

ON THE NATURE AND DEFINITION OF THE LUNULE, ESCUTCHEON AND CORCELET IN THE BIVALVIA

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'Before I begin to detail my system, I think it very necessary to settle the technical terms or names for the parts of the bivalves, useful for making their descriptions intelligible and easy, as also decent; for I hold in great detestation the obscene terms made use of by the Linnean School' (Da Costa, 1776, p. 239).

Textbooks of palaeontology have for many years included the terms lunule, escutcheon and corcelet in their treatment of general morphological terms used in Bivalvia. In addition, many systematic descriptions of new taxa in this class incorporate these terms as an essential part of the descriptive terminology of the bivalve shell. It is strange that no modern work has been done on either the detailed morphology of these structures or on their possible significance and function.

TERMINOLOGY OF SHELL STRUCTURE

Until the recent work of Oberling (1955, 1964) most workers on the shell structure of the Bivalvia used a generalized form of nomenclature, describing the macroscopically distinguishable layers of the shell as inner, middle and outer shell layers respectively.

Oberling (1955) proposed the terms ectostracum (for outer layer), mesostracum (for middle layer), and endostracum (for inner layer). These shell layers may be clearly distinct, or sometimes combined (e.g. mes-ectostracum). He also recognized as distinct those calcareous layers which are secreted at the site of muscle attachments—terming these myostraca of various types. The term periostracum was retained for the thin conchiolin layer covering the outer surface of the shell.

I have found these terms to be useful in that they are far more concise than the older terminology. However, they do tend to suggest an element of precision not implicit in the older terminology; this is deceptive precision as the new terms are exact equivalents of the previously used ones, as Oberling himself makes clear (1964, pp. 5-6). I do not suggest, by using these terms descriptively for the different major groups of bivalves, that they are necessarily exactly homologous throughout the class.

For the purposes of ascertaining the general shell structure underlying the features described in this paper, sections were made through the shell in the relevant regions. The cut surfaces, or acetate peels of them, were then examined under a binocular microscope.

HISTORICAL SUMMARY

The very earliest conchologists noted the main structural features of the bivalve shell and gave them somewhat imprecise names. Attempts to apply a systematic terminology to the class may usefully be taken to date from the 10th Edition of *Systema Naturae* (Linnaeus, 1758). Here we find Linnaeus giving a brief diagnosis of various genera and quite clearly recognizing the morphological features which modern workers term lunule and escutcheon.

Unfortunately Linnaeus' description and naming of the component parts of the shell was based on rather lurid sexual imagery which not only mediated against general acceptance, but actively offended many of his contemporary workers. This resulted in several alternative schemes of terminology being proposed in the years following the publication of the *Systema*.

It should be noted here that Linnaeus, and later workers, even up to Moquin-Tandon in 1855, oriented the shell in the opposite way to modern convention. That is to say the shell was oriented on its umbones with the open margins upwards and the ligament in front. The modern usage of anterior, posterior, dorsal and ventral may be taken to date from the excellent *Manuel de Conchylogie* of de Blainville (1825). In this work de Blainville gives a review of previously used terms, and points out the inconsistency of orientation to be found in most pre-1825 works.

THE LUNULE

History

A typical modern definition of lunule may be found in Moore, Lalicker and Fischer (1952): 'a depressed plane or curved area along the hinge line in front of the beak, equivalent to the anterior part of the cardinal area'. This corresponds to the area termed *anus* by Linnaeus.

Da Costa (1776) is the first post-Linnaean worker that I have been able to trace who defined alternative morphological terms to those of Linnaeus. He did not differentiate between lunule and escutcheon of modern usage, but lumped both under the term of *slopes* or *declivitas*.

Dodge (1950) proposed to replace lunule with the term *sigilla*; this has not been generally accepted.

The first usage of the term lunule appears in a paper by Lamarck (1799). The term is not defined but is used in description of *Meretrix* (... et une dent is ' ' ' sous la *lunule*), *Crassatella* (... munie d'une *lunule* ... enfoncées), *Tridac* baillante) and *Hippopus* (*lunule* pleine).

The term appears again in a work by Lamarck in 1801 and, in the same y

gives the first definition of the term that I have been able to find: 'la *lunule* est une impression circulaire, ovale ou lanceolée, plus ou moins profonde, placée au bas de la face postérieure [i.e. anterior in modern usage] des valves'.

In the *Nouveau Dictionnaire d'Histoire Naturelle* (1803–04) Lamarck (who had written the descriptions of the bivalve terms) writes: '*Lunule*. On nomme ainsi une impression ordinairement enfoncée, qui est placée au bas de la face postérieure [anterior in modern usage] de quelques coquilles, et dont chaque valve présente la moitié'.

