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

by W. J. KENNEDY, N. J. MORRIS, *and* J. D. TAYLOR

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, Crassatellacea, Lucinacea, and the rudists (Hippuritacea).

Most classifications have placed the Chamacea with the rudists; Newell (1965) placing them into the Hippuritoida, 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 *Cardita* in the early or middle Cretaceous. Similarities to the rudists are the result of convergent adaptions 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 origins 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 Megalodontacea 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 arcinella (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 Chamacea 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 Chamacea are rather less inequivalve than extant forms. The secondarily free genus *Arcinella* (Pl. 70, fig. 2) has returned to a more or less equivalve state. The shell of the Chamacea 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 squamae. 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 masculature 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 Chamacea 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 purely 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),

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and the rate of whorl translation parallel to the coiling axis (T) (for full details and deriva-
tion see Raup 1966). For most bivalves D is small, and in the Chamacea it is approxi-
mately zero. The shape, S, of the generating curve is difficult to define mathematically
and is not considered here.
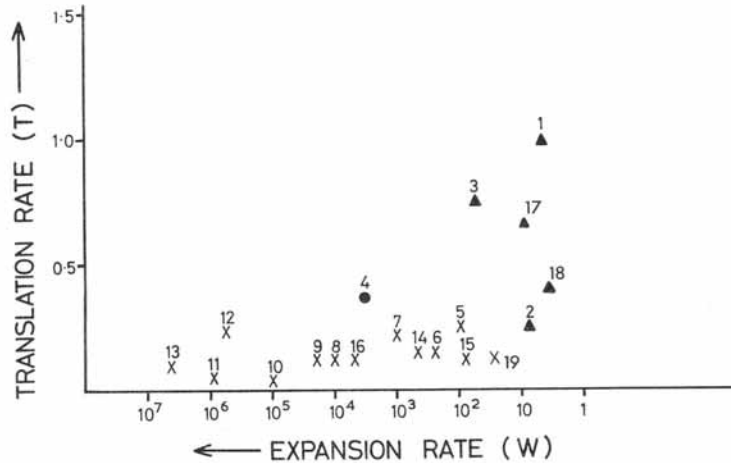
TEXT-FIG. 1. Shell geometry of the Chamacea in relation to other bivalves. Expansion rate (w) plotted
against translation rate (T) for a series of uncemented bivalves (x), cemented Chamidae (▲), and the
secondarily free *Arcinella arcinella* (●).

Key to numbers:

1, 2. *Chama imbricata* (1 = upper valve,
    2 = lower valve).
3. *Chama plicata* Sowerby. Upper valve.
4. *Arcinella arcinella* (Linnaeus). Both valves.
5. *Fragum unedo* (Linnaeus).
6. *Hippopus hippopus* Linnaeus.
7. *Trigonia pectinata* Lamarck.
8. *Codakia tigerina* (Linnaeus).
9. *Mytilus galloprovincialis* Lamarck.
10. *Chlamys varia* Linnaeus.

11. *Gloripecten pallium* (Linnaeus).
12. *Lima squamosa* Lamarck.
13. *Pinctada margaritifera* (Linnaeus).
14. *Crassatella decipiens* Reeve.
15. *Cerastoderma edule* (Linnaeus).
16. *Tellina virgata* (Linnaeus).
17, 18. *Chama gryphina* (Lamarck). (17 =
    lower valve, 18 = upper valve).
19. *Cardita bicolor* Reeve.

Accurate measurements of w and T are difficult to make in the Chamacea because of
the irregular growth form, ornament, and the corroded nature of most shells. Measure-
ments of w and T on *Chama gryphina* Lamarck (text-fig. 1) show that the expansion
rate of the lower valve lies between $10^{0.5}$ and $10^{0.9}$, and that of the upper valve is approxi-
mately 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. Measure-
ments of *Arcinella arcinella* (which has reverted to the uncemented mode of life) show
an expansion rate for both valves of approximately $10^{3.5}$. 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.

TEXT-FIG. 2. Sketch of *Chama bro-deripi* Reeve (with strongly enrolled umbos), Recent, Pacific. To show degree of ligament splitting. (Ligament in black.)

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 1953*b*).

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 *Chama*. 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, *Chama pellucida* Broderip, *Chama* 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.
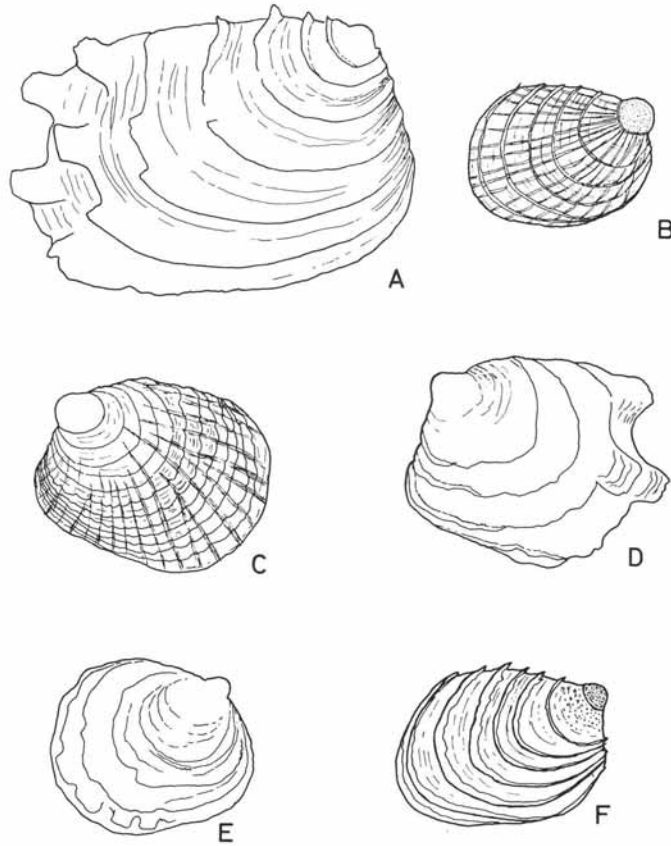
TEXT-FIG. 3. Prodissoconchs and dissoconchs of Recent Chamidae. A. *Arcinella arcinella* (Linnaeus), after Odhner (1919), ×60. B. *Chama pellucida* Broderip, Recent, California, ×60. C. *Chama pusilla* (Odhner), after Odhner (1919), ×40. D, E. *Chama gryphina* Linnaeus, after Odhner (1919), ×60. F. *Chama* sp. East Indies, ×70.

The sharp boundary between prodissoconch 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 uncemented, equivalve 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.

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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. jukesi* 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. 3). 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 teeth in these reversed 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

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EXPLANATION OF PLATE 71

Figs. 1, 2. *Chama pellucida* Broderip, Recent, California. 1, Prodissoconch, 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 prodissoconch and the dissoconch. Notice close bunching of growth lines as feeding ceases prior to metamorphosis. Scanning electron-micrograph, ×700.

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

Figs. 4, 5. Prodissoconch and dissoconch of *Chama* sp. from East Indies. 4, Scanning electron-micrograph, ×80. 5, Detail showing the contact between the prodissoconch 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 calcarata* (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 Chamacea 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 convertable to the Bernard system when homologous teeth are recognized. The two valves are illustrated beak to beak 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, nymph, and elastic ligament, etc.

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

Right valve	0 1 ⋮ n	(0) (1) 0 1 0 1	
Posterior	————	————————	Anterior.
Left valve	1 ⋮	n (0) (1) 0 1 0 1 0	

n = ligament nymph

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 nymphs. They are indicated in parentheses.

