THE SHELL STRUCTURE, MINERALOGY AND
RELATIONSHIPS OF THE CHAMACEA
(BIVALVIA)

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ABSTRACT. The superfamily Chamacea is a group which has constantly confused systematists concerning its relationship with other bivalves. Various authors have related it to the Cardiacea, Veneracea, Crossiellaceae, Lucinacea, and the rudists (Hippuritacea).

Most classifications have placed the Chamacea with the rudists; Newell (1965) placing them into the Hippuritacea, a relationship which Yonge (1967) considers beyond doubt. From a review of hard and soft part anatomy, especially shell-structure, dentition, and mineralogy, it seems likely that the Chamacea arose from a group of byssate Cardiina in the early or middle Cretaceous. Similarities to the rudists are the result of convergent adaptations to a similar mode of life, and there is no real indication of relationship.

The Chamacea should be removed from the order Hippuritoida and placed in the order Veneroida.

The Chamidae are the sole bivalve family placed in the Superfamily Chamacea (Newell 1965). They are a small group of cemented or secondarily free bivalves which have attracted the attention of zoologists for many years because of the problem of their origin and systematic position. Despite this attention, the systematics of the Recent species is in a very confused state.

Many authors have inferred that the Chamacea are closely related to the rudists (i.e. Odhner 1919, Yonge 1967) and the most recent review of bivalve classification (Newell 1965) places them in the Order Hippuritoida, together with the Megalodontaceae and Hippuritacea. We describe the shell structure and mineralogy of recent and fossil Chamidae below, and discuss the use of these features and the nature of the soft part anatomy to determine the natural relationships to other bivalve superfamilies. We have demonstrated elsewhere (Taylor, Kennedy, and Hall 1969) that shell structure and mineralogy are constant features within bivalve superfamilies, and that they are of value in assessing relationships within the Bivalvia.

The Chamacea are characteristic inhabitants of tropical and sub-tropical seas, although some species, such as Chama pellucida Broderip, range into cooler temperate waters along the coast of California (San Francisco), but are also present in warmer waters. One species, Chama gryphina Lamarck, is present in the Mediterranean.

Chama usually inhabits rocky shores, and is a typical member of the coral reef community. Individuals usually live cemented on rocky surfaces or upon dead coral. Coral-dwelling Chama species are usually found on the underside of coral colonies. Most species inhabit the sublittoral and sublittoral fringe environments, but some are intertidal.

Arcinella arcticella (Linnaeus), a Caribbean species, is usually found free living on a coarse gravel substrate (Nicol 1952) but occasionally cemented adults of this species are found. The loss of cementation in Arcinella is secondary, for traces of attachment are always to be seen on the juvenile parts of the shell. Certain fossil species such as

Chama calcarata Deshayes from the Calcaire Grossier of the Paris Basin (Eocene, Lutetian), a shell sand facies, also show this secondary loss of cementation.

THE SHELL

1. General morphology. The Chamaceae are generally inequivalve, asymmetrical, the free valve being the smaller. The lower valve is usually convex and the upper valve is frequently more or less flattened (Pl. 70, fig. 1). Many early Chamaceae are rather less inequivalve than extant forms. The secondarily free genus Arcinella (Pl. 70, fig. 2) has returned to a more or less equivalent state. The shell of the Chamaceae is thick; the umbones are prosogyrous; attachment can be by either valve.

Shell ornament is variable. Some species bear irregular, concentric lamellae, which may be long and foliaceous (Pl. 70, fig. 4); others are spinose, or have irregular, low squamellae. Some species have radial ribs as well as concentric lamellae. Ornament varies considerably with environmental conditions such as site of cementation, exposure to wave action and encrusting biota. Arcinella is the only genus which consistently bears long spines. Some specimens of Chama show a shallow groove running from the umbo to the posterior ventral margin; this is often marked by a supression of strong sculpture. A well-marked, heart-shaped lunule is present in Arcinella (Pl. 70, fig. 2).

The interior margin of the shell is frequently crenulate, while the area between the shell edge and the pallial line may be marked by irregular radial grooves and ridges, which are the impressions of the radial musculature of the mantle (Jaworski 1928).

The pallial attachment area (pallial line) is wide, and the dorsal side is overlapped irregularly by inner shell layer. The adductor muscle pads are massive and translucent; they and the pallial line fluoresce blue under ultra-violet light.

2. Shell geometry. Growth in the Chamaceae has been considered by Yonge (1967) in terms of radial, transverse, and tangential growth components, as discussed by Owen (1953a). As they stand, these terms are largely qualitative and have not been mathematically defined. As such they are of limited use in the discussion of shell form.

Lison (1949) described shell coiling in mathematical terms, and more recently Raup (1966) using the same logarithmic spiral, has provided a more comprehensive scheme for the quantitative description of shell coiling. Thus four basic parameters may be used to define the general form of the coiled shell. These are: the shape of the generating curve (s), the whorl expansion rate (w), the distance of the generating curve from the axis (d),

EXPLANATION OF PLATE 70

Fig. 1a. Chama macroraphylla Grunin, Recent, West Indies, cemented to a pebble, ×1. 1b, as above, view of right valve, ×1.

Fig. 2. Arcinella arcinella (Linnæus), Recent, West Indies, dorsal view showing lunule, cementation site and prodissoconch (arrow), ×1. 2a, as above, lateral view of right valve showing spinose ornament on radial ribs, ×1.

Fig. 3. Chama pellucida Broderip, Recent, California, view of inner surface of valve, showing outer translucent calcitic prismatic layer, ×1.

Fig. 4. Chama frondosa Broderip, Recent, West America, showing extreme development of frondose squamae, ×1.

Fig. 5. Gyropleura coniaventeris d'Orbigny, Cenomanian, Le Mans, France, cemented to valve of Scythrotrigonia, ×1.25.
and the rate of whorl translation parallel to the coiling axis (τ) (for full details and derivation see Raup 1966). For most bivalves τ is small, and in the Chamacea it is approximately zero. The shape, s, of the generating curve is difficult to define mathematically and is not considered here.

**Text-Fig. 1.** Shell geometry of the Chamacea in relation to other bivalves. Expansion rate (w) plotted against translation rate (τ) for a series of uncemented bivalves (x), cemented Chamidae (△), and the secondarily free Arcinella arcinella (●).

**Key to numbers:**

1. 2. *Chama imbricata* (*1 = upper valve, 2 = lower valve*).
5. *Fragum uncino* (Linnaeus).
15. *Ceratoderma edule* (Linnaeus).
17, 18. *Chama Gryphus* (Lamarck). (17 = lower valve, 18 = upper valve).

Accurate measurements of w and τ are difficult to make in the Chamacea because of the irregular growth form, ornament, and the corroded nature of most shells. Measurements of w and τ on *Chama Gryphus* Lamarck (text-fig. 1) show that the expansion rate of the lower valve lies between 10^6 and 10^8, and that of the upper valve is approximately 10. The translation rate of both valves is less than 1. In a specimen of *Chama Plicata* Sowerby, where the umbo of the lower valve is strongly enrolled, the translation rate lies between 3.0 and 3.5 whereas that of the upper valve is less than 0.5. Measurements of *Arcinella arcinella* (which has reverted to the uncemented mode of life) show an expansion rate for both valves of approximately 10^0.5. The translation rate is almost zero.
As can be seen from text-fig. 1 the expansion rate of both valves of the cemented Chamacea is low, usually between 10 and 10$^2$. In 'normal' free-living bivalves such as the Cardiacea and Veneracea, and in Arcinella, the expansion rate usually lies between 10$^2$ and 10$^4$.

It is clear that the translation rate of any one individual will be variable, according to the substrate upon which original cementation took place. Some repositioning during growth is evident in the attached valve of many individuals, with consequent changes in the translation rate.

3. The ligament. The ligament of the Chamacea is opisthodetic, massive, external, but often sunk into a deep groove.

The enrolment of the umbonal area causes the ligament to be widely split towards the anterior; each half of the split ligament curls back into the umbones (text-fig. 2).

Three ligament layers are present, an outer thin periostracum, a lamellar layer, and an inner fibrous layer. The outer lamellar layer is thick and wide, and the inner layer is calcified and aragonitic (Pl. 77, fig. 1).

The ligamental splitting is more pronounced than in other bivalves (Stasek 1963 a, b). Yonge (1967) states that this anterior splitting is due to the rate of growth of the ligament posteriorly exceeding the rate of growth of the valves; this does not seem meaningful as an explanation. The splitting is rather a result of the interumbonal growth produced by the low expansion rate of shell coiling, coupled with a small translation rate. The degree of splitting depends upon the translation rate, which may be rather higher in cemented Chamacea than in the free Arcinella. A similar degree of ligamental splitting as is seen in the Chamacea is present in Glossus (Owen 1953b).

During growth of the shell the ligament elongates in a posteriorward direction. Previously deposited sections of the ligament are overlain by the posteriorward growth of the massive hinge plate.

DEVELOPMENT

The dissoconch stages of Chamacea show a markedly different shell form to that of the adult.

Dissoconchs were examined on very small cemented individuals of Chamacea. Odhner (1919) figured and described some precementation dissoconchs (text-fig. 3, Pl. 71, figs. 1–5). In Arcinella arcinella the large dissoconch can frequently be seen preserved at the tips of the umbones on adult shells (Pl. 71, fig. 3).

The first of the shell growth stages is the prodissoconch, formed during the veliger stage. Part of this may be formed by the shell gland rather than the mantle edge. In the Chamacea examined, Chamacea pellucida Broderip, Chamacea sp., and Arcinella arcinella, the prodissoconchs (Pl. 71, figs. 1–5) are highly convex, subcircular in outline, translucent, and ornamented only by growth-lines. The form of the prodissoconch indicates a larva either feeding entirely upon the egg yolk during the planktonic stage
(i.e. lecitotrophic), or having direct development and some sort of brood protection (Ockelmann 1962). Yonge (1967) indicates that larval incubation could conceivably occur in *C. pellucida* and *C. exogyra* Conrad.


The sharp boundary between prodissococonch and dissoconch (Pl. 71, fig. 2) marks the settlement of the animal on to a substrate. The dissoconch which is secreted by the mantle in the Chamacea is unemented, equivale and possesses a sculpture and morphology differing from that of the adult. This stage usually lasts until the young *Chama* is from 0.5 to 1.5 mm. long, but in *Arcinella arcinella* the dissoconch may be prolonged until the individual is 2.5 mm. long. The dissoconch stage is terminated by cementation.
Dissoconch shape is somewhat variable, although a subrectangular or ovate outline is usual (text-fig. 3). Sculpture may consist of thin, widely spaced concentric ribs, as in *Arcinella arcinella* (Pl. 71, fig. 3), in which the outermost parts of the ribs may be projected into small squamae. A similar ornament is seen in *Chama gryphina*.

