic shell layer with growth increments.

The inner surface of the operculiform valve is concave outside of the projecting myophoral plates and hinge teeth (Pl. 4, Figs. 2–4; Pl. 5, Fig. 5). Its plane outer surface bears concentric growth lines and is of greatest width in anterior-posterior direction. The portion of this valve that extends onto the broad margin of the attached valve remained elastic. In many individuals where the opercular valve was pressed down during burial, the outer rim was bend during this process, and a groove formed where the margin to the calcified central region begins (Pl. 4, Fig. 1). The inner portion of the free valve is preserved as hollow space and was not filled by sediment. It represents the originally aragonitic inner shell layer that became dissolved during diagenesis when the carbonate particles surrounding the rudist had already been cemented.

Sauvagesia, short form

Plate 4, Figures 5, 6

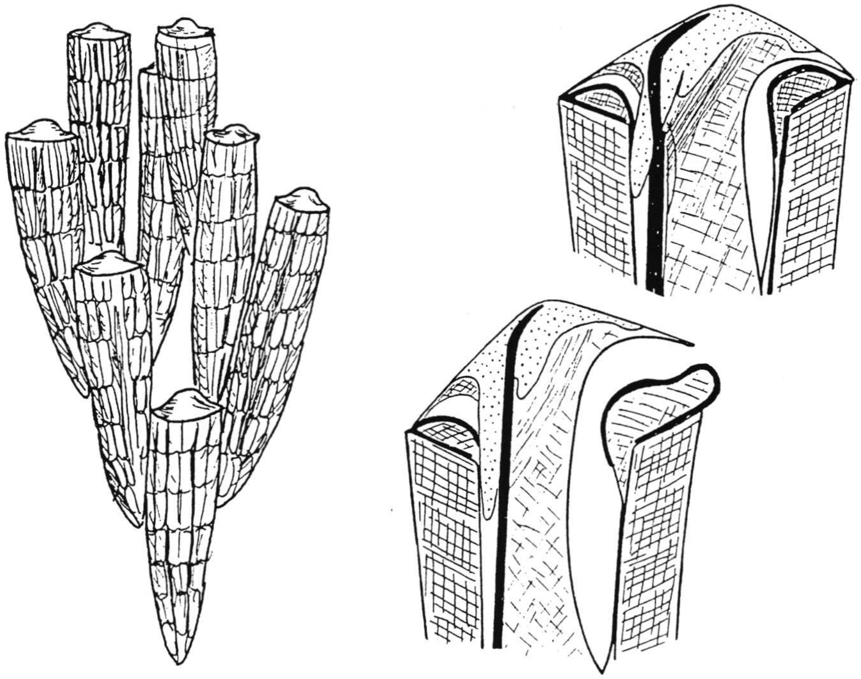
Description: The attached valve is about as wide as high. Its early portion is usually of gyroconical shape. Shell thickness increases rapidly after the valve has grown from 1 to 3 cm size. Growth increments form step-like interruption on the outer surface. *Sauvagesia* sp. resembles in all essential characters this smaller species of *Sauvagesia,* but differs in dimension and growth habits. It formed no clusters of several individuals attached to each other but only bundles of two to several individuals next to each other. In such bundles individuals grow in close connection and their outer walls may be fused.

Remarks to the taxonomy

Members of the family Radiolitidae arose in the Albian, and became extinct at the close of the Maastrichtian. The taxonomy of the radiolitids have been revised by DECHASEAUX & COOGAN (1969). According to CHUBB (1971) the attached valve of all advanced species has lost its single tooth, and the ligament is preserved only in more primitive species of the family. *Sauvagesia* sp. from Jordan represents such primitive radiolitid. Functional morphology was studied by YONGE (1967), VOGEL (1970, 1975), KAUFFMAN & SOHL (1974), SKELTON (1974, 1978, 1979) and the paleoecology was treated by PHILIPP (1972). This species from Istafena is part of *Eoradiolites syriacus* (CONRAD, 1852) described by BLANKENHORN, (1934).

Sauvagesia strategy

Hinge: The ligament is folded in and lies on the inner side of the calcitic shell layer of the conical valve. Here it is situated next to the sockets of the teeth. In the free valve it lies between the teeth and myophores. The ligament consists of a solid, thick, elastic ribbon which causes gaping of the two valves of the shell. Two large teeth of the opercular valve fit into slightly larger grooves of the conical valve that continue below the end of the teeth. When muscles are relaxed the ligamental tension inclines the opercular valve resulting in a gape. The long teeth in their narrow sockets allow only a narrow gape of the valves and inhibit rotation of the upper valve.



Text figure 2: Sketch of the growth form of *Sauvagesia* and opening of the operculiform valve.

Shell musculature: Two strong muscle bundles are broadly attached to inclined lateral projections (myophores) of the inner side of the opercular valve. When muscle fibres contract the opercular valve it is pulled onto the conical valve. Muscles were quite long and attached to the conical valve in extra tubes that lie in the aragonitic shell layer next to the teeth sockets.

Shell: The conical valve has a thick shell with an outer cellular layer that also covers the ligament. The cells are formed by calcitic prismatic crystallites, while their interior is filled with microprismatic aragonitic crystallites or chalky layer. The opercular shell is massively mineralized with aragonitic shell in its central part above the concavity of the conical valve and thin, calcitic outer layer. This outer layer continues to the portion above the broad rim of the attached valve. Here it is not underlain by additional deposits, and is elastic and flexible.