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

Right valve	0 1 n 0 1 0 1	
Posterior	———————	Anterior.
Left valve	1 (0) n 1 0 1 0	

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 has also occurred.

In *Arcinella arcinella* (an inverse form) a similar notation occurs, with the fusion of the cardinals and sockets:

$$\text{Posterior} \quad \frac{\text{Right valve} \quad \text{n 1} \mid \overset{\frown}{0\ 1\ 0}}{\text{Left valve} \quad \text{n 0} \mid \underset{\smile}{1\ 0\ 1}} \quad \text{Anterior.}$$

It will be shown below that the dentition of the early Chamacea shows great resemblances to that of the Carditacea.

ANATOMY

Studies on the anatomy of several species of Chamacea have been made by Anthony (1905), Pelseneer (1911), Grieser (1913), Odhner (1919), and most recently by Yonge (1967) who studied *Chama pellucida* 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

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EXPLANATION OF PLATE 72

Fig. 1. *Chama macerophylla* Gmelin, Recent, Bermuda. BMNH 1911.12.21.1322.3. *a*, Right valve, hinge teeth, ×2. *b*, left valve, ×2. Abbreviations: C, cardinal teeth; L, lateral teeth; n, ligament nymph; add, adductor muscle scar.

Fig. 2. *Chama calcarata* Deshayes, Eocene, Lutetian, Grignon, France. *a*, Right valve, showing hinge teeth, ×2. *b*, Left valve, ×2.

Fig. 3. *Chama* sp. Maastrichtian, Cotentin, France. Silicone rubber cast, ×2.

Fig. 4. *Chama haueri* Zittel, Cretaceous, Senonian Gosau Beds, Gosau, Austria. ×0·75. *b*, dorsal view.

Figs. 5, 6. *Ciplyella pulchra* (Ravn), Cretaceous, Danian, Faxe, Denmark ×1. 5, internal cast, left valve. BMNH L13601. 6, anterior view, BMNH L25558.

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 Odhner (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 Stasek (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 *Chama* in his type IIIa.

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

GEOLOGICAL HISTORY

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

Chama coquandi 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 *Chama* species.

Chama haueri 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. toeroeki* Pethö (1906, 269, pl. 19, figs. 15–16) from the Upper Cretaceous of Hungary are all good *Chama* species.

C. haueri 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 *haueri* 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).

Douvillé (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 à 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. moritzi* Strombeck (1863, 156) are all species of *Gyropleura*. *C. spondyloides* Bayle (1856, 365, pl. 14, fig. 1) is a monopleurid rudist. *C. triedra* Pictet and Campiche (1867, 5, pl. 140, figs. 4–5) and *C. gracilicornis* Pictet and Campiche (1867, 6, pl. 140, figs. 6–7) are both diceratid rudists. *C. boulei* 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* Griepenkerl (1899, 362, pl. 7, fig. 2), *C. costata* Roemer (1841, 67, pl. 8, fig. 20), *C. multicostata* 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 Koralkalk of Denmark seems to belong to the Monopleuridae (see p. 409). *Chama ciplyensis* Vincent (1928, 104, pl. 5, fig. 17) from the Danian or Montian Poudingue de Ciply of Belgium is little known. The description of its adductor scars suggest that it is a genuine *Chama*. *Chama ancestralis* 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*.

Arcinella (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 draconis* Dall (Nicol 1952).

Most of the fossil occurrences of *Chama* are in association with rich shallow marine faunas of tropical or subtropical aspect.

C. exogyra and *C. pellucida* 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 'Stereoscan' 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 ectostracum, mesostracum, and endostracum for three-layered shells, mesectostracum and mesendostracum 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 *myostracum* for the peculiar blocky prismatic aragonite laid down under sites of muscle attachment, i.e. the pallial, pedal, and adductor myostraca.

(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.
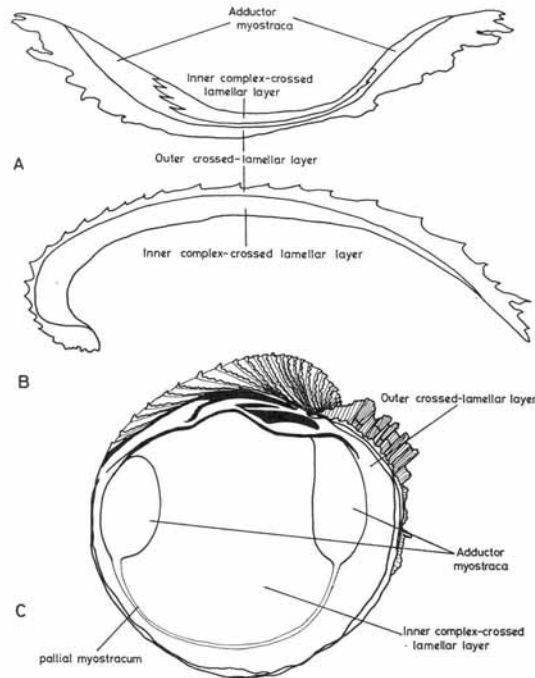
TEXT-FIG. 4. (A) Transverse section, (B) longitudinal section, and (C) interior of *Chama macerophylla* Gmelin to show distribution of shell layers.

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 Bøggild (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 (Bøggild 1930). These are in turn built of minute laths, about 1 μ in diameter and some

TABLE 1. Shell structure and mineralogy of recent and fossil Chamacea

Species	Horizon and locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Chama haueri Zittel	Senonian, Gosau, Austria	Aragonite	Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	
Chama calcarata Lamarck	Lutetian, Chaumont en Vexin, France		Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	
Chama calcarata Lamarck	Lutetian, Mouchy, France		Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	Myostracal sheets in inner layer locally folded (see text)
Chama lamellosa Lamarck	Lutetian, Damercy, France	Aragonite	Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	
Chama gigas Deshayes	Lutetian, Grignon, France		Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	Myostracal sheets in inner layer similar to those in *C. calcarata*
Chama selseiensis S. V. Wood	Lutetian, Brackle-sham, England		Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms and myostracal pillars	Prismatic	Prismatic	
Chama turgida Lamarck	Basal Auversian, Chavençon, France		Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms and myostracal pillars	Prismatic	Prismatic	Scattered tubules in inner layer
Chama fimbriata Defrance	Auversian, Auvers, France		Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	
Chama papyracea Deshayes	Auversian, Auvers, France		Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	
Chama squamosa Solander	Bartonian, Barton, England		Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	Scattered tubules in inner layer
Chama squamosa Solander	Ludian, Chavanion, France		Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms and myostracal pillars	Prismatic	Prismatic	Scattered tubules in inner layer

Species	Locality/Age					
Chama aquitanica Cossman and Pissarro	Aquitanian, Villandrani, Italy	Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	
Chama sp.	Miocene, San Domingo	Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	
Chama crassa Chenu	Pliocene, Florida	Crossed-lamellar	Complex crossed-lamellar with thin sheets of myostracal-type prisms	Prismatic	Prismatic	Scattered tubules in inner layer
Chama heilprini (Nicol)	Plio-Pleistocene, La Belle, Florida	Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms and myostracal pillars	Prismatic	Prismatic	Scattered tubules in inner layer
Chama brocchii Deshayes	Pleistocene, Asti?, giana, Italy	Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	Scattered tubules in inner layer
Chama gryphina Lamarck	Pleistocene, Piedmont, Italy	Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	
Chama gryphina Lamarck	Pleistocene, Asti-giana, Italy	Crossed-lamellar	Complex crossed-lamellar with thin sheets of myostracal-type prisms	Prismatic	Prismatic	
Chama nivalis Reeve	Pleistocene, Berbera, Somalia	Crossed-lamellar with scattered myostracal pillars	Complex crossed-lamellar with sheets of myostracal-type prisms and myostracal pillars	Prismatic	Prismatic	Myostracal pillars in the inner parts of the outer layer; scattered myostracal pillars in inner layer. Tubules in inner layer
Chama pulchella Reeve	Pleistocene, Berbera, Somalia	Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms and myostracal pillars	Prismatic	Prismatic	Tubules in inner layer
Arcinella arcinella antiquata (Dall)	Miocene, Colombia	Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	
Arcinella trachyderma (Pilsbry and Johnson)	Miocene, San Domingo	Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	