*Pseudochama* pusilla Odhner dissoconchs have reticulate ornament (Odhner 1919); *Chama reflexa* Reeve and *C. jukest* Reeve dissoconchs (Odhner 1919) have radiating ribs. Anthony (1905) figures an unidentified *Chama* dissoconch with fine radiating and concentric ribs. *Chama pellucida* (Pl. 71, fig. 1) has an ornament of fine radiating ribs crossed by about six larger concentric ribs. The early stages of the dissoconch in an unnamed *Chama* show a peculiar pitted ornament (Pl. 71, fig. 5), although the rest of the dissoconch bears concentric ribs only (Pl. 71, fig. 4).

The dentition of the dissoconch is known only from *Arcinella arcinella* (Odhner 1919), *Chama pellucida* (Dall 1903), and an unidentified species (Anthony 1905). In all of these, two cardinals are present in each valve.

An interesting feature of the dissoconch is the subrectangular shape, with a reduced anterior and an elongated posterior portion (text-fig. 5). It is well known that a byssate existence influences the shape of bivalves (Yonge 1962); thus in the Arcacea and some Carditidae a rectangular shape with a long ventral margin is developed. In some Cardita species there is a reduction in the anterior part of the animal, which is also seen in the Mytilacea. This purely morphological evidence strongly suggests that the dissoconch stage of some species of *Chama* is byssally attached prior to cementation. The presence of a much larger dissoconch in *Arcinella arcinella* suggests that the byssate existence was prolonged in this species. Unlike most other Chamacea *Arcinella arcinella* inhabits sandy substrates, and the long precementation byssate life may be an insurance against the choice of an unfavourable cementation site.

**Dentition and Inversion**

Study of the dentition of the Chamacea has given rise to much controversy in the past. The reason for this confusion is that some Chamacea can cement themselves by either the left or the right valve. As a result of attachment by the right valve, the hinge teeth normally present in the left valve appear in the same number and positions in the right valve. As Davis (1935) has pointed out, confusion arises in the interpretation of the teeth of this family by attempting to number individuals as though they were in a normal right valve. There are many records of species of *Chama* being attached by either the left valve or the right valve, and even those species which are

**Explanation of Plate 71**

Figs. 1, 2. *Chama pellucida* Broderip, Recent, California. 1, Prodissococonch, dissoconch and early adult shell. Note radial and concentric ornament on dissoconch, very different from the squamaceous ornament of the adult. Scanning electron-micrograph, ×140. 2, Detail of the sharp contact between the larval prodissococonch and the dissoconch. Notice close bunching of growth lines as feeding ceases prior to metamorphosis. Scanning electron-micrograph, ×700.

Fig. 3. Prodissococonch and dissoconch of *Arcinella arboresa* Linnaeus, Recent, West Indies showing concentric ornamentation. Scanning electron-micrograph, ×80.

Figs. 4, 5. Prodissococonch and dissoconch of *Chama* sp. from East Indies. 4, Scanning electron-micrograph, ×80. 5, Detail showing the contact between the prodissococonch and the dissoconch, with peculiar pitted ornamentation of the dissoconch. Scanning electron-micrograph, ×340.
usually attached by one valve sometimes show attachment by the other (Bayer 1943, Palmer 1928, Yonge 1967). *Chama calcarea* (Eocene, Paris Basin) shows attachment by left and right valves in approximately equal proportions, and this type of variation, plus others noted above, makes the use of the generic name *Pseudochama* Odhner 1919 for those species attached by the right valve of very doubtful validity.

Yonge (1967) stated that it is impossible to homologize the cardinal teeth of the Chamaea with those of other heterodont bivalves because of the great modifications caused by 'tangential growth'. The teeth of many recent species of *Chama* are indeed greatly modified in the adult stage, and it is perhaps easier to study dentition in some of the less modified, fossil forms. The hinge notation used here is that elaborated by Boyd and Newell (1968) from the Steinmann notation, in which every articulating ridge, prominence or depression of the hinge is numbered. This notation system is more objective than that of Bernard (1895) and Munier-Chalmas (1895) which requires knowledge of the ontogenetic development within each family.

The Boyd and Newell system is flexible and is readily convertible to the Bernard system when homologous teeth are recognized. The two valves are illustrated back to back with the right valve above the left valve (following Bernard) so that the posterior of the valves lies to the left. The notation is devised to be directly comparable with this. The right valve hinge is expressed by the upper of two lines of symbols and, in both lines, the symbols are arranged from left to right to reflect a traverse along the hinge from the posterior extremity to the anterior extremity. All the structures of the articulating surfaces are indicated. The Arabic numeral '1' represents teeth or potentially articular ridges. Inconspicuous or dubious teeth are indicated in brackets. Depressions in the articulating surface which generally function as tooth sockets are indicated as an '0'. Vertical lines, discontinuous in doubtful cases, are used to delimit cardinal from lateral teeth. Various letters such as 'r', 's', 'n', and 'e' are added to represent positions of the resilium, septum, nympha, and elastic ligament, etc.

The basic *Chama* dentition is Bernard's 'Lucinoid' type. The hinge notation of *Chama calcarea* (Eocene, Paris Basin) can be expressed as shown below, and in Plate 72, fig. 2:

<table>
<thead>
<tr>
<th>Right valve</th>
<th>0</th>
<th>1</th>
<th>(0)</th>
<th>(1)</th>
<th>0</th>
<th>1</th>
<th>0</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Posterior</td>
<td>(n)</td>
<td>(0)</td>
<td>(0)</td>
<td>(1)</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Left valve</td>
<td>1</td>
<td>(n)</td>
<td>(0)</td>
<td>(0)</td>
<td>(1)</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

\[ n = \text{ligament nympha} \]

In the left valve the anterior cardinal is large and solid, and the posterior cardinal is long and curved. In the upper right valve, the anterior cardinal is small and ill defined, and the posterior cardinal is long and curved. They are separated by a socket for the reception of the large anterior cardinal of the left valve. Extra articulating ridges are developed between the posterior laterals and the nympha. They are indicated in parentheses.

This species can be compared with the Recent species *Chama macerophylla* shown below and in Plate 72, fig. 1:

<table>
<thead>
<tr>
<th>Right valve</th>
<th>0</th>
<th>1</th>
<th>n</th>
<th>0</th>
<th>1</th>
<th>0</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Posterior</td>
<td>(0)</td>
<td>(0)</td>
<td>(1)</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

\[ n = \text{ligament nympha} \]
In the left valve the massive cardinal tooth is very large and grooved. The sockets for the reception of the cardinals of the right valve have fused to form an arcuate socket isolating the cardinal. In the right valve a comparable fusion of the two cardinals has taken place forming a single arcuate tooth. Loss of laterals also occurred in Arcinella arcinella (an inverse form) a similar notation occurs, with the fusion of the cardinals and sockets:

\[
\begin{array}{c|c|c|
\text{Right valve} & n & 1 \quad 0 \quad 1 \\
\text{Posterior} & \text{Anterior.} \\
\text{Left valve} & n & 0 \quad 1 \quad 1 \\
\end{array}
\]

It will be shown below that the denticity of the early Chamaecea shows great resemblances to that of the Carditacea.

**ANATOMY**

Studies on the anatomy of several species of Chamaecea have been made by Anthony (1905), Pelseneer (1911), Grieser (1913), Odhner (1919), and most recently by Yonge (1967) who studied *Chama pellicida* and *C. exogyra*. The general anatomical features of the soft parts are summarized below.

The mantle is similar to that of most bivalves, except that the three marginal folds are rather small. The mantle is fused by the inner fold only, to form posteriorly the inhalent and exhalent siphons, and at the anterior to delimit the more extensive pedal gape. The very short siphons represent extensions of the fused inner mantle fold. Yonge (1967) stated that the mantle dorsal to the pedal gape is fused at the inner fold and the inner part of the middle fold. A laterally compressed flap of mantle projects between the valves in the hinge area, forming the mantle isthmus, the termination of which secretes the ligament. The radial musculature of the mantle, which leaves radial markings on the inner shell surface, has been described by Jaworski (1928).

The mantle is attached to the shell by the broad, entire line of pallial muscles, and the adductor muscles. Other, local, points of attachment on the general outer mantle surface are described below. The adductor muscles are large and subequal. The anterior adductor is usually the larger, and curves ventrally to occupy most of the area immediately within the pedal gape.

The foot is small, compressed, and usually pointed. Yonge (1967) considers that the function of the foot is to assist in the cleansing of the mantle cavity, in particular the

**EXPLANATION OF PLATE 72**

Fig. 1. *Chama macerophyllea* Gmelin. Recent, Bermuda. BMNH 1911.21.1322.3. **a**, Right valve, hinge teeth, \( \times 2 \). **b**, Left valve, \( \times 2 \). Abbreviations: C, cardinal teeth; L, lateral teeth; n, ligament nymph; add, adductor muscle scar.

Fig. 2. *Chama exogyra* Deshayes. Eocene, Lutetian, Grignon, France. **a**, Right valve, showing hinge teeth, \( \times 2 \). **b**, Left valve, \( \times 2 \).

Fig. 3. *Chama* sp. Maastrichtian, Cévennes, France. Silicified rubber cast, \( \times 2 \).

Fig. 4. *Chama haueri* Zittel, Cretaceous, Senonian Gosau Beds, Gosau, Austria. \( \times 0.75 \). **b**, dorsal view.

Figs. 5, 6. *Clypeola palaeoca* (Ravn), Cretaceous, Danian, Faxe, Denmark \( \times 1 \). **5**, internal cast, left valve. BMNH L.13601. **6**, anterior view, BMNH L.25555.
area round the anterior adductor muscle. The posterior pedal retractor muscles are attached near the dorsal end of the adductor muscle.

The ctenidia are typically eulamellibranch and have been described in great detail by Othner (1919). They are highly plicate, and the gill ciliation pattern is type C (1) of Atkins (1937). The labial palps are small, and correspond to type 2 of Siasek (1963c), in which the ventral tips of the outermost filaments of the inner demibranches are inserted on to, and fused to, a distal oral groove. The stomach has been discussed by Purchon (1958, 1960) who places the stomach of two species in his types IV and V respectively. A more recent study by Dinamani (1967) places the stomach of Chamacea in his type IIIa.

Other features of the gut, heart, kidneys, nervous and reproductive systems have been described by Grieser (1913) and Othner (1919).