Mantle edge: The mantle edge is fixed to the shell edge and usually not retracted when the valves close. The elastic rim of the opercular valve is transparent. It can seal the valves even when the mantle is not contracted from the apertural edge. The complex shell structure of the outer shell layer of the conical valve can thus be deposited more easily. It consists of a regular network of calcite and aragonite or calcite of chalky composition deposited in the spaces between the calcitic sheets. Both structural modification of calcium-carbonate grow simultaneously within the extrapallial mucus produced by the margin of the mantle in contact to the broad edge of the conical valve. Symbiontic algae are cultured in the mantle margin. At the radial bands of the shell egestive and ingestive openings and mantle flaps channel water in and out the large mantle cavity.

Mantle cavity: The large gills produce a water stream that runs from the ingestive opening across their filaments to the egestive opening opposite to the hinge and next to the ingestive opening. Even a narrow shell gape together with the two embayments on the flanks of the attached valve enable the exchange of water for respiratory purposes through siphons.

Morphology of the soft body: The visceral mass is large and elongate filling much of the shell interior. The mantle edge is thick and well supplied with blood through a vascular system that imprints itself onto the shell surface.

Ecology: Shallow, clear, warm, illuminated water within and just below the tidal realm.

Remarks regarding functional morphology:

The active ligament was invaginated and not exposed to the outside since the outer layer fused above it. SKELTON (1979) calculated the effective length of the ligament with the valves fully closed as the vertical distance between the top of the right valve and the site of direct contact on the left valve. In a 5 cm long shell of *Radiolites angeoides* (DE LAPEIROUSE) from the Campanian SKELTON measured a little more than 1 mm as ligament length. This short ligament continued into both valves, as is documented by the cavity remainig after its disintegration after burial in the sediment in *Sauvagesia* from the Ajlun.

DOUVILLÉ (1886) interpreted the pair of radial bands on the posterior flanks of radiolitid shells as markings of the inhalent (ventral band) and exhalent (dorsal band) siphons, as is also assumed as correct in this study. This reconstruction was also accepted by YONGE (1967) who compared it with modern *Chama* where the inner mantle folds are fused. SKELTON (1979), in contrast, considered the restricted gaping of the valves of rudists as well as the general absence of mantle fusion in epifaunal bivalves (with exception of *Chama)* as indication for the absence of siphons. This author proposed a function for the short commissural zones marked by the radial bands on radiolitids as traces of two independent exits for pseudofaecal and faecal ejection. According to SKELTON, *Radiolites* and *Sauvagesia* would thus have siphons differing from those of all extant bivalves.

4. Reconstruction of *Hippurites*

Family Hippuritidae GRAY, 1848

Description: The sessile, epifaunal, species of the relation of *Hippurites* lived in shallow warm water of the Tethyan Ocean from Turonian to Maastrichtian time. Hippuritid rudists cemented themselves to the substrate by the umbonal apices of their conical right valves and lived as elevators. Each valve consists of a calcitic outer layer and an aragonitic inner layer. The larger cylindrical valve has two radial infoldings of the outer walls called pillars and an additional one, which supports the more or less reduced ligament. Internally the general cavity of the attached valve is small because of the development of many tabulae, which fill most of the valve's interior. This filling may consist of a series of voids or it may be of solid shell material. A radial canal and pore system in the outer shell layer characterizes the free left valve. The teeth and myophores of the left valve project into the right valve and are received in sockets lying on either side of the ligamentary infolding on the outer layer of the right valve. In the free valve the two principal infolds form apertures or oscules corresponding in position with the two principle pillars (DOUVILLÉ 1897, DECHASEAUX & COOGAN 1969, KENNEDY & TAYLOR 1968, CHUBB 1971).

Subfamily Hippuritinae

According to CHUBB (1971) the subfamily contains hippuritids with not more than three infolds, of which the ligamental may be small. The free, left valve is penetrated by a great number of thin walled, branching canals which radiate from its outer centre.

Genus *Hippurites* LAMARCK, 1801

Description: The hippuritid with conical right valve has an operculiform, nearly flat, left valve with two oscules. The flat valve is covered by a spongy layer and simple, linear, well separated pores.

Species *Hippurites requieni* MATHERON, 1842

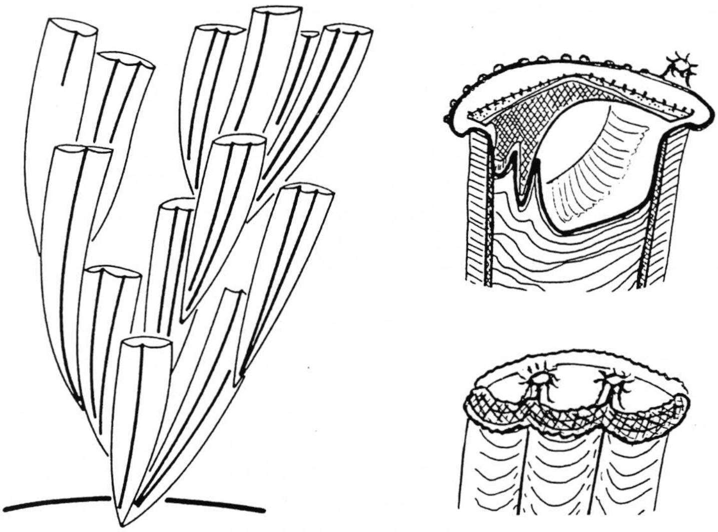
Plate 6, Figures 1-3; Plate 7, Figures 1-6