Species	Horizon and locality	Mineralogy	Outer layer	Inner layer	Myostraca Pallial	Myostraca Adductor	Observations
Arcinella arcinella arcinella (Linnaeus)	Pliocene, Caloosa-hatchee, Florida		Crossed-lamellar	Complex crossed-lamellar with sheets of myostracal-type prisms	Prismatic	Prismatic	
Arcinella arcinella (Linnaeus)	W. Florida	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic	Thick prismatic	Layers of myostracal-type prisms present in inner layer; other specimens have myostracal pillared tubules
Chama aspera Reeve	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic	Thick prismatic	Myostracal pillars in inner layer
Chama brassica Reeve	Philippines	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic	Thick prismatic	Thin bands of myostracal-type prisms and tubules in the inner layer
Chama gryphina Lamarck	Mediterranean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic	Thick prismatic	Myostracal pillars and scattered tubules in inner layer; some specimens have bands of myostracal-type prisms in this layer
Chama iostoma Reeve	Aden	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic	Thick prismatic	Abundant myostracal pillars and scattered pillars in inner layer. Other (? pedal) myostraca in some sections
Chama lazarus Wood	Mombasa, E. Africa	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic	Thick prismatic	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
Chama nubea Reeve	Philippines	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic	Thick prismatic	Abundant radially elongate myostracal pillars and scattered tubules in the inner layer

| Species	Location	Mineralogy					Remarks
Chama sarda Reeve	W. Indies	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic	Thick prismatic	Myostracal pillars and scattered tubules in the inner layer
Chama spinosa Broderip	Dunken Island, Cape York, Queensland	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic	Thick prismatic	Tubules present in the inner layer; myostracal pillars occur in some specimens
Chama spondylodes Menke	Queensland	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic	Thick prismatic	Tubules, sheets of myostracal-type prisms and myostracal pillars are present in the inner layer; the latter extend into the outer layer
Chama macerophylla Gmelin	W. Indies	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic	Thick prismatic	Myostracal pillars and abundant tubules in the inner layer
Chama corrugata Broderip	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
Chama radians Lamarck	W. Indies	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic	Thick prismatic	Abundant myostracal pillars in the inner layer
Chama pellucida Broderip	California	Aragonite and Calcite	Granular/prismatic calcite	*Middle layer* Crossed-lamellar aragonite	*Inner layer* Complex crossed-lamellar aragonite	*Myostraca* *Pallial* Thin prismatic aragonite	*Adductor* Thin prismatic aragonite
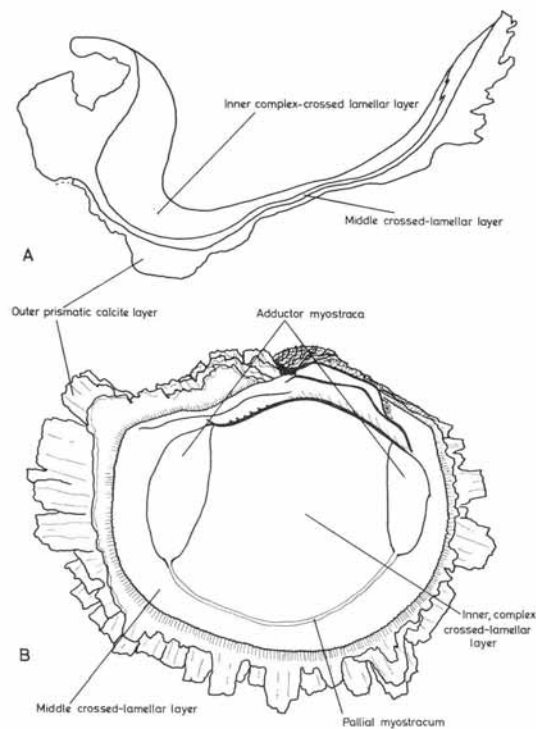
TEXT-FIG. 5. (A) Longitudinal section and (B) interior of *Chama pellucida*
Broderip to show the distribution of shell layers.

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 calcarata* Deshayes showing cone
shaped depressions in myostracal sheets, ×32.

Fig. 3. Planar section through the adductor myostracum of *Chama lazarus* 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 lazarus* Wood, ×20.

Fig. 7. Myostracal sheets in the inner complex crossed-lamellar layer of *Chama lamellosa* 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.
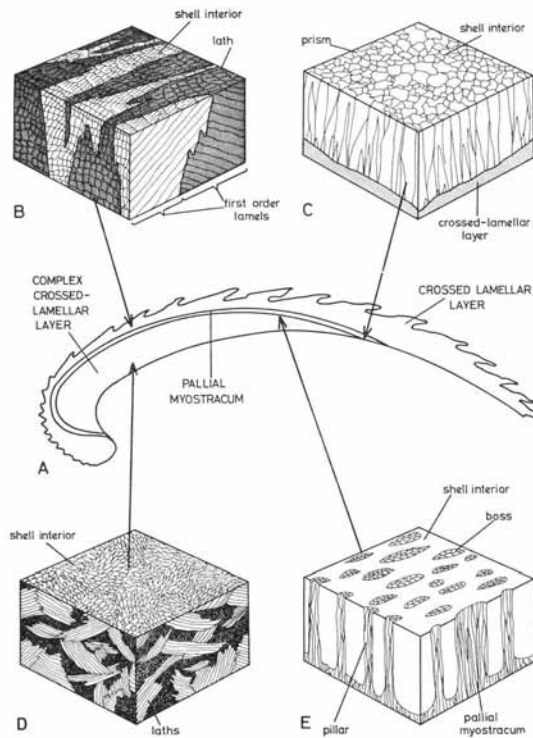
TEXT-FIG. 6. Radial section of a typical *Chama* (A) with block diagrams to show the microstructure of the crossed-lamellar layer (B), pallial myostracum (C), complex crossed-lamellar layer (D), and myostracal pillars (E).

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 Bøggild (1930). It is thus equivalent to 'complex' structure of Oberling (1964), which is not to be confused with 'complex' of Bøggild (1930)!

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

In some sections, small irregular patches of radiating laths are recognizable. Mac-Clintock (1967) has described these as sections of spherulitic growth. His patelloid 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 Pteriomorpha.

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

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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 radians*, showing laths joined into second-order lamels having variable orientations, ×240.

Fig. 4. Inner shell surface of *Chama radians*, showing the outcrop 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 radians* 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 conchiolin 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 Hall 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. 6e).

On shell interiors, myostracal pillars outcrop 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 *Chama 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. 73, fig. 1), and presumably reflect another mode of shell/mantle attachment.

(*e*) *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. 4*a*). 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 Mac-Clintock 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

Myochama. However, as it stands today, the superfamily Chamacea can be considered a homogeneous group.

The Chamacea have been related to the Lucinacea (Douvillé 1912, Nicol 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.