I propose that this latter definition should be taken in conjunction with the genera listed in 1799 by Lamarck in any consideration of the significance of the lunule in the Bivalvia. Modern workers would not consider that either *Tridacna* or *Hippopus* possess a lunule, but the term is extensively used today in descriptions of *Crassatella* and of most venerids. It is interesting to note that although Lamarck described *Venus* in 1799 he seemed to find no need of the term lunule, for it is not mentioned in his description of the genus.

Structure

Oberling (1964, p. 6) has noted that the hinge in bivalves is generally composed of mesostracum. However, it is not true, as Oberling suggests, that this is without exception in the class. As far as I have been able to determine, the Tridoniidae, Unioniidae, Crassatellidae and Astartidae, at least, have a hinge which is basically composed of endostracal material. It is likely that this is true of certain other groups of bivalves.

In every case that I have seen of a true lunule, it is clearly composed basically of the same shell layer as the dentition (mesostracum in most bivalves, endostracum in the Crassatellidae and similar forms) and represents the track on the external surface of the valve of the ever-lengthening antero-dorsal hinge edge. It is thus, in general, only present in bivalves with antero-lateral teeth, or with an antero-lateral extension of the hinge plate.

Where the lunule is bounded by an incised line, as in many venerids, this is due to the sharp termination of the ectostracum against mesostracum in the form of a slight nick in the valve edge; growth of this nick during ontogeny results in an incised line on the external surface of the valve. This incised line may be present in bivalves with no shell ornament other than concentric growth striae (*Callista chione* (L.), Fig. 1c); more commonly there is conspicuous ornament, the cutting out of which serves to emphasize the incised line bounding the lunule (*C. (Chionopsis) gnidia* (Brod. & Sow.), Plate 35F).

In some forms (e.g. *Meretrix*, one of the genera to which Lamarck originally alluded) there is no physical boundary to the lunule which is merely shown by a colour change. Furthermore, in forms (e.g. *Macra stultorum* (L.) = *M. corallina* (L.)) correctly considered to be without a lunule in the strict sense (in that there is no sign of any differentiated area on the outside of the valves immediately anterior to the beak), there is nonetheless a homologous *lunular sector* of the valves. This lunular sector corresponds externally to the extent of the antero-lateral dentition

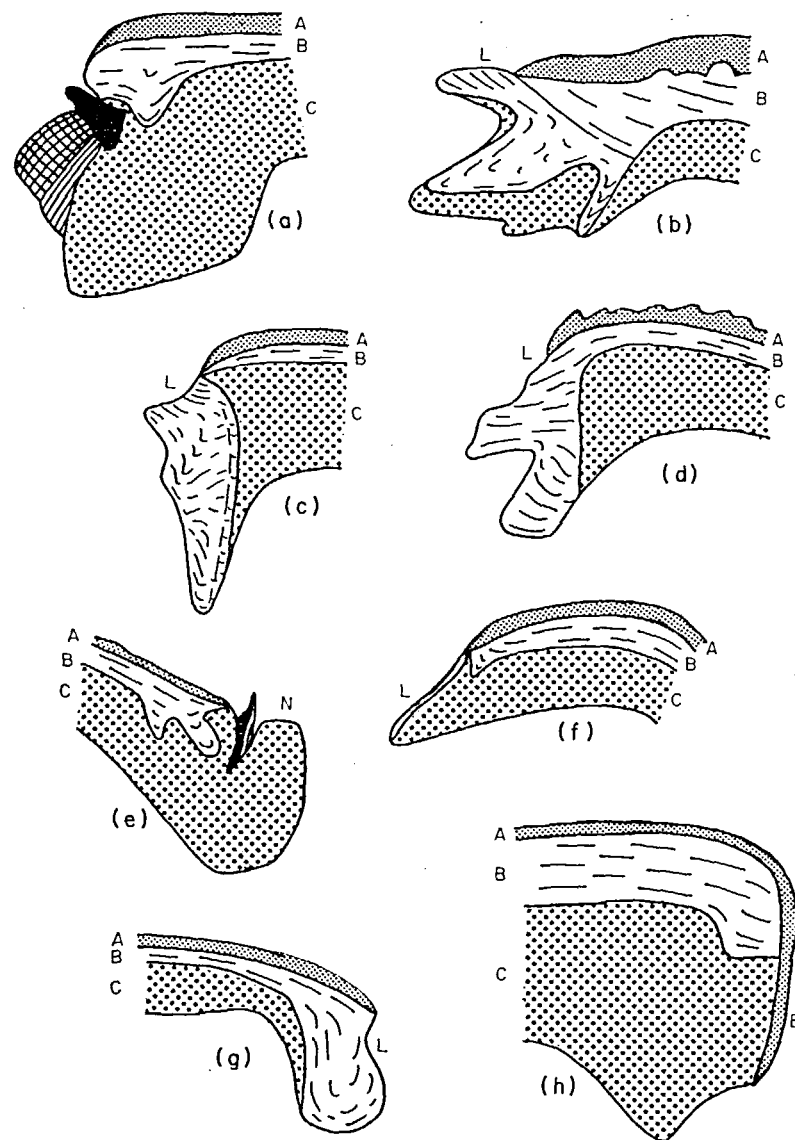


FIG. 1. (Legend on facing page)