Attached valves (right valves) are up to 15 cm long and 2.5 cm wide and of slender conical shape. Their exterior is radially ribbed, and three deeply indented folds of its interior are reflected in three grooves on its exterior. The outer surface bears fine and coarse, concentric growth rugae. Some individuals have many strong interruptions, where growth had been stunted, other individuals have not such interruptions. Tabulae that seal earlier valve portions lie more or less close to each other. Usually they leave one or several mm wide open space between them. The attached valve is indented and its outer layer of calcite covers an inner layer of aragonite. In well preserved individuals both layers have been transformed into quartz during diagenesis. The two posterior folds are rounded (pillars), while the ligamental fold ends sharply. The later is based on a raised platform into which the two tooth sockets and the two muscle scars are depressed. The rounded lamellae, in contrast, reach down to the base of the body cavity. The valve interior is as deep or deeper than wide while all older portions of the attached valve are closed off by saucer-like tabulae.

The interior of the attached valve is of quite variable shape. (Pl. 7, Figs. 1–4). Sockets of the two teeth as well as grooves of the muscle scars are excavated from the raised portion of the body cavity that lies below the ligamental fold. Each specimen has its individual arrangement of ridges between sockets and grooves and shape of base of the valve interior. Sockets as well as the muscle scars differ in depth, and the ridge between sockets may be absent or, in contrary, extend into a tooth like structure. The body cavity is always rounded and smooth from valve margins to its base.

The left valve forms a small opercular cap to the right valve. The outer layer incorporates a radial canal system as noted by DOUVILLÉ (1897). Two slit-like holes are present above the pillars and a short additional one above the ligamental infold. (Pl. 7, Figs. 5, 6). The teeth of the posterior adductor myophore project sharply down into the respective sockets with close fit. The two teeth of the hinge lie next to the ligament groove. The outer surface of the free valve is covered by radial ribs representing the base of the canals. The spongy layer above and marginal to the canals has usually not been preserved in the silizified individuals of the species from Ajlun.

In the quarry behind the forest station at Istafena, the corroded surface of a former beach rock has been settled by *Hippurites*. Individuals occur gregareously and are rarely solitary. (Pl. 6, Figs. 1, 3). Usually up to 6 levels of individuals attached to each other form clusters of mound-like or hemispherical shape that are up to 50 cm high. These autochthonous bushes consist of a few basal individuals attached to the beach rock surface while the other individuals are anchored by their umbonal apex. The colony thus has the shape of a branching cactus. One to three individuals are attached to the one below. In a thicket individual animals are commonly 10 to 15 cm long and 2.3 to 2.5 cm wide at their valve margins. Within a bush-like colony or cluster the individuals continued to grow until fully grown, and all individuals may have been alife at the same time and may also have died more or less at the same time. But certainly the lower individuals must have had a longer life. Here the opercular valve is usually lost but may be found still in place on single individuals that have brocken off and have rapidly been covered by debris. (Pl. 6, Fig. 2). Often the whole interconnected structure has been dislodged and fallen to the side or even turned on their top without disintegrating. The reason for free valves loosing contact to the attached valves may be due to the presence of only a thin ligament that was rapidly destroyed after death of the bivalve. Teeth of the free valve interlock tightly into their sockets of the attached valve when the shell is closed but do not reach down deeply as is the case in *Sauvagesia* and *Caprinula*. When the ligament is gone, the free valves are thus easily detached from the conical valve.



Text figure 3: Sketch of the growth form of *Hippurites requieni* and reconstruction of operculiform valve with mantle edge and gill.

Functional morpholgy of *Hippurites requieni*:

Hinge: The ligament is very thin and in a position within a fold between the tooth sockets that projects into the conical valve. It connects both valves to each other like a rubber band. It is not able to push both valves into gaping position. Two large and wide teeth and a tooth-like muscle attachment ramp of the opercular valve fit into wide grooves in the conical valve. Their arrangement varies considerably among individuals. Grooves in the attached valve are excavated from the internal space of the bivalves interior, so that the opercular valve can be lifted in total from the conical valve.

Shell musculature: Two strong bundles of retractor muscles are quite short. Their attachment to the opercular valve lies on a ramp in one case and in a depression in the other case. When contracted muscle fibres pull the opercular valve into the top of the conical valve. They interlock firmly and connect tightly to each other. The shell opens when muscles are released and mantle tissue expands due to body liquid pumped into it. Since muscles are of different length the opercular valve is rotated a bit as soon as the teeth have been pulled out of their short sockets. Siphons unfold and expand through the gape formed between pillars of the conical valve and slits in the opercular valve.

Shell: The conical valve is moderately thick with a dominant, calcitic, outer layer and a thinner, aragonitic, inner layer. The opercular valve is of similar construction but, in addition, consists of a porous outer layer added to the shell secundarily from the outside. Canals increase in length and width in accordance with the enlargement of the shell and they continue into grooves on the lower margin of the opercular valve. Here the tentacles of the canals are fused to the mantle. The tentacular mantle margin excretes a calcareous porous mesh that covers and protects the whole opercular valve and forms a free margin on its rim.