**GEOLOGICAL HISTORY**

The generic name Chamacea was used by early workers for many different groups of Cretaceous bivalves, including rudists, Exogyra, and other oysters. Picket and Campiche (1864–7), Stoliczka (1870), and Kutassy (1934) have removed many of these; of the remainder, only five appear to be valid Chamacea species.

*Chama cupani* Vidal (1877, 92, pl. 3a, fig. 1) is a remarkable Campanian species, in need of reinvestigation. It is inequivalve, but shows no traces of a cementation area, there is no trace of an external ligamental groove or of muscle scars on the internal mould, and the hinge is unknown. The morphology of the valve margin (Vidal 1877, pl. 4, fig. 6) is comparable to that seen in other Chamacea species.

*Chama haneri* Zittel (1865, 147, pl. 7, figs. 3 a–c; see herein Pl. 72, fig. 4) and *C. detrita* Zittel (1865, 147, pl. 7, figs. 4 a–b) from the Gosau Beds, Austria, of Senonian age; *C. callosa* Noetling (1902, 50, pl. 12, figs. 9–10) from the Upper Cretaceous of Baluchistan; and *C. toeroki* Pethő (1906, 269, pl. 19, figs. 15–16) from the Upper Cretaceous of Hungary are all good Chamacea species.

*Chama is based on material retaining the shell, C. detrita on internal moulds. From our knowledge of variation in other species, these are probably synonyms, the trivial name haneri taking priority. C. callosa may also be a synonym.

All these Cretaceous forms are similar in having an ornament of concentric lamellae (Pl. 72, figs. 3, 4).

Douville (1913, 453) also records Chamidae from the Upper Cretaceous of France, but from horizons above that of the Gosau material. We have also seen an undescribed form from the Calcaire a baculites (Maastrichtian) of Cotentin, France (Pl. 72, fig. 3).

*Chama angulosa* d'Orbigny (1844, 690, pl. 464, figs. 8–9), *Chama gasoli* Vidal (1877, 93, pl. 4, figs. 7 a–b), and *C. moritz* Strombeck (1863, 156) are all species of *Gyropeirus*, *C. spondyloides* Bayle (1856, 365, pl. 14, fig. 1) is a monopleurid rudist. *C. triedra* Picket and Campiche (1867, 5, pl. 140, figs. 4–5) and *C. gracilicornis* Picket and Campiche (1867, 6, pl. 140, figs. 6–7) are both diereatid rudists. *C. bodei* Basse (1933, 43, pl. 7, fig. 6) is probably a *Spondylus*. *C. deplanata* Stoliczka (1870, 235, pl. 22, fig. 5) is probably a *Plicatula*. *C. bifrons* Grieppenkerl (1899, 362, pl. 7, fig. 2), *C. costata* Roemer (1841, 67, pl. 8, fig. 20), *C. multicosata* Wegner (1905, 192, text-fig. 19), and *C. geometrica* Roemer (1840, 35, pl. 18, fig. 39) are all oysters.
Chama cretacea d’Orbigny (1846, 689, pl. 463, figs. 1–2) is generically indeterminate, but does not seem to be a Chama. Chama suborbiculata d’Orbigny (1822, 100), is not figured. Whilst d’Orbigny’s description is brief, it may be a Chama, but is best regarded as a nomen dubium until re-studied.

Little is known of Chama in Danian, Montian or Thanetian rocks. Ciplyella pulchra (Ravn) (1902, 127, pl. 4, figs. 12–15) from the Danian Koral-kalk of Denmark seems to belong to the Monopleuridae (see p. 409). Chama ciplyensto Vincent (1928, 104, pl. 5, fig. 17) from the Danian or Montian Poulingue de Ciply of Belgium is little known. The description of its adductor scars suggest that it is a genuine Chama. Chama ancosbalis Cossmann (1908, 44, pl. 1, figs. 38–40) from the Montian Calcaire Grossier of Belgium is known from two specimens only and needs reinvestigation.

In the Eocene Chama becomes much more common, being represented by such familiar forms as Chama squamosa, C. lamellosa, and C. gigas. Arca navis (type species Chama arcinella Linnaeus) is a tropical American chamid which appears in the early Miocene of the Florida region. It is thought to be derived from the early to middle Miocene species Chama dracoins Dall (Mico 1952).

Most of the fossil occurrences of Chama are in association with rich shallow marine faunas of tropical or subtropical aspect. Chama exogyra and C. pellicida occur associated with cooler water faunas, as do living members of the same species.

**SHELL STRUCTURE AND MINERALOGY**

Shells of more than thirty species of recent and fossil Chamidae were examined in connection with this work.

Mineralogical determinations were carried out by means of standard X-ray diffraction techniques. Optical examinations of shell structure were made on shell interiors, fractured sections, acetate peels of polished and etched sections (method in Kummel and Raup 1965), and petrographic thin sections.

Fine structure was studied on surfaces, fractured and polished and etched sections, which were examined with a Cambridge Instrument Company Scanning electron microscope.

The shell of most species examined is wholly aragonitic, with a two-layered shell. Exceptions are Chama pellucida and Chama exogyra which have an additional outer prismatic calcite layer. The significance of this is discussed below.

The results of our observations are summarized in Table 1. It will be seen that we use the terms inner, middle, and outer shell layers. This is an entirely topographic, and thus unambiguous division. We reject Oberling’s (1964) use of the terms ektrostracum, mesostracum, and endostracum for three-layered shells, mesostracum and endostracum for two-layered shells as this implies homology between layers in different shells. It further suggests that two-layered shells may be derived from three-layered forms.

As well as speaking of shell layers, we have adopted Oberling’s (1964) term myostrostracum for the peculiar blocky prismatic aragonite laid down under sites of muscle attachment, i.e. the pallial, pedal, and adductor myostracum.
(a) Structure of the crossed-lamellar layer. Crossed-lamellar structure forms the outer shell layer of most species (text-fig. 4), but the middle layer of *Chama pellucida* and *C. exogyra* (text-fig. 5).

Conventional microscopy shows the inner surface of the shell layer as a series of elongate, branching, interdigitating lenses. These lenses are arranged with their long axes running concentrically, i.e. essentially parallel to the shell margin over most of the shell.

![Diagram](image)

**Text-fig. 4.** (a) Transverse section, (b) longitudinal section, and (c) interior of *Chama macrospyphila* Gmelin to show distribution of shell layers.

More variable orientations are developed on spines, squamae, and in the umbonal region. These lenses correspond to the outcrop of the first order lamels of Boggild (1930).

In section first-order lamels run normal to the inner surface of the shell layer (Pl. 73, fig. 1). Traced towards the shell exterior they twist and turn however, producing complicated patterns. The first-order lamels branch and interdigitate in sections in much the same way as they do on shell interiors. A strong, interlocking structure is thus produced.

First-order lamels are up to several millimetres long and of the order of 0.5 mm thick. Sections and peels show a striking colour banding, adjacent lamels being straw-yellow or red-brown in colour.