(*b*) The *Cardita* group, consisting of byssate forms, ovoid to subrectangular in outline. 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 uncemented 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* Bruguière, Recent, Seychelles is:

$$\begin{array}{l} \text{Right valve} \quad n\,0\,1\,0\,1\,0\,|\,1 \\ \text{Posterior} \,\rule{3cm}{0.4pt}\, \text{Anterior} \\ \text{Left valve} \quad n \;\; 0\,1\,0\,1\,|\,0\,1 \\ \qquad\qquad\qquad\; D\,d \end{array}$$

TABLE 2. Main features of the bivalve superfamilies Chamacea, Carditacea, Lucinacea, Crassatellacea, Cardiacea, and Veneracea.

Superfamily	Mode of life	Shell structure characters						Ligament	Hinge teeth	Mantle fusion
		Outer layer	Middle layer	Inner layer	Myostracal pillars	Myostracal sheets	Tubules			
CHAMACEA	Cemented	*Crossed-lamellar	—	Complex crossed-lamellar	Present	Present in some	Present	External opisthodetic	Lucinoid	Inner fold
CARDITACEA	Byssate or burrowing	Crossed-lamellar	—	Complex crossed-lamellar	Present in some	Present in some	Present	External opisthodetic	Lucinoid	Inner fold fused between inhalent/exhalent areas
LUCINACEA	Burrowing	Composite prismatic	Crossed lamellar	Complex crossed-lamellar	Rare	Present in some	Rare	Sub-internal	Lucinoid	Inner fold
CRASSATELLACEA	Burrowing	Crossed-lamellar	—	Homogeneous in Crassatellidae, prisms in Astartidae	Absent	Present in Astartidae	Absent	Astartidae: external opisthodetic Crassatellidae: internal resilium	Cyrenoid	Inner fold, fusion at point between exhalent/inhalent areas
CARDIACEA	Burrowing	Crossed-lamellar	—	Complex crossed-lamellar	Absent	Thin sheets in inner layer	Absent	External opisthodetic	Lucinoid	Inner fold and inner surface of middle fold
VENERACEA	Burrowing, rarely byssate	Crossed-lamellar homogeneous	—	Complex crossed-lamellar or homogeneous	Absent	Thin sheets in inner layer of some species	Absent	External opisthodetic	Cyrenoid	Inner fold and inner surface of middle fold

* C. pellucida and C. exogyra have an outer prismatic calcite layer, middle crossed-lamellar layer and inner complex-crossed lamellar layer.

Superfamily	Siphons	Labial palp Ctenidia Grade (Stasek 1963c)	Gill type (Ridewood 1903)	Gill cilia (Atkins 1937)	Stomach type (Purchon 1958, 1960)	Stomach type (Dinamani 1967)	External ornament
CHAMACEA	Short inner fold	Type 2	Plicate	C 1	4 and 5	3a	Radial and concentric squamae, or spinose
CARDITACEA	No siphons	Type 2	Non-plicate	Not examined	4	3a	Radial ribs, some squamate and reticulate
LUCINACEA	If siphon present then inner fold	Type 3	Non-plicate homorhabdic	G 1	4	Not examined	Concentric, some radial and reticulate
CRASSATELLACEA	No siphons	Type 3 (Crassatellidae) Type 1 (Astartidae)	Non-plicate	C 1	4	Not examined	Concentric, costae and striae
CARDIACEA	Inner and middle fold	Type 2	Plicate heterorhabdic	C 1	5	3	Radical ribs or concentric, some spines
VENERACEA	Inner and middle fold	Types 2 and 3	Plicate heterorhabdic	C 1 and C 2	5	3	Concentric, some radial, reticulate or spinose

and for *Cardita tenuicosta* Sowerby, Cretaceous (Albian), Gault, Folkestone (Pl. 75, fig. 1)

Right valve $\quad$ 1 0 1 n $\mid$ 0 1 0

Posterior $\quad\rule{3cm}{0.4pt}\quad$ Anterior.

Left valve $\quad$ 0 1 0 n $\mid$ 0 1 0 1

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 *Fenestricardita 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 opisthodetic ligament of the Carditidae is frequently sunk between the dorsal valve margins. A similar condition is seen in several heterodont superfamilies, including the Chamacea.

The dissoconch of the Chamacea 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 *Fenestricardita 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 *Trapezicardita* (Casey 1961, p. 581; Keeping 1883, 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 possibly these or similar carditids that are the ancestors of the Chamacea.

2. *Comparisons with the Lucinacea*

Douvillé (1912) proposed that the Chamacea 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. *amelliae* d'Archiac, Upper Cretaceous, Ga'ara, Ruthbah, Iraq. Right valve, BMNH LL22245; ×0·75.

Fig. 3. *Mytilicardia crassicosta* Lamarck, Pleistocene, Limestone creek, Gleneig River, Victoria. BMNH L6570, ×1.

Fig. 4. *Mytilicardia 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. *Fenestricardita fenestrata* (Forbes) Cretaceous, Aptian, Sevenoaks, England. Left valve, BMNH L23280, ×3.

This apparent resemblance between the Lucinacea and the Chamacea is well seen only in *Arcinella*. Some Lucinacea have a groove on the posterior part of the exterior of the shell running from the umbo to the postero-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 (1958) 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 inhalent current. This anterior inhalent current is peculiar to the Lucinacea. In the Chamacea however, both inhalent and exhalent 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.
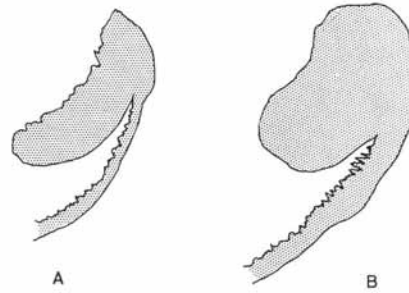
TEXT-FIG. 7. Diagram of the anterior adductor muscle pad and pallial line of (A) *Codakia punctata* Linnaeus and (B) *Chama macerophylla* Gmelin to show the comparable detachment of the ventral end of the muscle pad in the Lucinacea and Chamacea.

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

As can be seen from Table 2 the labial palps, gill type, and gill cilia of the Lucinacea differ from those of the Chamacea, while they have the anterior inhalent current. Some species have a small posterior exhalent 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-lameller layer, and an inner complex crossed-lamellar layer. This arrangement has been present since the Lower Lias (as in *Lucina limbata* Terquem and Piette) 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 primitively '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:

Lucina pensylvanica (Linnaeus)

Right valve	0 1 0 1 n	(1) 0 $\overline{1}$ (0) (1) 0 1	0 1 0	
Posterior				Anterior.
Left valve	1 0 1 n	0 1 0 1 0	1 0 1	

Codakia punctata (Linnaeus)

Right valve	(1)	ne nc nc	1 0 1	1 0	
Posterior					Anterior
Left valve	(1) (0) (1) ne nc nc	(1) 0 1 (0)	1 0 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, Astartidae, and Cardiniidae. The first two families are extant but the latter family became extinct during the Jurassic.

The Astartidae 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 'cyrenoid' patterns. Boyd and Newell (1968) have recently re-examined the dentition of this superfamily. They find that recent examples of Crassatellidae and Astartidae have rather similar hinges. For the crassatellid *Hybolophus speciosus* (Adams) the notation is:

Right valve	1 0 (1) e r	1 0 1 0 1	1 0 1	
Posterior				Anterior
Left valve	1 0 1	e r (0) 1 0 1 0 (1) 0 1		

e = elastic ligament.
r = resilifer.

For *Astarte castanea* Say:

Right valve	1 0 (1) n	1 0 1 0 (1)	1 0 1	
Posterior				Anterior.
Left valve	1 0 1	n 0 1 0 1 (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.