Mantle cavity: Gills on the visceral mass lie on both sides and keep incoming and outgoing currents in motion. Water flows through the openings formed by the infoldings of the opercular valve and the pillars of the conical valve when retractor muscles are relaxed. Thus respiration as well as food filtration is possible when the opercular valve is raised. When it is pulled down and slightly rotated the shell becomes closely sealed to the outside.

Mantle edge: The margin of the mantle extends around the shell edge of the opercular valve during activity of the animal and covers this valve with its tentacles. When the shell is closed at low tide the siphons are pulled in and muscle contraction rotates the opercular valve back to a perfect fit of the indentations onto the pillars of the conical valve. Due to the crenulation of the inner margin of the opercular valve mantle tentacles can be left on the outer surface of this valve. The mantle is here protected by a mesh of calcitic shell deposits. Mantle tentacles reshape, and repair the canal system and the protective calcareous net above and beside the opercular valve throughout life. The mantle tissue holds symbiontic algae that are exposed to the sun within its tentaculate and papillate surface.

Shape of the soft body: The visceral mass is small and the conical valve grows in length by a continuous series of internal tabulae raising the body of the small animal in its fast growing shell.

Ecology: Shallow warm and well illuminated lagoonal sea water within and just below the intertidal area.

Remarks to the functional morphology

Chubb (1971) reconstructed the soft body with siphons as local modifications of the periphery of the mantle in both valves producing oscules in the left valve and pillars in the right. Yonge (1967) supposed that the inner mantle folds of the hippuritids were fused around most of the margin as is the case in *Chama*. Perkins (1969) noted that a ligament could hardly have been effective in opening the valves. Skelton (1976) calculated the length of the muscles to be only very small allowing a marginal gape of about 0.5 to 0.8 mm in an individual with 2 cm commissural diameter. According to the reconstructions of Antony (1924) and Dechaseaux & Coogan (1969) a direct up-and-down motion of the left valve is all that would have been allowed by the closely interlocking myocardial elements.

Chubb (1971) following Douvillé (1880) in this matter suggested that the opercular valve was vertically uplifted when the hinge teeth were to be withdrawn from their sockets. Formation of oscules in the free valve in turn necessitate the development of pillars in the attached valve to close the oscules when the opercular valve is pulled down onto the conical valve. *Lapeirousia* and *Barrettia* with osculi far up on the opercular valve had to construct longer infoldings.

The complex canal and pore system of the opercular left valve have been interpreted by KLINGHARDT (1930), ZAPFE (1937), MILOVANOVIC (1957) and VOGEL (1960, 1970) as holding tentacles of the mantle margin. It was assumed that water ran through the porous upper layer of the upper valve. KAUFFMAN & SOHL (1974) and SKELTON (1976) found that the pores were preserved and kept clear and free from epibionts throughout the animals' development. According to SKELTON (1976) growth increments occurred along the canal interiors. From this he concluded that invaginations of the mantle margin extended into the canals as was assumed by ZAPFE (1937) and MILOVANOVIC (1957).

SKELTON (1976) reconstructed the canals as hollow-centred linings of mantle tissue. In his model the pores should have functioned as passageways and the tips of the mantle invaginations were punctured. He assumed that cilia on the mantle linings of the radial canals found on the upper valve generated a water current which entered the canals via the external pores. In SKELTON's model food particles were trapped upon the expanded radially crenulate margin of the right mantle lobe and not by the gill, as is the usual case among bivalves. According to SKELTON's model currents were directed from the canals across the mantle-edge inward to be picked up by the ctenidia and/or palpes. Hippuritids thus would have been equipped with a double food collecting device compared with other bivalves which collect food only by the gills. Material rejected within the mantle cavity according to SKELTON's model was passed out as pseudofaeces via the ventral oscule, whilst faeces were ejected from the anus via the dorsal one. This bivalve thus should have two egestion siphons or egestive pathways as has also been suggested by SKELTON (1979) in the case of *Radiolites*.

At SKELTON's model hippuritids have moved the current and entrapment function from the ctenidia onto the mantle margin. Accordingly hippuritids were reconstructed as not opening and closing their valves when active. Rather, the left valve was fixedly held in place by the short and very broad adductor muscles, with a permanent tiny gape of a few tenth of a millimeter between the commarginal ridges. The large muscles thus are reconstructed as just holding the valves in place. SKELTON's model envisages a bivalve that does not only look strange but also functioned like no living bivalve. It had large muscles but not to pull, it reconstructed the mantle into a sieve-like canal system, it used the siphons only the expell faeces and water, and its gill did not function as main water pump but passed over this activity to the ciliated mantle of the opercular valve.

Summary

The evolution of the advanced hippuritoids represented in the three families Caprinidae, Radiolitidae and Hippuritidae is characterized by the enlargement of the mantle and its attachment to and in the shell. In the Caprotinidae transition to the Caprinidae is seen in genera like *Pachytraga* PAQUIER, 1900 from the Urgonian with only one or few accessory cavities next to the myophores. *Sellaea* DISTEPHANO, 1889 from the Albian has two conical valves, and in *Retha* COX, 1965 these have multiplied into a whole row of tunnels in the wall. At the same time the outer calcitic layer remains thin and the inner aragonitic layer develops into the receptor of mantle tentacles. *Caprinula* from the Old World and *Capri-*

nuloidea in the New World give rise to *Titanosarcolites* with extremely many tubes and canals that have also infested hinge teeth. Thus the mantle has increased in surface considerably within these developmental lineages ranging from the upper lower Cretaceous into the Maastrichtian.