Within each first-order lamel (text-fig. 6b) there are sheet-like second-order lamels (Boggild 1930). These are in turn built of minute laths, about 1 μ in diameter and some
<table>
<thead>
<tr>
<th>Species</th>
<th>Horizon and locality</th>
<th>Mineralogy</th>
<th>Outer layer</th>
<th>Inner layer</th>
<th>M. Mysococcoma</th>
<th>Adductor</th>
<th>Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chama haurei</td>
<td>Zittel</td>
<td>Aragonite</td>
<td>Complex crossed-lamellar with sheets of myoskeletal type prisms</td>
<td>Prismatic</td>
<td>Prismatic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chama ecaeterata</td>
<td>Lamarck</td>
<td></td>
<td>Complex crossed-lamellar with sheets of myoskeletal type prisms</td>
<td>Prismatic</td>
<td>Prismatic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chama ecaeterata</td>
<td>Lamarck</td>
<td></td>
<td>Complex crossed-lamellar with sheets of myoskeletal type prisms</td>
<td>Prismatic</td>
<td>Prismatic</td>
<td></td>
<td>Mysococcoma sheets in inner layer locally folded (see text)</td>
</tr>
<tr>
<td>Chama lavelloisa</td>
<td>Lamarck</td>
<td>Aragonite</td>
<td>Complex crossed-lamellar with sheets of myoskeletal type prisms</td>
<td>Prismatic</td>
<td>Prismatic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chama gigas</td>
<td>Deshayes</td>
<td></td>
<td>Complex crossed-lamellar with sheets of myoskeletal type prisms</td>
<td>Prismatic</td>
<td>Prismatic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chama seiferensis</td>
<td>S. V. Wood</td>
<td></td>
<td>Complex crossed-lamellar with sheets of myoskeletal type prisms</td>
<td>Prismatic</td>
<td>Prismatic</td>
<td></td>
<td>Mysococcoma sheets in inner layer similar to those in C. ecaeterata</td>
</tr>
<tr>
<td>Chama turgida</td>
<td>Lamarck</td>
<td></td>
<td>Complex crossed-lamellar with sheets of myoskeletal type prisms and myoskeletal pillars</td>
<td>Prismatic</td>
<td>Prismatic</td>
<td></td>
<td>Scattered tubules in inner layer</td>
</tr>
<tr>
<td>Chama simbraeiia</td>
<td>Defrance</td>
<td></td>
<td>Complex crossed-lamellar with sheets of myoskeletal type prisms</td>
<td>Prismatic</td>
<td>Prismatic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chama papyrea</td>
<td>Deshayes</td>
<td></td>
<td>Complex crossed-lamellar with sheets of myoskeletal type prisms</td>
<td>Prismatic</td>
<td>Prismatic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chama squamosa</td>
<td>Solander</td>
<td></td>
<td>Complex crossed-lamellar with sheets of myoskeletal type prisms</td>
<td>Prismatic</td>
<td>Prismatic</td>
<td></td>
<td>Scattered tubules in inner layer</td>
</tr>
<tr>
<td>Chama squamosa</td>
<td>Solander</td>
<td></td>
<td>Complex crossed-lamellar with sheets of myoskeletal type prisms and myoskeletal pillars</td>
<td>Prismatic</td>
<td>Prismatic</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
| Clamia aquitanica  
| Cosman and Pessaro | Aquitanian, Villandri, Italy | Crossed-lamellar | Complex crossed-lamellar with sheets of myostracal-type prisms | Prismatic | Prismatic |
| Clamia sp. | Miocene, San Domingo | Crossed-lamellar | Complex crossed-lamellar with sheets of myostracal-type prisms | Prismatic | Prismatic |
| Clamia crassa  
| Ehrenberg | Pliocene, Florida | Crossed-lamellar | Complex crossed-lamellar with sheets of myostracal-type prisms | Prismatic | Prismatic |
| Clamia helvira  
| (Nicol) | Plio-Pleistocene, La Belle, Florida | Crossed-lamellar | Complex crossed-lamellar with sheets of myostracal-type prisms and myostracal pillars | Prismatic | Prismatic |
| Clamia brevicaulis  
| Deshayes | Pleistocene, Asti, Italy | Crossed-lamellar | Complex crossed-lamellar with sheets of myostracal-type prisms | Prismatic | Prismatic |
| Clamia gryphina  
| Lamarck | Pleistocene, Piedmont, Italy | Crossed-lamellar | Complex crossed-lamellar with sheets of myostracal-type prisms | Prismatic | Prismatic |
| Clamia gryphina  
| Lamarck | Pleistocene, Asti, Italy | Crossed-lamellar | Complex crossed-lamellar with thin sheets of myostracal-type prisms | Prismatic | Prismatic |
| Clamia navillis  
| Reeve | Pleistocene, Berbera, Somalia | Crossed-lamellar | Complex crossed-lamellar with sheets of myostracal-type prisms and myostracal pillars | Prismatic | Prismatic |
| Clamia pulchella  
| Reeve | Pleistocene, Berbera, Somalia | Crossed-lamellar | Complex crossed-lamellar with sheets of myostracal-type prisms and myostracal pillars | Prismatic | Prismatic |
| Arcinella arcinella  
| antiquata (Dall) | Miocene, Colombia | Crossed-lamellar | Complex crossed-lamellar with sheets of myostracal-type prisms | Prismatic | Prismatic |
| Arcinella trapezioides  
<p>| (Pilsbry and Johnson) | Miocene, San Domingo | Crossed-lamellar | Complex crossed-lamellar with sheets of myostracal-type prisms | Prismatic | Prismatic |</p>
<table>
<thead>
<tr>
<th>Species</th>
<th>Horizon and locality</th>
<th>Mineralogy</th>
<th>Outer layer</th>
<th>Inner layer</th>
<th>Myostraca Pallial</th>
<th>Adductor</th>
<th>Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arcinella arcinella (Linnaeus)</td>
<td>Pliocene, Caloosahatchee, Florida</td>
<td>Aragonite</td>
<td>Crossed-lamellar</td>
<td>Complex crossed-lamellar with sheets of myostracal-type prisms</td>
<td>Thin prismatic</td>
<td>Thick prismatic</td>
<td>Layers of myostracal-type prisms present in inner layer; other specimens have myostracal pillared tubules</td>
</tr>
<tr>
<td>Arcinella arcinella (Linnaeus)</td>
<td>W. Florida</td>
<td>Aragonite</td>
<td>Crossed-lamellar</td>
<td>Complex crossed-lamellar</td>
<td>Thin prismatic</td>
<td>Thick prismatic</td>
<td>Myostracal pillars in inner layer</td>
</tr>
<tr>
<td>Chama aspera Reeve</td>
<td>Indian Ocean</td>
<td>Aragonite</td>
<td>Crossed-lamellar</td>
<td>Complex crossed-lamellar</td>
<td>Thin prismatic</td>
<td>Thick prismatic</td>
<td>Thin bands of myostracal-type prisms and tubules in the inner layer</td>
</tr>
<tr>
<td>Chama brasica Reeve</td>
<td>Philippines</td>
<td>Aragonite</td>
<td>Crossed-lamellar</td>
<td>Complex crossed-lamellar</td>
<td>Thin prismatic</td>
<td>Thick prismatic</td>
<td>Myostracal pillars and scattered tubules in inner layer; some specimens have bands of myostracal-type prisms in this layer</td>
</tr>
<tr>
<td>Chama gryphiina Lamarck</td>
<td>Mediterranean</td>
<td>Aragonite</td>
<td>Crossed-lamellar</td>
<td>Complex crossed-lamellar</td>
<td>Thin prismatic</td>
<td>Thick prismatic</td>
<td>Myostracal pillars and scattered pillars in inner layer. Other (?) pedis myostracal in some sections</td>
</tr>
<tr>
<td>Chama lastoma Reeve</td>
<td>Aden</td>
<td>Aragonite</td>
<td>Crossed-lamellar</td>
<td>Complex crossed-lamellar</td>
<td>Thin prismatic</td>
<td>Thick prismatic</td>
<td>Abundant myostracal pillars and scattered pillars in the inner layer. The internal ligament is aragonitic</td>
</tr>
<tr>
<td>Chama lazzarus Wood</td>
<td>Mombasa, E. Africa</td>
<td>Aragonite</td>
<td>Crossed-lamellar</td>
<td>Complex crossed-lamellar</td>
<td>Thin prismatic</td>
<td>Thick prismatic</td>
<td>Abundant myostracal pillars and scattered tubules in the inner layer. Tubules may be present in the marginal parts of the outer layer. The internal ligament is aragonitic</td>
</tr>
<tr>
<td>Chama tubera Reeve</td>
<td>Philippines</td>
<td>Aragonite</td>
<td>Crossed-lamellar</td>
<td>Complex crossed-lamellar</td>
<td>Thin prismatic</td>
<td>Thick prismatic</td>
<td>Abundant radially elongate myostracal pillars and scattered tubules in the inner layer</td>
</tr>
<tr>
<td>Chamna aculeata</td>
<td>W. Indies</td>
<td>Aragonite</td>
<td>Crossed-lamellar</td>
<td>Complex crossed-lamellar</td>
<td>Thin prismatic</td>
<td>Thick prismatic</td>
<td>Myostracal pillars and scattered tubules in the inner layer.</td>
</tr>
</tbody>
</table>
| Chamna spinosa | Dunkan Island, Cape York, Queens-
| Broderip | land | Aragonite | Crossed-lamellar | Complex crossed-lamellar | Thin prismatic | Thick prismatic | Tubules present in the inner layer; myostracal pillars occur in some specimens. |
| Chamna spinythodes | Queensland | Aragonite | Crossed-lamellar | Complex crossed-lamellar | Thin prismatic | Thick prismatic | Tubules, sheets of myo-
| Menke | stracal-type prisms and myostracal pillars are present in the inner layer; the latter extend into the outer layer. |
| Chamna nucerephysila | W. Indies | Aragonite | Crossed-lamellar | Complex crossed-lamellar | Thin prismatic | Thick prismatic | Myostracal pillars and abundant tubules in the inner layer. |
| Gmelin | Ecuador | Aragonite | Crossed-lamellar | Complex crossed-lamellar | Thin prismatic | Thick prismatic | The inner layer has a rather coarse fabric, and myostracal pillars in the umbonal area. |
| Chamna radicans | W. Indies | Aragonite | Crossed-lamellar | Complex crossed-lamellar | Thin prismatic | Thick prismatic | Abundant myostracal pillars in the inner layer. |
| Lamareck | | | | | | | |
| Chamna palliata | California | Aragonite and Calcite | Granular/prismatic calcite | Crossed-lamellar aragonite | Middle layer | Inner layer | Myostraca Adductor |
| Broderip | | | | | Complex crossed-
| lamellar aragonite | Thin prismatic | aragonite |
| | | | | Thin prismatic | aragonite | |
| | | | | | | |
TEXT-FIG. 5. (A) Longitudinal section and (B) interior of Chama pellucida Broderip to show the distribution of shell layers.

EXPLANATION OF PLATE 73

All sections are acetate peels.

Fig. 1. Outer crossed-lamellar layer of Arcinella arcinella (Linnaeus), showing first-order lamels aligned normal to the shell interior in the inner part of the layer (lower), and the 'bladed' outer part where they are aligned parallel to the shell interior. Radial section, ×32.

Fig. 2. Radial section inner complex crossed-lamellar layer of Chama eulamellata Deshayes showing cone shaped depressions in myostracal sheets, ×32.

Fig. 3. Planar section through the adductor myostracum of Chama lazarua Wood, ×100.

Fig. 4. Contact between the outer crossed-lamellar layer (left) and the adductor myostracum of Chama radians Lamarck, radial section, ×80.

Fig. 5. Myostracal pillars in the inner, complex crossed-lamellar layer of Chama radians Lamarck. Radial section, ×80.

Fig. 6. Radial section of the inner complex crossed-lamellar layer of Chama lazarua Wood, ×20.

Fig. 7. Myostracal sheets in the inner complex crossed-lamellar layer of Chama lamellata Lamarck, ×80.

Fig. 8. Contact between the outer, prismatic, calcitic layer (top) and the middle aragonite crossed-lamellar layer of Chama pellucida Broderip, ×80.

Fig. 9. Planar section of the outer prismatic, calcitic layer of Chama pellucida Broderip, ×80.
tens of microns long, joined in side-to-side contact. These sheets of laths, i.e. second-order lamels, lie normal to the sides of the first-order lamels, the long axes of the laths being parallel to the plane of the first-order lamels.

Second-order lamels are inclined to the shell interior, with opposite inclinations of dip in adjacent first-order lamels. Optical work suggests that the whole layer is built of crystallites with only two crystallographic orientations.

These observations are summarized in text-fig. 6b. Fine structure is shown in Plate 74, fig. 1.

As well as the carbonate, there is a well-developed proteinaceous organic matrix in the crossed-lamellar layer (Pl. 74, fig. 2). This is intimately associated with the carbonate, surrounding each lath of the crossed-lamellar structure. Unlike the regular, fenestrate sheets of nacre organic matrix (Grégoire 1957, 1959, 1960, 1967), crossed-lamellar matrix has a much more open, irregular structure.
The variation in attitude of first-order lamels seen in sections is a result of their growth normal to the secreting surface, i.e. the marginal parts of the mantle. Where this is variable in form, as in ribs, or in the reflected margin of Arcinella, irregularities will develop. Indeed, in Arcinella, growth of lamels normal to the surface of the margin produces a structure which superficially resembles the composite prismatic structure developed in the Lucinacea (Pl. 73, fig. 1).

(b) Structure of the complex crossed-lamellar layer. Complex crossed-lamellar structure forms the inner shell layer of all Chamacea. We use 'complex crossed-lamellar' in the original sense of Beggild (1930). It is thus equivalent to 'complex' structure of Oberling (1964), which is not to be confused with 'complex' of Beggild (1930).

This shell structure type is built of the same basic building blocks as crossed-lamellar structure, i.e. minute lamels (Text fig. 6d). Instead of building first-order lamels, the lamels build much more irregular blocks (Pl. 73, fig. 6; Pl. 74, fig. 3), and many different attitudes and orientations of lamels are present within the layer.

In some sections, small irregular patches of radiating lamels are recognizable. McClintock (1967) has described these as sections of spherulitic growth. His pellucidae structures are, however, different in detail from structures present in bivalves.