Cardiacean 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:

$$\begin{array}{lll} \text{Right valve} & 1\ 0\ 1\ (0)\ n\ \vdots\ 1\ 0\ (1)\ \vdots\ 1\ 0\ 1 & \\ \text{Posterior} & \rule{4cm}{0.4pt} & \text{Anterior} \\ \text{Left valve} & \ \ \ 1\ 0\ \ 1\ \ n\ \vdots\ 0\ 1\ \ 0\ \vdots\ \ \ 1\ 0 & \end{array}$$

and *Fragum unedo* (Linnaeus)

$$\begin{array}{lll} \text{Right valve} & \ \ 1\ 0\ 1\ \ \ \ n\ \vdots\ 0\ 1\ 0\ \vdots\ \ 1\ 0\ (1) & \\ \text{Posterior} & \rule{4cm}{0.4pt} & \text{Anterior.} \\ \text{Left valve} & 1\ 0\ (1)\ n\ \vdots\ 1\ 0\ 1\ \vdots\ 1\ 0\ 1\ \ 0 & \end{array}$$

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 'cyrenoid' 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 Albian is:

$$\begin{array}{lll} \text{Right valve} & n\ \ \ 0\ \overset{\frown}{1\ 0\ 1}\ 0\ 1\ 0\ 1\ \big|\ (0)\ (1)\ 0\ 1\ \ 0 & \\ \text{Posterior} & \rule{4cm}{0.4pt} & \text{Anterior} \\ \text{Left valve} & n\ 0\ 1\ \ \ 0\ \ \ 1\ 0\ 1\ 0\big/\ \ \ \ \ \ 1\ 0\ (1) & \end{array}$$

and *Notochione columbiensis* (Sowerby), Recent, Ecuador:

Right valve   (n) | (0) (1) 0 1 0 1 0 1 0
Posterior   ―――――――――――――――――――   Anterior.
Left valve   n | (1) 0 1 0 1 0

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 *Gafrarium* 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 Megalodontacea, a Silurian to Lower Cretaceous group of pachydonts, 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 Chamacea 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 Chamacea. Similar arguments can be applied to the Caprinidae (Aptian to Maastrichtian).

Greater resemblance to the Chamacea is shown by the Monopleuridae, Diceratidae, possibly the Requinidae, some Caprotinidae, and the Megalodontacea.

(*a*) *Megalodontacea*. 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 *Durga 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 Lycett) is shown below and in Plate 76, fig. 4; Plate 77, fig. 3.

Eumegalodon cucullatus:

Right valve	(1) 0 1 n │ 0 $\overbrace{(1\ 0\ 1\ 0\ 1\ 0\ 1\ 0\ 1\ 0\ 1)}$ 0
Posterior	———————————————— Anterior.
Left valve	0 1 (0) n │ 1 $\underbrace{(0\ 1\ 0\ 1\ 0\ 1\ 0\ 1\ 0\ 1\ 0)}$ 1

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.

Pachyrisma grande:

Right valve	1 0 n ┊ (0) 1 0 1 ┊ (1) 0 1
Posterior	—————————————— Anterior.
Left valve	0 1 n ┊ 0 1 0 ┊ 0 1

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 Megalondontacea; changes in the geometry, dentition, and musculature result from the acquisition of the cemented habit.

The dentition is simplified from the megalodontid pattern of *Pachyrisma*. 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 exogyriform shape of the shell.

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

Right valve	1 0 n ┊ 1 0 1
Posterior	——————— Anterior.
Left valve	0 1 n ┊ 0 1 0

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*) *Requieniidae*. 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 *Apricardia toucasi* (d'Orbigny) from the Lower
Campanian of Var, France, show an outer, calcitic 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
exogyriform 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 foreshortening 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)	$\overline{010\ 1\ 0}$	
Posterior	———————	Anterior.
Left valve (free)	$\underline{101\ 0\ 1}$	

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. *Diceras arietum* Lamarck. Jurassic (Oxfordian), Chatel-Censoir, Yonne, France, BMNH
L33915, ×1. *a*, right valve, *b*, left valve.

Fig. 2. *Caprotina semistriata* (d'Orbigny). Cretaceous, Cenomanian, Le Mans, France, ×2. *a*, left (free)
valve. BMNH L96200. *b*, right (cemeted valve) BMNH L96203.

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

EXPLANATION OF PLATE 77

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

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

Fig. 3. *Pachyrisma grande* Morris and Lycett, Jurassic, Great Oolite, Minchinhampton, England.
×0·5. *a*, Left valve showing hinge teeth; *b*, Right valve. Abbreviations: C, cardinals; L, laterals;
n, ligament nymph; aa, anterior adductor muscle scar.

(*e*) *Monopleuridae* (Kimmeridgian–Danian). The Monopleuridae can be derived from the Diceratidae through *Valletia*. Certain members of this family, for example *Gyropleura cenomanensis* (d'Orbigny) (Pl. 70, fig. 5) and *Ciplyella pulchra* (Ravn) (Pl. 72, fig. 5), show remarkable similarity in morphology to *Chama*. They are small to medium-sized, strongly exogyriform and radially ribbed. *Ciplyella 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 Caprotinidae, but without the incipient splitting of the posterior tooth in the left valve seen in *Caprotina* (Pl. 76, fig. 2).

The teeth of *Gyropleura* are illustrated in a sketch by Deschaseaux (1952, 335, text-fig. 177). *Gyropleura cornucopiae* (d'Orbigny) from the Middle Cenomanian of north-western Europe, and *G. inequirostrata* (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 notation of *Gyropleura cornucopiae* (d'Orbigny) is shown below:

Right valve (fixed)	0 1 0	
Posterior	———	Anterior.
Left valve (free)	1 0 1	

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 inequirostrata* (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 Megalodontacea, 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 Caprotinidae 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 exogyriform 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. pellucida* and *C. exogyra*), 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 haueri*, 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 Ga'ara, 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.
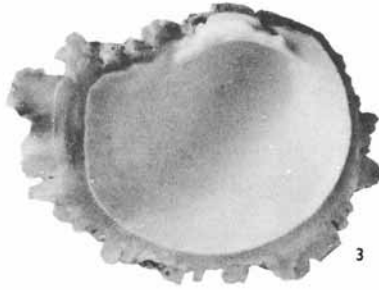
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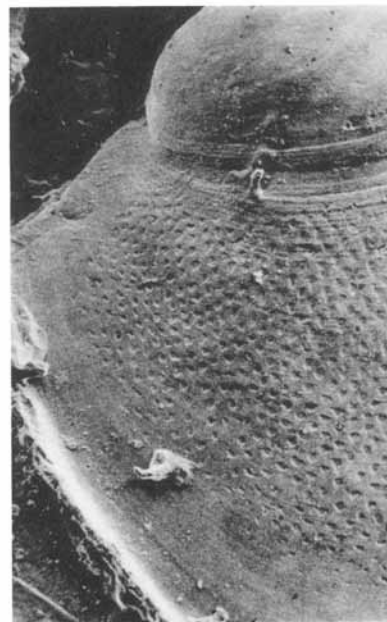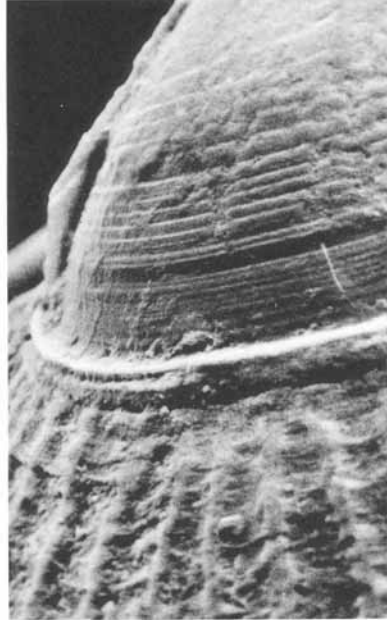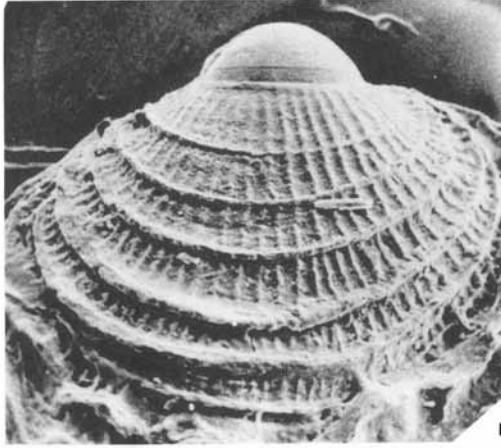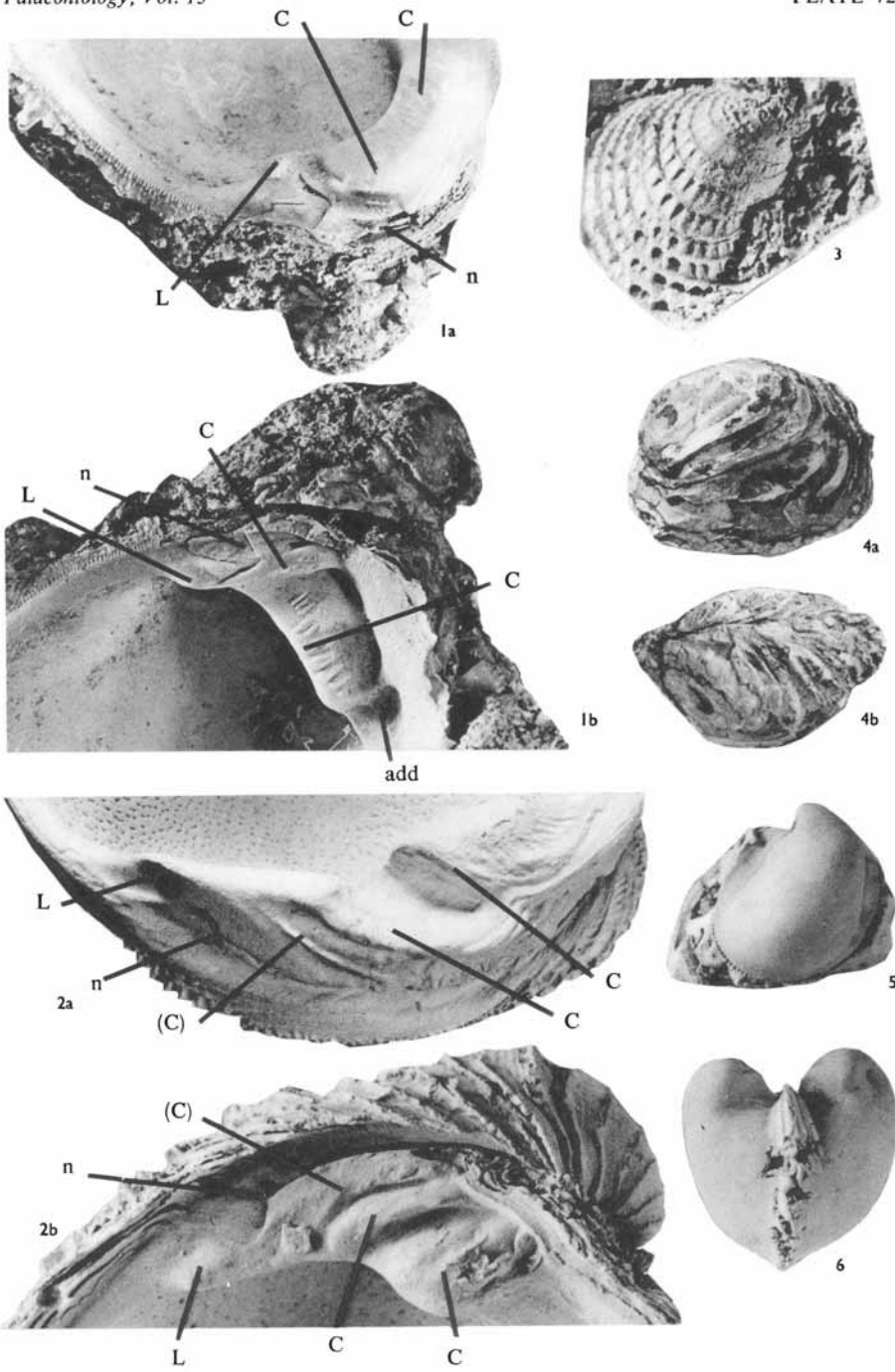KENNEDY, MORRIS and TAYLOR, Chamacea