Pachytraga like ancestors can also have given rise to the Radiolitidae but with a different tendency in development. Here the multiplication of accessory tubes in the inner layer played a minor role while the outer calcitic layer was modified. It became wide in the conical valve and reduced in thickness in the opercular valve. The two siphos exhalent and inhalent leave evidence of their existence in the form of sinuses across the comissure, below which there may be bands on the outside of the shell. Within the group the margin of the conical valve was strongly modified in the Lapeirousiinae so that the mantle here became very thick, and its vascular system is clearly imprinted onto its surface as is the case in *Durania* or *Vautrina*.

In the Hippuritidae the position of the siphons are reflected in infolds of the shell substance which penetrate the body cavity as pillars. Here mantle spread out on and within the opercular valve with the tentacles becoming quite independent from the closure of the upper valve. Within the species of *Barrettia* from the Maastrichtian of Jamaica and *Pironea* from the same time in Italy the conical valve was also penetrated by mantle tentacles, but in contrast to the radiolitids on the outer layer. The Barrettinae CHUBB, 1971 differ from ordinary hippuritids by having multiple infolds of the thin outer shell layer and within their folds rows of vertical tubes *(Barrettia)* or sheets like depressions *(Pironea)* that penetrate the shell margin. These have been protected by the rim network of the opercular valve and where thus below porous shell cover just as the tentacles of the central region of that valve. Thus surface for mantle tissue was enlarged in comparison to *Hippurites*. The indentations of the edge of the opercular valve present in Hippurites were moved toward the middle forming two shell pores in *Vaccinites* and *Torreites*.

The relative independance from a food supply outside of the symbiontic algae enabled the rudists to live close together in huge numbers spread out over large areas. D. SCHUMANN (pers. comm.) noted settlements composed of one or few species spread out over flat shallow seabottom of Maastrichtinan Oman from tenth of km width and length (up to 250 square kilometers). Requirements for rudists were warm, well illuminated, clear sea water of normal salinity, fairly similar to what modern reef building coral need. But one important difference explains the differences of distribution of corals and rudists. The latter did not feed on zooplanplankton. Here symbionts produced oxygen during their photosynthesis and thus currents bringing oxygen rich water were not so important. Shallow shelf areas could thus be populated. As soon as water is turbid due to increased plankton production or much suspended material, rudist lived only in the very shallow illuminated zones. Where water was very clear they exploited deeper bottoms as well, resembling in this regard modern bivalves with photosynthetic symbionts like *Tridacna*.

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Plate 1

All figures show *Caprinula boissyi* from Ajlun.

Fig. 1: In the 12 cm long steinkern of the inner cavity the two valves are fitted into each other by the teeth of the hinge.

Fig. 2: The same steinkern as in Fig. 1 seen from the side demonstrates the partitioning of the internal cavity.

Fig. 3: Steinkern of juvenile individual with both valves still in contact measures 7.5 cm across.

Fig. 4: A single valve of a juvenile shell measuring about 2 cm across has a less complex construction of shell wall tubes than later ontogenetic stages.

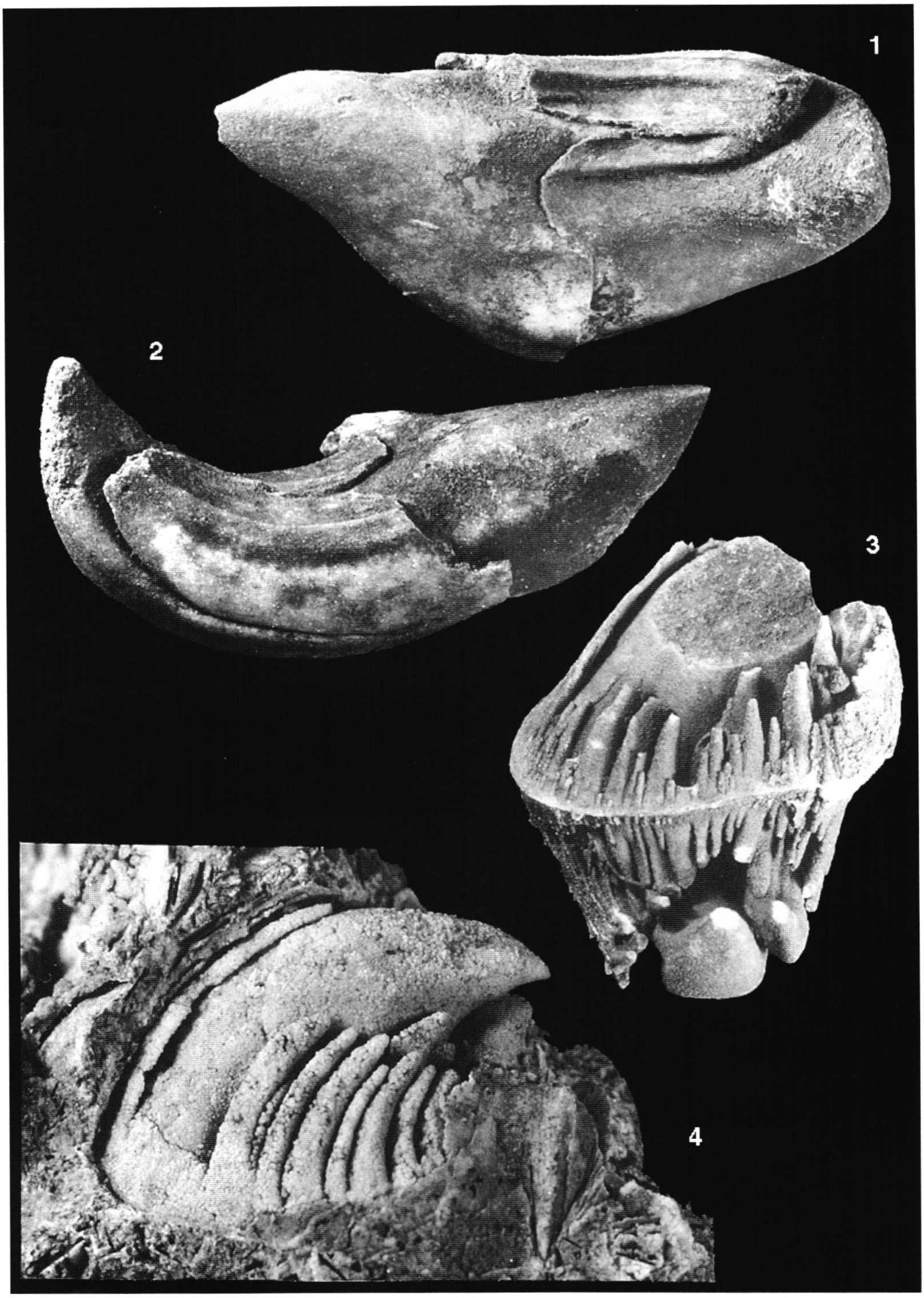
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Plate 2