(c) Structure of the prismatic layer. An outer, calcite prismatic layer is present in two recent species of Chama, C. pellucida, and C. exogyra. The occurrence in C. pellucida has been noted by previous workers (Lowenstam 1954 a, b, 1963, 1964; Kennedy and Taylor 1968), but the present record from C. exogyra represents only the second occurrence of calcite in extant bivalves other than the Pebrinomorpha.

However, matters are far from simple in respect of these two species.

Examination of the type specimens of C. exogyra and C. pellucida (in the collections of the British Museum (Natural History)) shows that the specimens appear distinctive. C. pellucida is rounded in outline, is 'normal' (i.e. attached by the left valve), and bears striking translucent squamae. C. exogyra is irregular, elongate, reversed (i.e. attached by right valve), and lacks conspicuous squamae. Other specimens of C. exogyra we have examined show rather more conspicuous ridges, and are 'normal'—attached by the left valve. These normal specimens closely resemble C. pellucida, whilst reversed C. pellucida closely resembles C. exogyra.

These similarities, the identical and highly unusual mineralogy and structure, together with the similar geographical range of the two species (Yonge 1967) plus the problems

**EXPLANATION OF PLATE 74**

All figures are scanning electron-micrographs.

Fig. 1. Polished, etched (HCl) radial section of the middle crossed-lamellar layer of Chama pellucida, showing three adjacent first-order lamels, ×700.

Fig. 2. As above, showing contact between the outer prismatic layer (left) and the middle crossed-lamellar layer; notice the lace-like organic matrix network, ×700.

Fig. 3. Fractured section of the inner complex crossed-lamellar layer of Chama radiata, showing lamels joined into second-order lamels having variable orientations, ×240.

Fig. 4. Inner shell surface of Chama radiata, showing the outercrop of myostracal prisms, ×1,100.

Fig. 5. Polished, etched (HCl) radial section of the outer prismatic layer of Chama pellucida, ×700.

Fig. 6. Inner shell surface of Chama radiata showing the opening of a tubule, ×2,250.
of inversion in the Chamacea generally, have led us to suspect that these species may be synonymous. This is, however, a field problem, which we cannot resolve on the basis of material available to us.

In both species the structure of the outer prismatic layer is very similar, and different from that occurring in all other extant bivalves. In hand specimen, the layer has a distinctive, translucent, 'pellucid' appearance (Pl. 70, fig. 3).

In peels and thin sections (Pl. 73, figs. 8 and 9) it appears grey against the browns and yellows of the adjacent crossed-lamellar layer. It is built up of minute, irregular, blade-like prisms, which are orientated more or less normally to the mantle and shell interior at the time of secretion. The prisms are rather variable in their attitude (in part as a result of their being involved in ribs and squamae), and are arranged into blocks with irregular polygonal outlines (Pl. 73, fig. 8). These larger blocks pass into extinction quite irregularly, and there is thus no uniformity of attitude within the blocks.

These observations are confirmed by electron-microscopy. In fractured sections, the large prism blocks show prominent transverse striae, and are clearly built up of smaller units (Pl. 77, fig. 2). Etching brings out these smaller units (Pl. 74, fig. 5), which correspond to the fine prisms seen at optical level. These fine prisms are surrounded by sheaths of organic matrix, but there are no thick concholin sheets such as characterize the other prismatic calcite layer of Pinna, Pinctada, and many other bivalves.

(d) Structure of the myostracal layers. These layers show similar features in all Chamacea we have examined. At optical level (Pl. 73, figs. 3, 4, 5, 7) myostraca are a characteristic grey colour, contrasting with the adjacent shell layers. The myostraca are built up of prisms, with highly irregular outlines. These prisms are orientated with their long axes normal to the surfaces of the myostracum, with crystallographic axes lying in the same direction (text-fig. 6c). There are no well-developed interprismatic protein walls, but thin organic matrix envelopes surround each prism.

The pallial myostracum is a thick sheet, extending into the umbo (text-fig. 6a). The adductor myostraca are thick, well-developed pads. In addition to these features, areas of myostracal structure are present in the Chamacea away from well-authenticated areas of muscle attachment. Sheets of myostracal-type prisms are present within the inner shell layer of many species, and represent interruption of deposition of normal shell fabric (Pl. 73, fig. 7). This may be due to periodic attachment of the mantle surface, but there is no direct evidence for this, although structure and fluorescence properties are identical with those of normal myostracum. Pillar-like areas of myostracal structure, called myostracal pillars (Taylor, Kennedy, and Hull 1969) occur in the inner layer of most species of Chamacea and in the crossed-lamellar layer of a few species (Table 1).

These pillars appear in sections as elongate ovoids or strips of myostracal structure, the long axes running normally to the shell interior (Pl. 73, fig. 5). In the inner layer they usually extend upwards from the pallial or adductor myostracum (text-fig. 6c).

On shell interiors, myostracal pillars open as minute bosses, usually 0.5–1.0 mm. in diameter, or as elongate ovals, often arranged in lines radiating from the umbo.

Electron-microscopy shows that the surfaces of the bosses consists of a series of irregular prisms, corresponding to those seen at optical level (Pl. 74, fig. 4). The prisms are separated by grooves, of uncertain origin.

Sections of the mantle of Chamacea jukesii reveal the presence of minute papillae all over
the mantle surface, corresponding in size and distribution to the myostracal pillars of the shell. These papillae result from elongation of the normal mantle cells, and we take them to be sites of additional shell and mantle attachment.

A peculiar modification of the sheets of myostracal type prisms present in the inner shell layer is seen in *Chama calcarata* and *Chama gigas*. Here, the inner surface of the inner shell layer is pitted. These pits correspond to depressions in the surfaces of the myostracal sheets (Pl. 72, fig. 1), and presumably reflect another mode of shell/mantle attachment.

(c) *Layer contacts.* Crossed-lamellar and complex crossed-lamellar layers are separated by the pallial and adductor myostraca. There is usually a transition zone at the layer/myostracum contact, rich in organic matrix. The organic matrix of the myostracum and the crossed-lamellar or complex crossed-lamellar layers is in structural continuity. There is often a complex interdigitation of adductor myostracum and shell layers (text-fig. 40). This is probably the result of slight shifting of the animal within its shell during growth.

The contact of the crossed-lamellar layer and the outer prismatic layer of *C. pellucida* and *C. exogyra* shows several unusual features (Pl. 73, fig. 8). The surface at contact is minutely corrugated, the corrugations apparently originating at the shell margin, as a reflection of the position of the pallial muscles. They are subsequently buried below the middle layer, filled by a thin zone of fine-grained aragonite, rich in organic matrix (Pl. 74, fig. 2). Elsewhere, this layer is replaced by a complex and irregular junction with minute angular crystals protruding into the crossed-lamellar layer, as though a highly irregular surface was grown over by crossed-lamellar structure. These relationships closely resemble the results of partial recrystallization of aragonite to calcite.

The organic matrix of prismatic and crossed-lamellar layers is in direct structural continuity.

(f) *Tubules.* Many species of Chamacea possess the remarkable shell feature which Oberling (1964) described as tubules (Pl. 74, fig. 8).

These are minute cylindrical perforations, only a few microns in diameter, which open at the interior surface of the shell and penetrate the shell layers. Tubules are a primary feature of the shell (Oberling 1964; Taylor, Kennedy, and Hall 1969), and appear as minute hollow cylinders penetrating the finest elements of the shell fabric (Pl. 74, fig. 8). On the shell interior, *Chama* tubules lie in minute pits. The function of tubules is at present unknown.

(g) *Ligament.* The ligament of the Chamacea is calcified and aragonitic, as in other bivalves with calcified ligaments (Lowenstam 1964; Taylor, Kennedy, and Hall 1969) (Pl. 77, fig. 1).

(h) *Banding.* All shell layers show prominent daily growth bands (Panella and MacClintock 1968).

**COMPARISON OF THE CHAMACEA WITH OTHER GROUPS**

The systematic position of the Chamacea has always been in doubt. Consideration of their affinities in the past was not helped by the allotment to this superfamily of several other cemented bivalves such as the rudists and the pandoraceans, *Cleidothaerus* and
Myochara. However, as it stands today, the superfamily Chamacea can be considered a homogeneous group.

The Chamacea have been related to the Lucinacea (Douvillé 1912, Nicoll 1952), Carditacea (Dall 1903), the Cardiacea (Anthony 1905), Crassatellacea (Boehm 1891), Veneracea (Fischer 1886), and to the Hippuritacea (see references in Odhner 1919, Newell 1965, Yonge 1967). Of all these possibilities that of relationship to the rudists is the most commonly held. Odhner (1919) came to this conclusion after a detailed study of Chama, and Cox (1960) in deference to the thoroughness of Odhner’s work accepted the conclusion but thought they should constitute a separate superfamily.

The similarities of the Chamacea to the various superfamilies listed above are discussed below. A summary of some of the more easily tabulated characters of possible relatives amongst living bivalve superfamilies is given in Table 2. The affinities with the extinct rudists are more difficult to examine because of the lack of soft parts, but Yonge (1967) has made certain inferences concerning rudist soft parts based on a study of the inner shell morphology.

1. Comparison with the Carditacea

Two distinct groups can be recognized within the Carditacea.
(a) The Venericardia group, which are burrowers with generally rounded shell outlines, the hinge plate is short and high, and the ornamentation usually consists of radial ribs. The hinge plate is usually elongate and the anterior adductor muscle is somewhat reduced. The ornament is usually of radial ribs, but some species can produce squamae. This group contains many tropical species associated with coral reefs and rocky shores.

It is to this second group that the Chamacea may be compared. As can be seen from Table 2 some soft part characters such as the degree of mantle fusion and the gill plication are different, but others, such as labial palps and stomach types, are similar.

The greatest similarity between the Chamacea and the Carditacea is seen in shell characters such as the shell structure, dentition, ornament, and the similarity of the unincemented dissoconch of Chama to the adult byssate Cardita.

Thus the outer shell layer of the Carditacea consists of crossed-lamellar structure, with rather fine first-order lamels. The inner layer is built up of complex crossed-lamellar structure. Myostracal pillars are present in most species; in some the pillars are confined to the inner layer but in others they occur in both layers. Myostracal-type prisms can also be present, as fine sheets interbanded with complex crossed-lamellar structure in the inner layer. Tubules were present in all the species we have examined.