internally. We may similarly speak of an *escutcheonal sector* posterior to the umbones. Stolickzka as long ago as 1871 proposed a similar distinction which has apparently never gained general acceptance. He termed *lunular* the margin of the shell just below and in front of the umbones; and *areal* that similar area behind the umbones where the ligament is attached. If the margins of these two regions were marked in any way, then he suggested the terms *lunula* and *area* be applied to them.

Periostracum is always continuous over the lunule (though not, of course, over the commissure between the two halves of the lunule). The postero-dorsal edge of the lunule is often bordered by a thin extension of the ligament—the anterior outer ligament layer. Allen (1960, p. 27) has shown that the 'primary ligament extends from the anterior end of the lunule' in the Lucinacea.

The tangential growth component and the shape of the lunule

Stasek (1963, p. 228) has suggested that 'where interumbonal growth occurs in antero-posterior gradient, a tangential component of growth also appears'.

This statement appears to me to be incorrect; a gradient of interumbonal growth, as seen in a marked form in some arcids, might be considered to result in elongation of one end of the shell relative to the other, but it does not, of itself, result in a tangential component of growth appearing. I hope to deal more fully elsewhere with the question of representing shell growth in terms of vector analysis, and to conclude that for many purposes it is unsatisfactory.

In order to explain the shape of the lunule it is only necessary to recognize the fact that the edge of the lunule (i.e. the incised line on the valves marking the cutting out of the ectostracum) marks a growth sector of the mantle edge.

Lison (1949, p. 29 *et seq.*) has shown that all bivalves with a planar commissure may be considered to possess a *directive plane*, i.e. a plane at right angles to the

FIG. 1. Diagrammatic transverse sections of the dorsal valve margin in the region of the hinge in various bivalves.

(a) *Venerupis* sp., Recent, U.K. 14 mm posterior to the umbones; $\times 4$. Note the lack of a true escutcheon, due to the ligament stretching as far posteriorly as the hinge.

(b) *Cardium edule* L., Recent, U.K. About half way between the umbones and the anterior end of the hinge; $\times 4$. Note the appearance of a small but marked lunule due to the cutting out of the ectostracum.

(c) *Callista chione* (L.), Recent, U.K. 3 mm anterior to the umbones; $\times 1\frac{1}{2}$.

(d) *Venus fasciata* (da Costa), Recent, U.K. 1 mm anterior to the umbones; $\times 4$. A typical and well-marked venerid type lunule.

(e) *C. edule* L. A similar section to (b), only posterior to the umbones. There is no escutcheon at the point of section.

(f) *Crassatella* sp., Eocene, America. Some 7 mm anterior to the umbones; $\times 4$. Note especially that the hinge and lunule are dominantly composed of endostracum.

(g) *Lucina* (*Callucina*) sp., Recent, Miami. 2 mm anterior to the umbones; $\times 4$. Note the essential similarity of this lucinid type lunule to the venerid type.

(h) *Crassatella* (*Scambula*) *melinus* (Conrad), Miocene, America. 20 mm posterior to the umbones. Note especially the endostracal nature of the hinge plate and escutcheon, and the thin cover of 'ectostracum' over the escutcheon.

A, Ectostracum; B, mesostracum; C, endostracum; E, escutcheon; L, lunule; N, nymph.