All figures show *Caprinula boissyi* from Ajlun.

Fig. 1: The median steinkern of two valves meeting each other with the tooth from the upper valve fitted into the groove of the lower valve.

Fig. 2: The same specimen as in Fig 1 with the part above the tooth fitted in place and the canal system visible in the upper valve, but broken off from the central filling in the lower valve, 8 cm high and 7 cm wide.

Fig. 3: The 13 cm long steinkern shows one valve preserved and the other fractured. The preserved valve has the central cavity filled and tooth socket canals as well as the outer more narrow canals are seen projecting from the shell margin.

Fig. 4: The detail to Fig. 3 with shell margin and narrow outer canals, wider inner canals that overlie the tooth sockets. The canals of the lower valve are visible inclined to the left.

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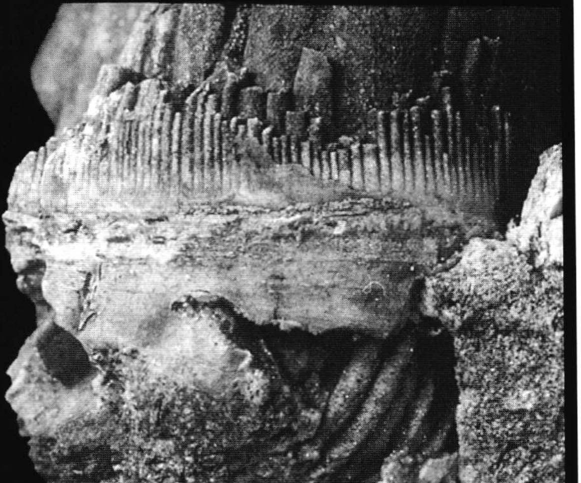

Plate 3

All figures show *Caprinula boissyi* from Ajlun.

Fig. 1: The valve sectioned near its hinge of maximally 9 cm width has a central cavity (lower right), larger tooth sockets (upper right) and a separated off part (left). The valve wall is riddled by canals of different width and shape.

Fig. 2: The section of a more median portion of the valve with maxium diameter of 7 cm has more cavities that are split off by septa from the main cavity.

Fig. 3: The 10 cm wide section of the valve cut near the hinge in comparison to that figured in Fig. 1 is quite differently organized regarding canals and septa.

Fig. 4: A 7 cm wide steinkern seen from the umbilicus toward the hinge demonstrates the larger cavities of the teeth sockets (lower part) and the median cavity surrounded by the porous outer shell wall.

Fig. 5: The same individual as in Fig. 4 seen from the side with hinge margin and one tooth socket.

Fig. 6: Same as in Fig. 5 but with missing portion replaced displays the wall separating off the tooth socket area from the central cavity.

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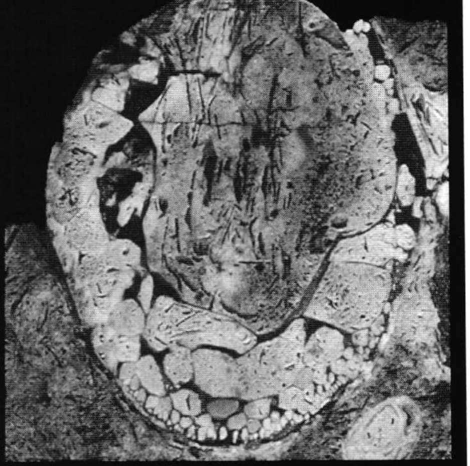

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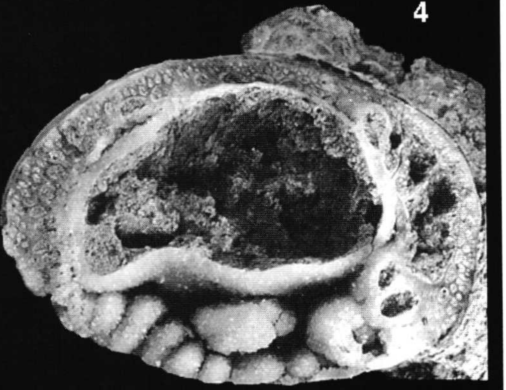