The dentition of the Carditidae shows striking similarities to that of the Chamacea. Both families have a ‘lucinoid’ dentition. The notation for Cardita variegata Bruguère, Recent, Seychelles is:

<table>
<thead>
<tr>
<th>Right valve</th>
<th>n 0 1 0 1 0</th>
<th>Anterior</th>
</tr>
</thead>
<tbody>
<tr>
<td>Posterior</td>
<td>n 0 1 0 1 0</td>
<td></td>
</tr>
<tr>
<td>Left valve</td>
<td>n 0 1 0 1 0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>d d</td>
<td></td>
</tr>
</tbody>
</table>
### Table 2. Main features of the bivalve superfamilies Chamacea, Carditacea, Lucinacea, Crassatellacea, Cardiacea, and Veneracea

<table>
<thead>
<tr>
<th>Superfamily</th>
<th>Mode of life</th>
<th>Outer layer</th>
<th>Middle layer</th>
<th>Inner layer</th>
<th>Mysidial pillars</th>
<th>Mysidial sheets</th>
<th>Tubules</th>
<th>Ligament</th>
<th>Hinge teeth</th>
<th>Musculature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chamacea</td>
<td>Cemented</td>
<td><em>Crossed-lamellar</em></td>
<td>Complex crossed-lamellar</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td>External opisthodetic</td>
<td>Lucinoid</td>
<td>Inner fold fused between inhalent/exhalent areas</td>
</tr>
<tr>
<td>Carditacea</td>
<td>Byssoic or burrowing</td>
<td>Crossed-lamellar</td>
<td>Complex crossed-lamellar</td>
<td>Present in some</td>
<td>Present in some</td>
<td>Present</td>
<td>Present</td>
<td>External opisthodetic</td>
<td>Lucinoid</td>
<td>Inner fold</td>
</tr>
<tr>
<td>Lucinacea</td>
<td>Burrowing</td>
<td>Composite prismatic</td>
<td>Crossed lamellar</td>
<td>Rare</td>
<td>Present in some</td>
<td>Rare</td>
<td>Sub-internal</td>
<td>Lucinoid</td>
<td>Inner fold</td>
<td></td>
</tr>
<tr>
<td>Crassatellacea</td>
<td>Burrowing</td>
<td>Crossed-lamellar</td>
<td>Homogeneous in Crassatellidae, prisms in Asthariae</td>
<td>Absent</td>
<td>Present in Asthariae</td>
<td>Absent</td>
<td>Asthariae: external opisthodetic</td>
<td>Crossatellida: internal resilinum</td>
<td>Cyrenoid</td>
<td>Inner fold, fusion at point between inhalent/exhalent areas</td>
</tr>
<tr>
<td>Cardiacea</td>
<td>Burrowing</td>
<td>Crossed-lamellar</td>
<td>Complex crossed-lamellar</td>
<td>Absent</td>
<td>Thin sheets in inner layer</td>
<td>Absent</td>
<td>External opisthodetic</td>
<td>Lucinoid</td>
<td>Inner fold and inner surface of middle fold</td>
<td></td>
</tr>
<tr>
<td>Veneracea</td>
<td>Burrowing, rarely byssate</td>
<td>Crossed-lamellar or homogeneous</td>
<td>Complex crossed-lamellar or homogeneous</td>
<td>Absent</td>
<td>Thin sheets in inner layer of some species</td>
<td>Absent</td>
<td>External opisthodetic</td>
<td>Cyrenoid</td>
<td>Inner fold and inner surface of middle fold</td>
<td></td>
</tr>
</tbody>
</table>

* C. pellucida and C. exogyra have an outer prismatic calcaite layer, middle crossed-lamellar layer and inner complex-crossed lamellar layer.
<table>
<thead>
<tr>
<th>Superfamily</th>
<th>Siphons</th>
<th>Labial palp</th>
<th>Gill type</th>
<th>Gill cilia</th>
<th>Stomach type (Purchon 1958)</th>
<th>Stomach type (Dinant 1967)</th>
<th>External armature</th>
</tr>
</thead>
<tbody>
<tr>
<td>CHAMACEA</td>
<td>Short inner fold</td>
<td>Type 2</td>
<td>Plicate</td>
<td>C 1</td>
<td>4 and 5</td>
<td>3a</td>
<td>Radial and concentric squamae, or spinose</td>
</tr>
<tr>
<td>CARDITAEEA</td>
<td>No siphons</td>
<td>Type 2</td>
<td>Non-plicate</td>
<td>Not examined</td>
<td>4</td>
<td>3a</td>
<td>Radial ribs, some squamae and reticulate</td>
</tr>
<tr>
<td>LUCINACEA</td>
<td>If siphon present then inner fold</td>
<td>Type 3</td>
<td>Non-plicate</td>
<td>G 1</td>
<td>4</td>
<td>Not examined</td>
<td>Concentric, some radial and reticulate</td>
</tr>
<tr>
<td>CRASSATELLACEA</td>
<td>No siphons</td>
<td>Type 3 (Crassatellidae)</td>
<td>Non-plicate</td>
<td>C 1</td>
<td>4</td>
<td>Not examined</td>
<td>Concentric, costae and striae</td>
</tr>
<tr>
<td>CARDIACEA</td>
<td>Inner and middle fold</td>
<td>Type 2</td>
<td>Plicate heterorhabdic</td>
<td>C 1</td>
<td>5</td>
<td>3</td>
<td>Radial ribs or concentric, some spines</td>
</tr>
<tr>
<td>VENERACEA</td>
<td>Inner and middle fold</td>
<td>Types 2 and 3</td>
<td>Plicate heterorhabdic</td>
<td>C 1 and C 2</td>
<td>5</td>
<td>3</td>
<td>Concentric, some radial, reticulate or spinose</td>
</tr>
</tbody>
</table>
and for Cardita tenuicosta Sowerby, Cretaceous (Albian), Gault, Folkestone (Pl. 75, fig. 1)

<table>
<thead>
<tr>
<th></th>
<th>Right valve</th>
<th>Posterior</th>
<th>Left valve</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anterior</td>
<td>1 0 1 n</td>
<td>0 1 0</td>
<td>0 1 0 1</td>
</tr>
</tbody>
</table>

If these are compared with that of a relatively unmodified Chama from the Eocene, striking similarities are seen. The subsequent modification of the teeth in Chama has been associated with the cemented habit. Both early Chama and recent Cardita have one stout anterior cardinal and a long arcuate posterior cardinal.

Radial ribbing is the most frequent ornamentation pattern of Carditidae but some byssate species such as Cardita crassicostata Reeve can develop large squamae (Pl. 75, fig. 4). Many Cretaceous species such as Fenestrocardita fenestrata (Forbes) (Pl. 75, fig. 6) have a reticulate ornament. Cardita distorta Reeve, a Red Sea species which lives byssally attached amongst coral, has become inequivalve and very Chama-like in appearance (Pl. 75, fig. 5).

The external opisthidetic ligament of the Carditidae is frequently sunk between the dorsal valve margins. A similar condition is seen in several heterodont superfamilies, including the Chamaeacea.

The dissoconch of the Chamaeacea shows striking resemblances to the byssate Carditidae (text-fig. 3, Pl. 71, fig. 1) both externally and internally, including the dentition. These similarities could, however, be morphological convergence as the result of the byssate attachment.

 Certain adult Cretaceous carditid genera show a remarkable similarity in morphology to the dissoconchs of some Recent Chama species. For instance Fenestrocardita fenestrata (Forbes) (Pl. 75, fig. 6), Aptian, England, while being a typical carditid shell shape has an ornament very similar to that shown on many Chama (Pl. 71).

The less-common Trapesiocardita (Casey 1961, p. 581; Keeping 1983, pl. 6, figs. 5a and b; Woods 1907, p. 148, pl. 28, figs. 12–15) from the Upper Aptian of England, has the same ornament. More interestingly it has the shell shape of the Recent byssate Carditidae. It is possible these or similar carditids that are the ancestors of the Chamaeacea.

2. Comparisons with the Lucinacea

Douvillei (1912) proposed that the Chamaeacea were derived from the Lucinacea during the late Cretaceous. This view was supported by Nicol (1952) on the basis of shell morphology.

EXPLANATION OF PLATE 75

Fig. 1. Cardita tenuicosta Sowerby, Cretaceous (Albian), Gault, Folkestone, England. a, right valve showing hinge teeth; b, left valve. Both × 4.

Abbreviations: C, cardinal teeth; L, lateral teeth.

Fig. 2. Cardita beaumonti var. amelacia d’Archiac, Upper Cretaceous, Gafar, Rutba, Iraq. Right valve, BMNH L.22245; × 0·75.

Fig. 3. Mystilocardis crassicosta Lamarck, Pleistocene, Limestone creek, Glenelg River, Victoria. BMNH L6570, × 1.

Fig. 4. Mystilocardis crassicosta Lamarck, Recent, New Holland. Left valve, × 2.

Fig. 5. Cardita distorta Reeve, Recent, Red Sea. a, Type, BMNH 1963686/2, ×1·5. b, Dorsal view.

Fig. 6. Fenestrocardita fenestrata (Forbes) Cretaceous, Aptian, Sevenoaks, England. Left valve, BMNH L.23280, × 3.
This apparent resemblance between the Lucinacea and the Chamacea is well seen only in *Archeilla*. Some Lucinacea have a groove on the posterior part of the exterior of the shell running from the umbo to the posterior-ventral margin. This is reflected on the inside of the shell as a low ridge at the anteriorward termination of the posterior adductor muscle scar, and is present at the shell margin as a slight nick. A similar groove on the exterior surface is seen in some Chamacea, although it is often obscured by the irregular surface ornament. The function of this exterior groove and internal ridge is uncertain, but it may be associated with the insertion of the posterior adductor muscle.

In many Lucinacea and a few species of *Chama* the ventral end of the anterior adductor muscle scar is detached from the pallial line (text-fig. 7) and extended in an anterior direction. Allen (1898) has shown that in the Lucinacea the elongate anterior adductor muscle is ciliated, and serves as a preliminary sorting area for food particles brought in by the anterior inhalant current. This anterior inhalant current is peculiar to the Lucinacea. In the Chamacea however, both inhalant and exhalant siphons are situated at the posterior end. Yonge (1967) has described how the foot of *Chama pellucida* protrudes and moves dorsally along the outer surface of the anterior adductor muscle, as in other cemented genera, assisting in the cleansing of the anterior mantle cavity.

The elongation in this instance is thus possibly related to the facility of mantle cleansing.

As can be seen from Table 2 the labial pulps, gill type, and gill cilia of the Lucinacea differ from those of the Chamacea, while they have the anterior inhalant current. Some species have a small posterior exhalant siphon which, although formed by fusion of the inner mantle fold, has a unique inversion retraction mechanism.