KENNEDY, MORRIS and TAYLOR, Chamacea

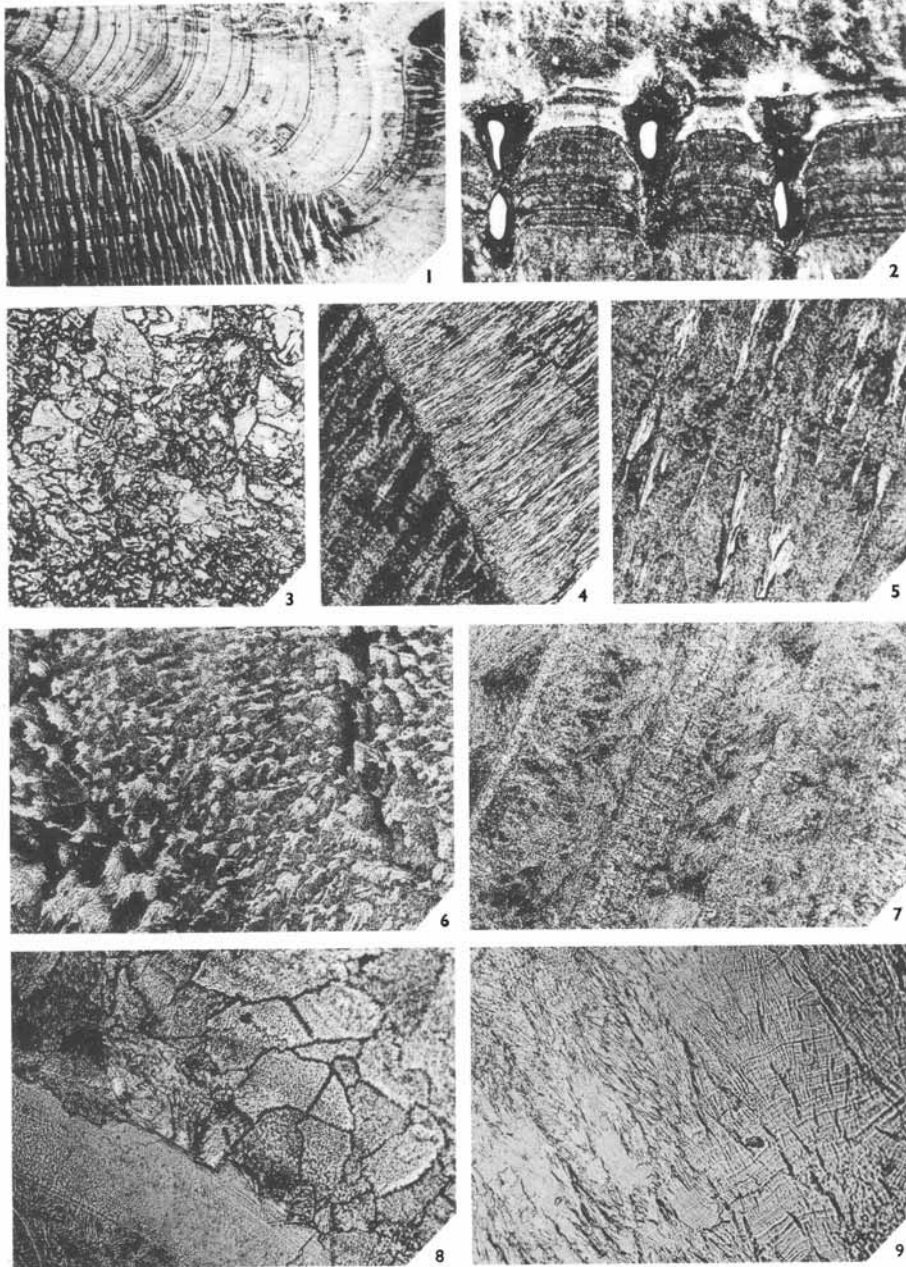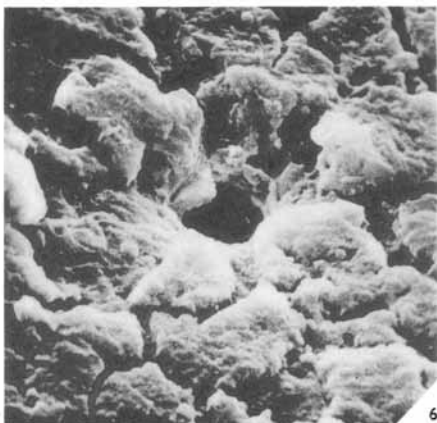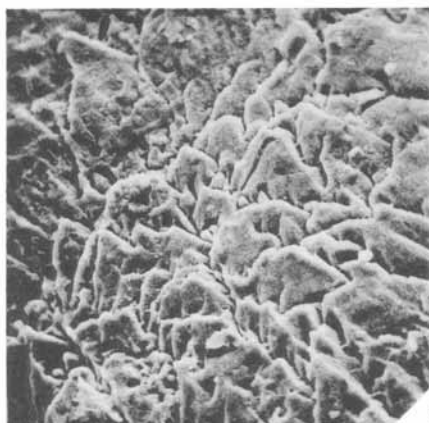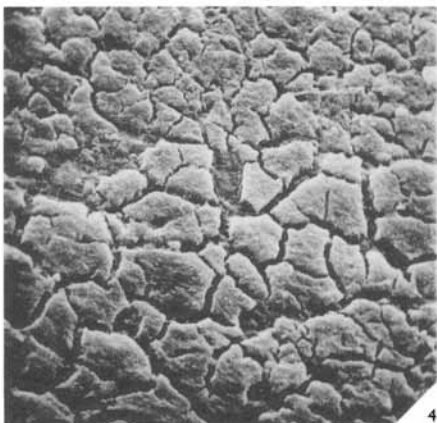KENNEDY, MORRIS and TAYLOR, Chamacea

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PLATE 76
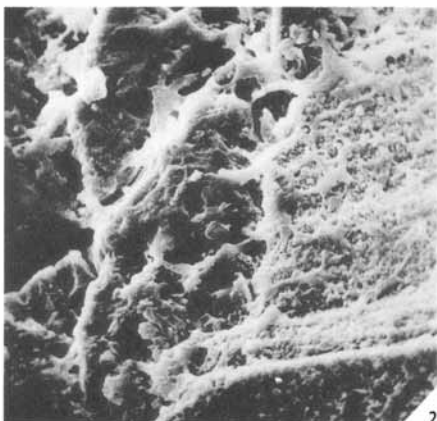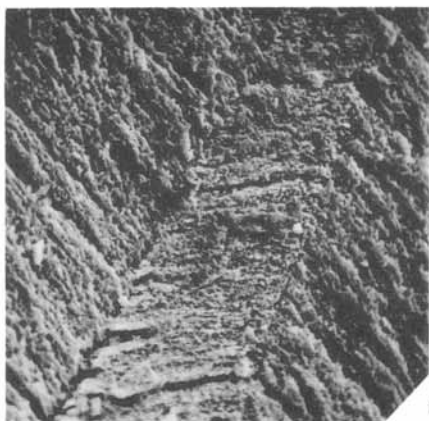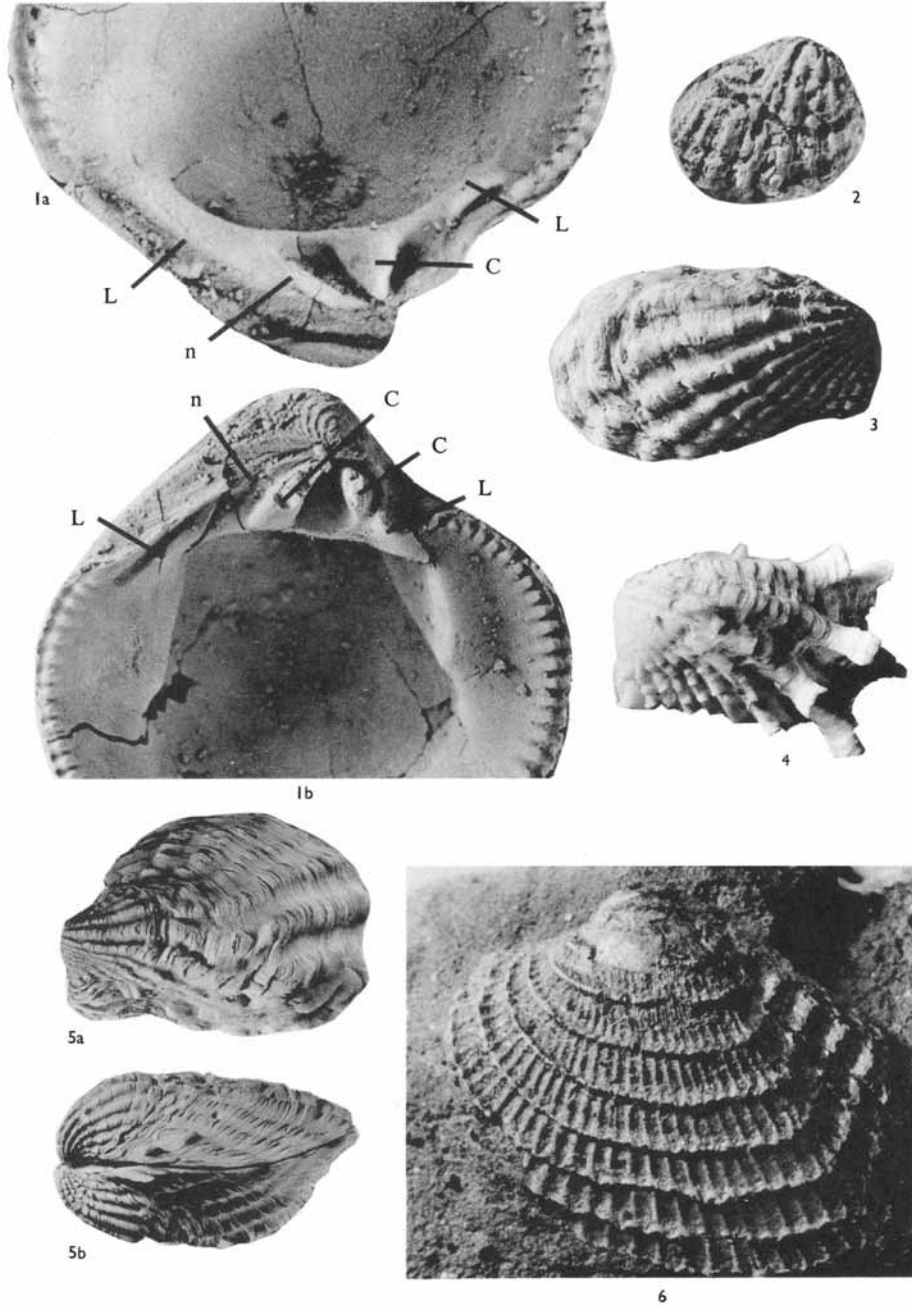