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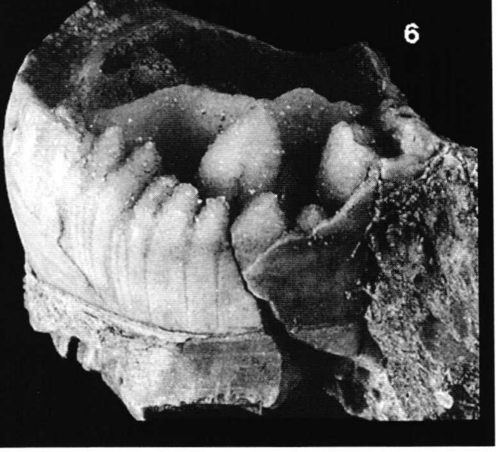

Plate 4

All figures show *Sauvagesia* from Ajlun.

Fig. 1: The operculiform valve with 5 cm diameter has a thin rim.

Fig. 2: The ligamental fold is well visible in the steinkern of the attached valve and free valve in the 7 cm wide individual.

Fig. 3: Side view of a 5.5 cm wide steinkern with ligamental fold and secundarily hollow teeth in their grooves.

Fig. 4: Same specimen as in Fig. 3 with view onto the inner side of the operculiform plate with hollow teeth (secondarily).

Fig. 5: The steinkern of the small species demonstrates the tooth sockets and the ligamental furrow. The fossil is 1.8 mm wide at its upper end.

Fig. 6: The steinkern of the small species lies in the cavity formed by its former shell wall and demonstrates the operculiform valve (3 cm wide) with cavitities of the former teeth.

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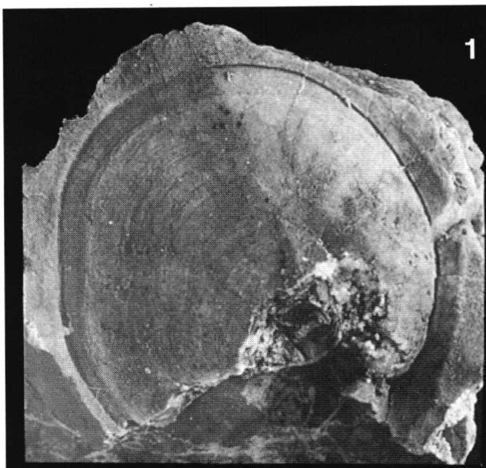

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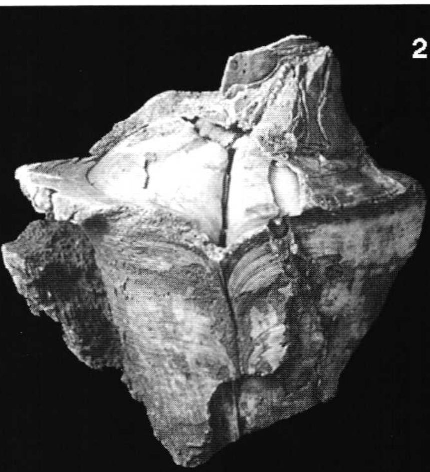

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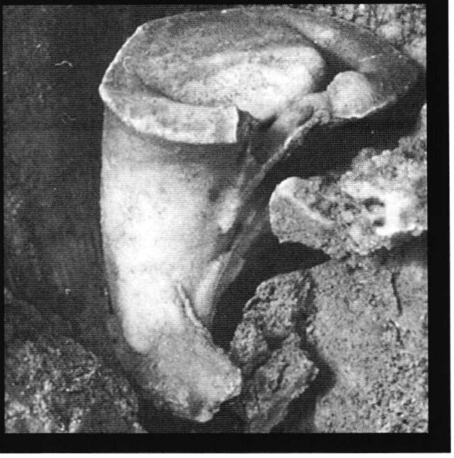

Plate 5

All figures show *Sauvagesia* from Ajlun.

Fig. 1: The ligament fold continues from the conical valve to the attached valve and relicts of the cellular outer shell layer are preserved in the 7 cm wide fossil.

Fig. 2: Three individuals each of about 3 cm width are attached to each other and are preserved as casts that feature the outer shell morphology with longitudinal ridges and growth increments.

Fig. 3: The 12 cm long steinkern with inner growth lines of the shell and the groove formed by the ligamental infold.

Fig. 4: Steinkern with central cavity, tooth sockets and accompanying canals as well as the median ligament fold preserved in an almost 10 cm long fragment.

Fig. 5: The 7 cm long conical valve has relicts of the cellular shell wall attached to the steinkern and is connected with the opercular valve preserved with its inner surface.