The shell of the Lucinacea consists of three layers. There is an outer composite prismatic layer, a middle crossed-lamellate layer, and an inner complex crossed-lamellate layer. This arrangement has been present since the Lower Lias (as in *Lucina limhata* Terquem and Piétre) at least. Myostracal pillars are not found, although thin sheets of myostracal-type prisms may be present in the inner layer. Tubules are very rare; we have found them only in the genus *Codakia*. Here, tubules, larger and sparser than in other bivalve groups, are found penetrating the inner shell layer only.

The dentition is primitive 'lucinoid' but many Lucinacea have lost teeth, and some are edentulous. The hinge notation for *Lucina pensylvanica* Linnaeus and *Codakia punctata* (Linnaeus) are given below:

<table>
<thead>
<tr>
<th></th>
<th>Right valve</th>
<th>Posterior</th>
<th>Left valve</th>
<th>Anterior</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0101n</td>
<td>(1)01(0)</td>
<td>1010</td>
<td></td>
</tr>
<tr>
<td>Anterior</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Codakia punctata (Linnaeus)

Right valve  (1) ne ne 10 1 10
Posterior
Left valve  (1)  (0) (1) ne ne 10 0 (0) 10 1
ne = ridge-bearing elastic ligament.
nc = ridge-bearing calcified ligament.

This pattern shows similarities to the Chamacea but also to the Carditacea.

All living species of Lucinacea are burrowers, and fossil forms seem to have been so since the Ordovician (McAlester 1965). Shell ornament varies from fine concentric growth-lines to radial ribs or a reticulate pattern. The sculpture is always fairly subdued.

3. Comparisons with the Crassatellacea

The superfamily Crassatellacea is divided into three families, the Crassatellidae, Astarticdae, and Cardiniidae. The first two families are extant but the latter family became extinct during the Jurassic.

The Astartinidae and Crassatellidae show rather different characters, and Boyd and Newell (1968) have suggested that the Crassatellacea may have had a diphyletic origin.

Both the Crassatellacea and the Astartacea have a two-layered shell. The outer layer of both consists of crossed lamellar structure. The inner layer of the Crassatellacea is homogeneous, whereas that of the Astartacea is made up of 'myostracal type' prisms with only small traces of complex crossed-lamellar structure. The shell structure characters of the Astartidae have been present since the Lower Jurassic.

The dentition of the Crassatellacea has been related to both the 'Lucinoid' and 'Cerebrinaeoid' patterns. Boyd and Newell (1968) have recently re-examined the dentition of this superfamly. They find that recent examples of Crassatellidae and Astartidae have rather similar hinges. For the crassatellid Hybolithus speciosus (Adams) the notation is:

Right valve  10 (1) e 10 10 1 10 1
Posterior
Left valve  10 1 e (0) 10 10 (1) 10 1
e = elastic ligament.
er = resilifer.

For Astartae castanea Say:

Right valve  10 (1) n 10 10 (1) 10 1
Posterior
Left valve  10 1 n 01 10 (0) (1) 0 1

Thus both examples have rather more complex hinge teeth structures than any of the early Chamacea.

The ligament of the Astartidae is external and opisthodetic but in the Crassatellidae there is an internal resilium.

The sculpture of both families is concentric, frequently with raised costae but they are often smooth or concentrically striate. Radial sculpture is never developed.

Members of both the Crassatellidae and Astartidae are shallow burrowers.
4. Comparison with the Cardiacea

The Chamacea were considered to have arisen from the Cardiacea by Anthony (1905). His evidence was based primarily upon the ctenidia and the hinge teeth.

It can be seen from Table 2 that although the main shell layers in the Chamacea and Cardiacea are similar, neither tubules nor myostracal pillars are developed in the latter.

Cardiacea dentition is of a 'lucinoid' pattern, but with well-developed laterals as well as the usual cardinals. The development of these widely spaced laterals is a characteristic of the group. The hinge of Acanthocardia aculeata (Linnaeus) can be expressed as:

| Right valve | 1 0 1 (l) n | 1 0 (l) | 1 0 1 | Anterior |
| Posterior   | 1 0 1 n    | 0 1 0  | 1 0   |
| Left valve  | 1 0 1 n    | 0 1 0  | 1 0   |

and Fragum unedo (Linnaeus)

| Right valve | 1 0 1 | n 0 1 0 | 1 0 (l) | Anterior |
| Posterior   | 1 0 (l) n | 1 0 1  | 1 0 1 0 |
| Left valve  | 1 0 (l) n | 1 0 1  | 1 0 1 0 |

A hinge which, contrary to the opinion of Anthony (1905), is not like that of Chama. The ctenidia of the Cardiacea, although similar to those of Chama, show similarities to several other heterodont groups (Table 2).

All recent species of Cardiacea are shallow burrowers, although the Eocene genus Lithocardium which gave rise to the Tridacnacea was in all probability a byssate form.

The first Cardiacea appeared in the Upper Trias and have been distinct since, early members appearing morphologically very like Recent species.

5. Comparison with the Veneracea

The Chamacea were related to the Veneracea by Fischer (1887), who considered that the dissoconch stage of Arcinella showed similarities of external sculpture to the adult Venerupis.

Table 2 shows that many of the anatomical characters of the Veneracea are quite different from those of the Chamacea. The stomachs according to the classification of both Purchon (1958, 1960) and Dinamani (1967) are quite different. Mantle fusion is much more extensive in the Veneracea, fusion being by way of the inner mantle folds and the inner surface of the middle fold. Well-developed siphons are formed from these regions of the mantle.

The dentition of the Veneracea is typically of the 'eyrenoid' pattern, with three cardinals in each valve. This is an altogether more complex dentition than that found in the Chamacea. The notation of Callistina plana (Sowerby) from the Albion is:

| Right valve | n 0 1 0 1 0 1 1 | (0) (l) 0 1 0 | Anterior |
| Posterior   | n 0 1 0 1 0 1 0 |
| Left valve  | n 0 1 0 1 0 1 0 | 1 0 (l) |
and *Notochione columbiensis* (Sowerby), Recent, Ecuador:

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>(0)</th>
<th>(0)</th>
<th>1</th>
<th>0</th>
<th>1</th>
<th>0</th>
<th>1</th>
<th>0</th>
<th>0</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right valve</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Posterior</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left valve</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The Veneracea have an outer crossed-lamellar shell layer and an inner layer usually consisting of homogeneous structure, although in some species it is complex crossed-lamellar. The outer layer shows certain distinctive characters. Because the shell margin is frequently reflected, the first-order lamels of the outer part of the crossed-lamellar layer are arranged radially. They become arranged concentrically when traced inwards, and appear vertical in radial section. Frequently they grade into homogeneous structure at the shell interior. The outer layer thus appears to be built of three distinct shell structures. Both tubules and myostracal pillars are absent.

Most members of the Veneracea are burrowers, and a pallial sinus is developed in many species. However, some species such as *Gefrarium* can under unfavourable conditions, become byssate.

The ornamentation of the shell is mainly concentric, but reticulations, spines and squamae can be developed.

6. *Comparison with the rudists*

It is generally thought that the origin of the rudists lies in the Megalodontaecae, a Silurian to Lower Cretaceous group of pachyodonts, one of which, *Pachyrisma* (Lower to Upper Jurassic), became cemented, and gave rise to *Diceras* (Oxfordian to Tithonian) and subsequently the rest of the rudists (Cox 1933, Dechaseaux 1952).

Derivation of the Chamaecae from the Hippuritacea (Turonian to Maastrichtian) and Radiolitidae (Aptian to Maastrichtian) is unlikely. These forms, with their extensive changes in symmetry, the massive conical lower valves and lid-like upper valves, the porous calcitic shell layers, and the atrophied ligaments, are morphologically too divergent to be considered the ancestors of the Chamaecae. Similar arguments can be applied to the Caprinidae (Aptian to Maastrichtian).

Greater resemblance to the Chamaecae is shown by the Monopleuridae, Diceratidae, possibly the Requiniidae, some Caprotnidae, and the Megalodontaecae.

(a) *Megalodontaecae.* Members of this family were uncemented, and considering the reduction of the anterior part of the shell, were apparently byssally attached.

The shell structure of some well-preserved examples was examined. Examples of *Megalodon pumilis* Benecke and *Pachymegalodon crassus* Böhm from the Lower Lias of Valle del Paradiso, Crezzana, Italy, showed a two-layered aragonitic shell, with an outer homogeneous layer and an inner homogeneous to complex crossed-lamellar layer. The two layers are separated by the prismatic trace of the pallial myostracum. Some thin sheets of myostracal type prisms are present in the inner layer. Specimens of *Dugia trigonalis* Böhm, from the Lias near Verona, Italy, are badly recrystallized, but show what was an originally wholly aragonitic shell with two homogeneous layers separated by the trace of the pallial myostracum.

The hinge teeth of Megalodontidae show the pachydont condition, with massive cardinals, the notation for *Eumegalodon cucullatus* (J. Sow.) and *Pachyrisma grande* (Morris and Lycect) is shown below and in Plate 76, fig. 4; Plate 77, fig. 3.
Eumegalodon cucullatus:

\[
\begin{array}{c|c|c|c|c|c|c|c|c}
\text{Right valve} & 1 & 0 & 1 & n & 0 & 1 & 0 & 1 \\
\text{Posterior} & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 0 \\
\text{Left valve} & 0 & 1 & 0 & n & 1 & 0 & 1 & 0 \\
\end{array}
\]

The traces of small teeth and sockets (bracketed above) between the two large teeth of the left valve are remnants of an original actinodont condition.

Pachyrhisma grande:

\[
\begin{array}{c|c|c|c|c|c|c|c|c}
\text{Right valve} & 1 & 0 & n & 0 & 1 & 0 & 1 \\
\text{Posterior} & 1 & 0 & 1 & 0 & 1 & 0 \\
\text{Left valve} & 0 & 1 & n & 0 & 1 & 0 \\
\end{array}
\]

In these early derivatives of the actinodonts the ligament and its nymph are basically dorsal to the hinge teeth. Although the dentition appears to be disrupted into cardinals and laterals it is a modified actinodont dentition. The apparent cardinals and laterals are not necessarily homologous with those found in the veneroid type of heterodont dentition.

As is the case with the other rudist families discussed, this is a typical pachydont dentition with a reduced number of large cardinal-like teeth often with their greatest dimension vertical in relation to the plane between the valves.

Both species show a rather more complex notation than that of early Chamacea. Furthermore, the arrangement of the more massive teeth seen in this family is very distinctive.

(b) Diceratidae. This family can be derived directly from the Megalodontaceae; changes in the geometry, dentition, and musculature result from the acquisition of the cemented habit.