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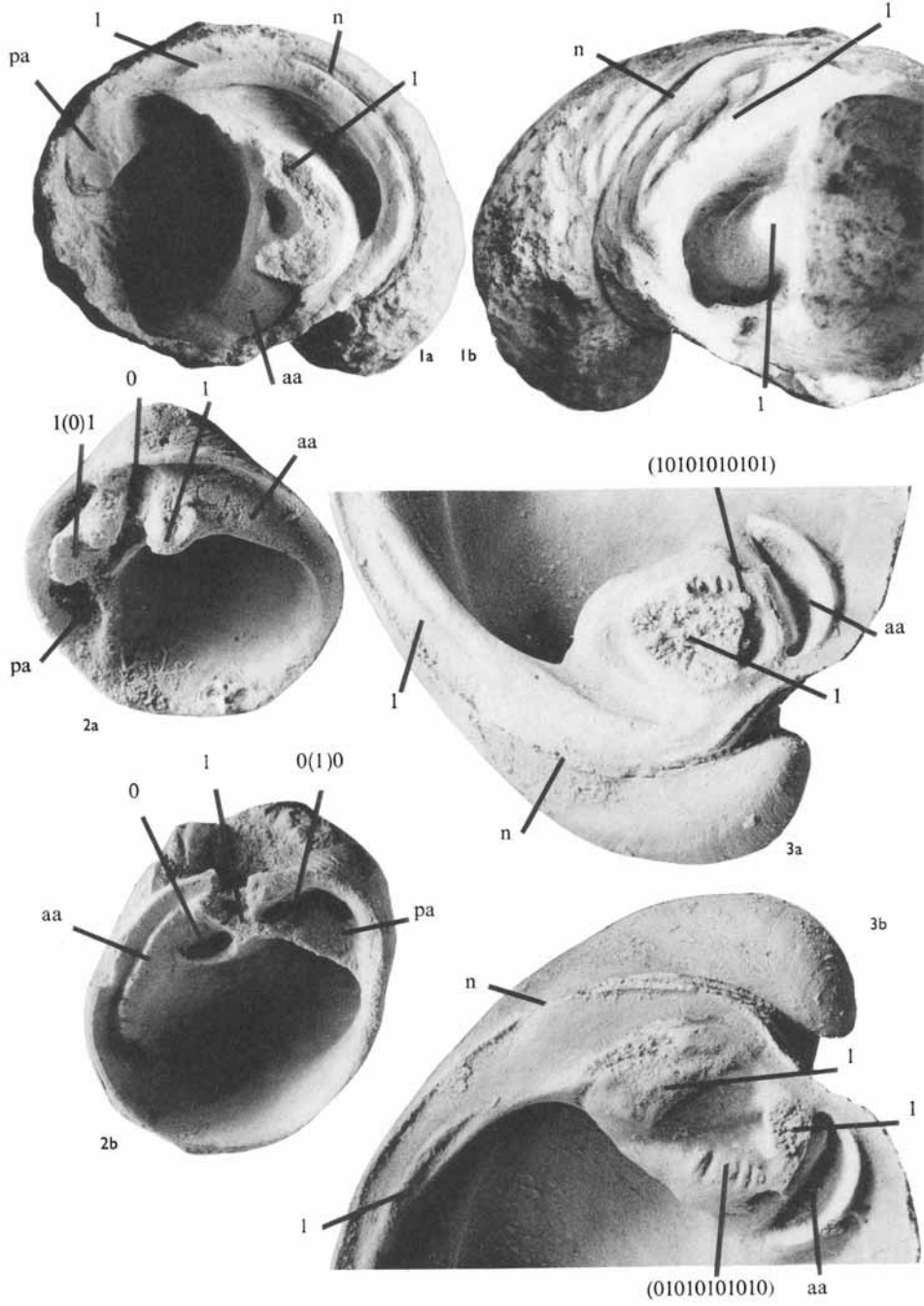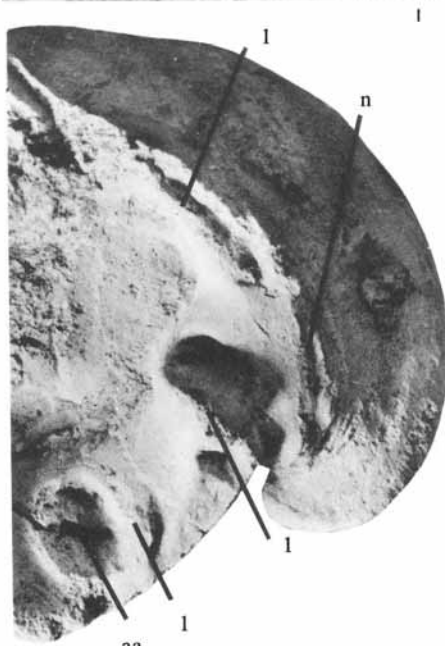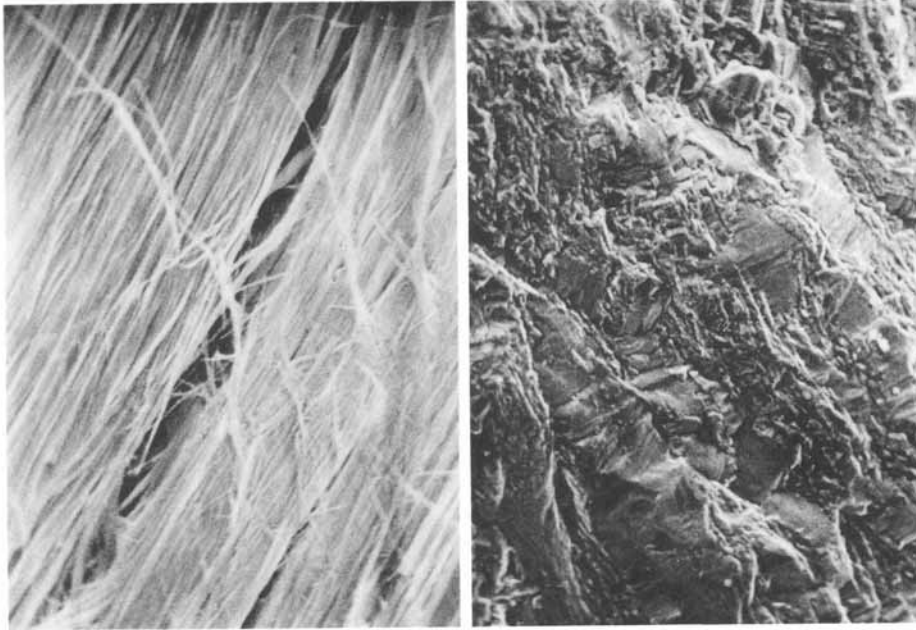KENNEDY, MORRIS and TAYLOR, Chamacea