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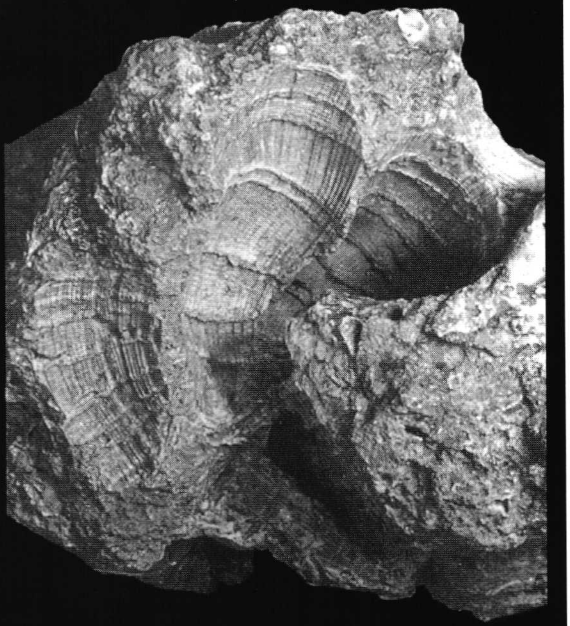

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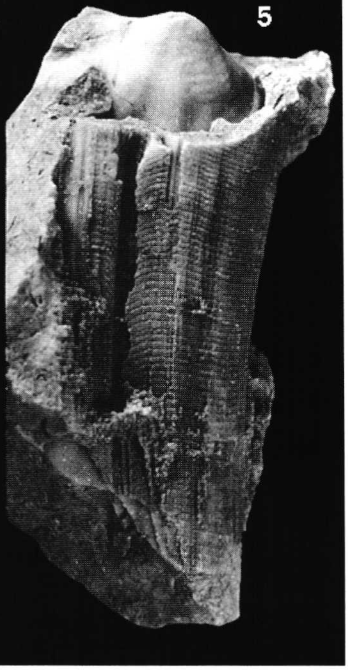

Plate 6

All figures show *Hippurites requieni* from Ajlun.

Fig. 1: Individuals used an older shell for attachment. The large individual measures 2 cm across.

Fig. 2: The 3 cm high juvenile individual with both valves in place.

Fig. 3: Small colony forming a cluster of losely attached individuals each measuring about 2 cm across.

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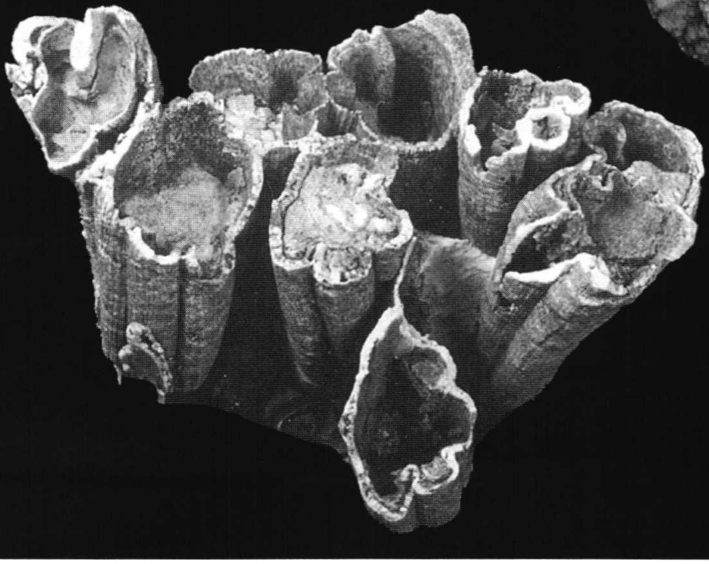

Plate 7

All figures show *Hippurites requieni* from Ajlun.

Fig. 1: The cavity of the conical valve is of rather variable shape as demonstated when figures 1-4 are compared. Width about 2.5 cm.

Fig. 2: The central cavity is deeper and the tooth sockets are wider than in Fig. 1. with same shell size.

Fig. 3: Socket arrangement differs from that seen in Fig. 1 and Fig. 2 while the shell size is the same.

Fig. 4: The ligamental pillar is from the right in the four specimen figured in fig 1-4.

Fig. 5: The operculiform valve fits well and has the widest embayment above the ligamental pillar(lower left).

Fig. 6: Like the operculiform valve in fig 5 the size here is 2.5 cm across and the outer shell layer is not preserved, showing the inner layer with grooves formed by the individual canals.

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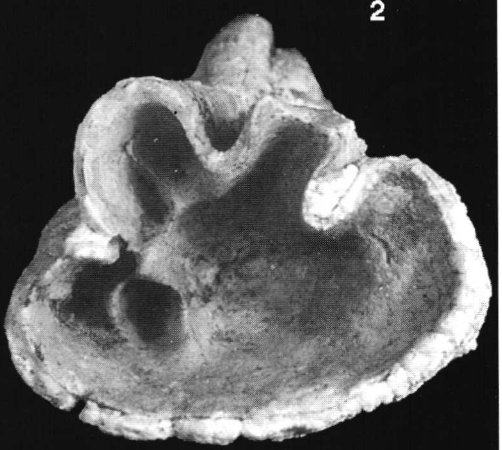

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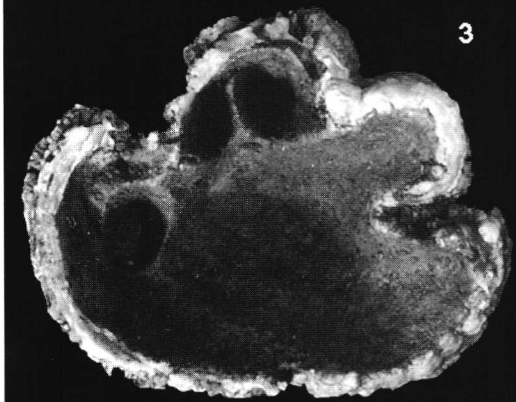

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