The dentition is simplified from the megalodontid pattern of Pachyrhisma. The smaller anterior teeth are lost. The large tooth in the left valve and the two large teeth in the right valve become larger, longer, and twisted. These changes are reflected externally by the exogyroform shape of the shell.

The notation of Diceras arietum Lamarck is shown below and in Plate 76, fig. 1.

\[
\begin{array}{c|c|c|c|c|c|c|c|c}
\text{Right valve} & 1 & 0 & n & 1 & 0 \\
\text{Posterior} & 0 & 0 & 1 \\
\text{Left valve} & 0 & 0 & 1 & 0 \\
\end{array}
\]

We have not found any specimens of Diceras well enough preserved to determine the original shell structure.

The rudists were cemented by either the right or the left valve and evolved a virtual inversion of dentition in later forms. Some later forms attached by the left valve have a single tooth in that valve and two teeth in the right valve, while forms attached by the right valve have one tooth in the right valve and two in the left valve. It is this point of resemblance with the Chamacea which has most impressed palaeontologists and zoologists. However, early ribbed oysters could be attached by either valve, but later oysters
are attached only by the left valve. It would thus seem that cementation by either valve may be a characteristic of the early history of cementation within a group. Resemblance of Diceras to the Chamacea is thus purely coincidental.

(c) Requiiniidae. This family shows certain features (such as the hinge teeth) in common with the Diceratidae, but additional modifications such as siphonal bands and accessory cavities appear.

Moderately unaltered specimens of Apricardiata tuscasi (d'Orbigny) from the Lower Campanian of Var, France, show an outer, calcite prismatic layer, and middle and inner aragonitic homogeneous layers. Thin prism sheets are seen in the inner layer.

(d) Caprotinidae (Neocomian-Turonian). Many species in this family are small and exogyriiform with an ornament of radial ribs. Together with the Monopleuridae they show the closest morphological resemblance to Chama among the rudists.

Material sufficiently unaltered for shell structure studies was not available, but it seems that Caprotina semistriata (d'Orbigny) from the Cenomanian of Le Mans had an outer calcitic layer and an inner aragonitic layer or layers.

The pattern of teeth has changed from that of Diceras by a shortening of the hinge plate, increase in size of the posterior tooth in the left valve, near atrophy of the ligament, and loss of the anterior tooth in the right valve. These changes are associated with the reduction of the free valve to a cap-shaped or opercular form. The notation can be expressed as below:

Right valve (fixed)  \begin{tabular}{c}
\hline
0 & 1 & 0 \\
\hline
\end{tabular}

Anterior.

Left valve (free)  \begin{tabular}{c}
\hline
1 & 0 & 1 \\
\hline
\end{tabular}

The position of the ligament in Caprotina is indicated by an infolding of the shell wall, marked by a shallow groove on the outer surface. The ligament is disposed vertically in relation to the valve commissure, so that the functional distance is therefore very short. It is doubtful whether the ligament in this case was a very effective mechanism for the opening of the valves. No comparable ligamental structure is found in the Chamacea.

**Explanation of Plate 76**

Fig. 1. *Diceratina urielanum* Lamarck, Jurassic (Oxfordian), Chatel-Censoir, Yonne, France, BMNH I.33915, ×1, 1, right valve, b, left valve.

Fig. 2. *Caprotina semistriata* (d'Orbigny), Cretaceous, Cenomanian, Le Mans, France, ×2, a, left (free) valve. BMNH I.6260. b, right (cemented valve) BMNH I.6260.

Fig. 3. *Eumegalodon cuculatus* (J. Sowerby). Devonian, Parthain, Cologne, Germany, ×2, a, right valve; b, left valve. Abbreviations: C, cardinal; L, lateral; n, ligament nympha; aa, anterior adductor muscle scar.

**Explanation of Plate 77**

Fig. 1. Fractured section of the inner calcified ligament of *Chama mucrosphyla* Gmelin. Scanning electron-micrograph, ×1000.

Fig. 2. Fractured section of the prismatic layer of *Chama pellicia* Broderip. Scanning electron-micrograph, ×280.

Fig. 3. *Pickeringia granda* Morris and Lyell, Jurassic, Great Oolite, Minchinghampton, England, ×9, a, Left valve showing hinge teeth; b, Right valve. Abbreviations: C, cardinals; L, laterals; n, ligament nympha; aa, anterior adductor muscle scar.
(e) Monopleuridae (Kimmeridgian–Danian). The Monopleuridae can be derived from the Diceratidae through Valleritia. Certain members of this family, for example Gyropleura cenomanensis (d’Orbigny) (Pl. 70, fig. 5) and Ciphyella pulchra (Ravn) (Pl. 72, fig. 5), show remarkable similarity in morphology to Chama. They are small to medium-sized, strongly exogyriform and radially ribbed. Ciphyella pulchra has commonly been considered to be a Chama, but the form of the adductor scars and the near atrophy of the ligament show that it is a rudist closely related to Gyropleura (N. J. M. and J. D. T., in litt.).

The dentition of the Monopleuridae resembles that of the Caprotilidae, but without the incipient splitting of the posterior tooth in the left valve seen in Caprottila (Pl. 76, fig. 2).

The teeth of Gyropleura are illustrated in a sketch by Deschaseaux (1952, 335, text-fig. 177), Gyropleura cornucopiæae (d’Orbigny) from the Middle Cenomanian of northwestern Europe, and G. inequirostra (Woodward) from the Campanian and Lower Maastrichtian of the same area, have a similar arrangement. The dentition of Monopleura (Deschaseaux 1952, 335, text-fig. 176) is also not significantly different.

The notations of Gyropleura cornucopiæae (d’Orbigny) is shown below:

<table>
<thead>
<tr>
<th>Right valve (fixed)</th>
<th>0</th>
<th>1</th>
<th>0</th>
</tr>
</thead>
<tbody>
<tr>
<td>Posterior</td>
<td></td>
<td></td>
<td>Anterior.</td>
</tr>
<tr>
<td>Left valve (free)</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

As is the case with the other rudist families discussed, this is a typical pachydont dentition with no differentiation into heterodont cardinals and laterals. It contrasts remarkably with the dentition of the earlier Chamacea. The teeth of Chama calcarata, for example (Pl. 72, fig. 2), although twisted to lie sub-parallel to the line of the ligament, still diverge slightly below the umbones and in the fixed valve may be matched tooth for tooth with many fossil and recent Carditidae.

No well-preserved material was available for shell structure studies. Specimens of Gyropleura cenomanensis from the Cenomanian of Le Mans, France, however, appear to have an aragonitic inner layer or layers and a calcitic outer layer. The preservation of a specimen of Gyropleura inequirostra (Woodward) from the Upper Campanian Chalk of Sidestrand, Norfolk, England, indicates the same arrangement.

Major differences occur in the adductor musculature between the Chamidae and the Monopleuridae together with all other rudists. In the Melegodontaceae, the posterior adductor scar is associated with a plate or myophoric septum (Pl. 76, fig. 3) which seems to add strength to the shell in the form of a buttress. The anterior adductor scar is in the form of a shallow, cup-shaped socket (Pl. 76, fig. 3; Pl. 77, fig. 3). In Diceras, the animal becomes attached by one valve and presumably takes up a posture reclining on one side. The umbones become widely separate, each valve becoming cornucopia shaped. The adductor musculature attachment has had to compensate in order to remain near normal to the direction of adduction. This compensation took the form of certain modifications of the muscle attachment area. In the Caprotilidae and the Requeniidae, the anterior adductor scar occurs on a raised platform in either valve so that the actual length remains at a minimum. At the same time this muscle became extended parallel to the valve margins. The posterior adductor muscle attachment sank deeper into the space between the myophoric septum and the hinge plate in the Requeniidae. In the
Caprotinidae, the same septum joined with the hinge plate to form a deep accessory cavity to house the posterior adductor muscle. In the Monopleuridae both the posterior and the anterior muscles form elongate scars on raised platforms which tend to form extensions to the hinge plate. They are somewhat less prominent in the fixed valve. The Monopleuridae retain a somewhat reduced posterior myophoric septum.

In marked contrast to these developments in the rudists, the adductor muscle scars of the Chamidae are broadly similar to those of most other heterodont groups, except that the dorsal portion of the anterior adductor scar of both valves impinges somewhat upon the hinge plate.

The resemblance of Gyropleura and other Monopleuridae to Chama is merely that of convergent adaptions to the same cemented mode of life under similar habitat conditions. Similar exogyrisiform shapes are found in totally unrelated bivalves, e.g. Ostreacea, Pandoracea, Spondylidae, Unionacea, and the Chamacea.

**DISCUSSION**

From the comparison of the Chamacea with their possible relatives, it appears to us that amongst these groups only the superfamilies Carditacea and Lucinacea are likely to be closely related.

The rudists, for so long considered closely related to the Chamacea show certain similarities, but these are only the result of convergence because of the cemented habit.

The shell structure characters of the Carditacea match exactly those of the Chamacea (except for the development of calcite in *C. pelletoida* and *C. exogyros*), whereas the Lucinacea have an extra outer shell layer. The dentitions of the Chamacea, Lucinacea, and Carditacea are all very similar. Certain shell morphology features such as the shape of the anterior adductor muscle scar, and the groove on the exterior, suggest similarities with the Lucinacea.

The Carditacea, however, contain many species which are byssally attached, and are asymmetrical; some are inequivalve. The Lucinacea are all burrowers. The Lucinacea and the Carditacea have had a distinct history at least as far back as the Ordovician (McAlester 1965).

The weight of evidence suggests to us that the Chamacea were derived from a byssate *Cardita* during the late Cretaceous. *Chama lanteri*, the first authenticated *Chama*, is a 'good' *Chama* but rather less inequivalve than many Recent species. Transitional forms (other than the assumption of the byssate habit) between Carditacea and Chamacea are lacking; however, if the Cardita origin is not accepted, then possible transitional forms are not found between the Chamacea and any other group. However, possibly byssate *Cardita* are common in the Cretaceous, for example forms from the Upper Cretaceous of Gharra, Ruthbah, Iraq (BMNH LL2245–8) labelled *Cardita beaumonti var. amelliae d’Archiac. They are thick-shelled, subrectangular in shape with coarse radial and concentric ornament, on which short spines are developed (Pl. 75, fig. 2). Although perhaps too late in time to be thought of as ancestral to the Chamacea, they show the forms among which the origin of the group should be sought. An alternative would be probably byssate forms such as *Fenestricardita* (Pl. 75, fig. 6).

The superfamily Chamacea should be removed from the Order Hippuritoida and placed in the Veneroida.
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