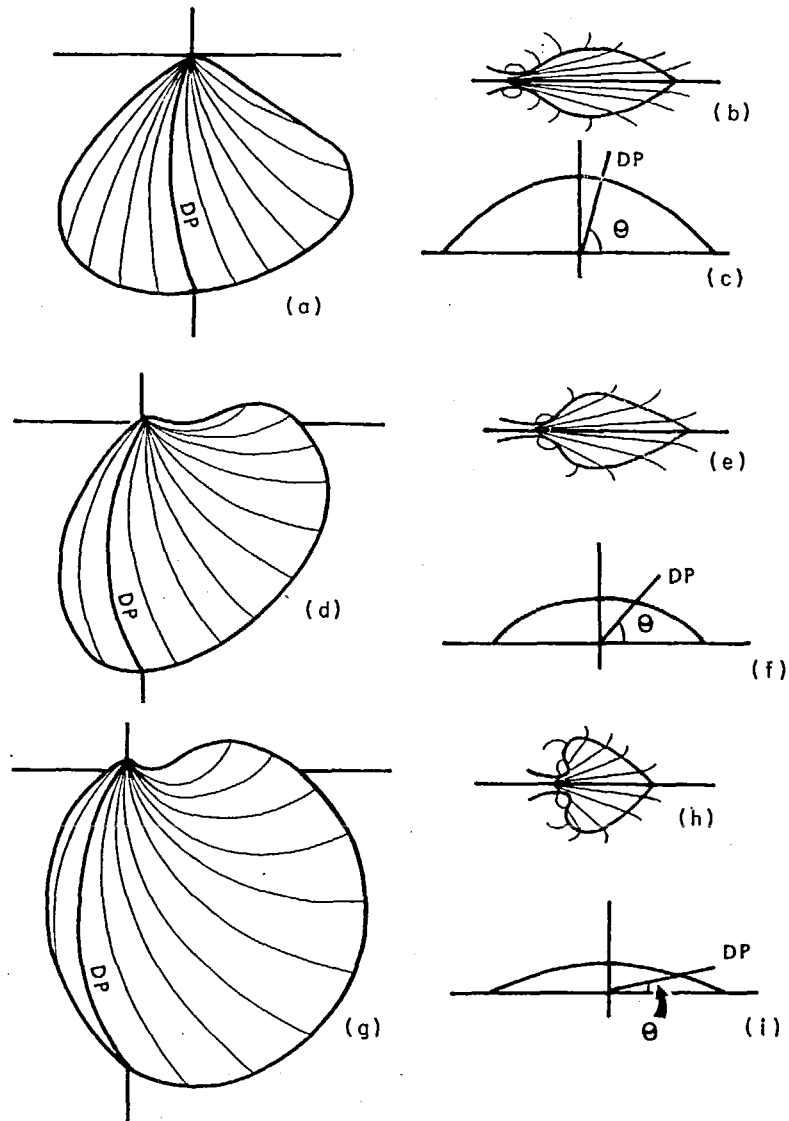


FIG. 2. (Legend on facing page)

axis of coiling of the logarithmic spiral of the shell, which contains a planispiral logarithmic spiral. Further, he has shown that sectors of the shell lateral to this directive plane have the form of dextral or sinistral logarithmic spirals with a larger spiral angle than the spiral in the directive plane. The absolute magnitude of the spiral angle of non-directive spirals is determined by the fact that their projection into the directive plane must have the same spiral angle as the spiral of the directive plane. Because of this, the further away laterally a sector of shell growth is from the directive plane, the more markedly turbinate it is, and hence the more marked is the apparent 'tangential growth component' of the shell (Owen, 1953).

Thus, given models of shell shape which are identical apart from the angle that the directive plane makes with the commissure (defined as θ by Lison), the shape of the lunule will be controlled by this angle.

A morphological series may be constructed following this line of reasoning.

A form such as *Meretrix* (Fig. 2a) has directive plane situated almost symmetrically in the centre of the shell (i.e. $\theta = c. 80^\circ$, Fig. 2c). The shape of the lunule (and the escutcheon) is relatively lanceolate (Fig. 2b).

Consider next a shell in which the directive plane is situated to one side (usually posterior) of the centre of the shell (Fig. 2d) and hence makes a moderate angle with the plane or the commissure (i.e. $\theta = c. 50^\circ$, Fig. 2f). The lunule now has a less lanceolate and more heart-shaped form (e.g. *Callista*, Fig. 2e and Plate 35C).

Finally in a shell like *Dosinia* (Fig. 2g), the directive plane may make an angle as low as 20° with the plane of the commissure (Fig. 2i) and the lunule has now become definitely heart-shaped (Fig. 2h and Plate 36E).

This morphological series is, of course, not exact, for the shape of the generating curve varies somewhat from one genus to another of those genera that we have considered. However, it is precise enough to illustrate the general principle.

Exactly similar geometrical principles govern the shape of the escutcheon. If the directive plane should be asymmetrically positioned, but to the anterior side of the shell (e.g. *Nucula*), the result is what we term an opisthogyrous shell. Predictably, the escutcheon is in this case heart-shaped for, though it is situated morphologically

FIG. 2. To illustrate the relationship between shell geometry and lunule shape. (a), (d) and (g): lateral views of right valves; (b), (e) and (h): lunule (with growth lines) of both valves; (c), (f) and (i): diagrammatic representation of the angle θ between the directive plane and plane of the commissure.

(a-c) *Meretrix*. An example of a form where the directive plane makes a high angle ($c. 80^\circ$, Fig. 2c) with the plane of the commissure. The resultant shell form is almost bilaterally symmetrical (Fig. 2a); the lunule has a lanceolate shape (Fig. 2b).

(d-f) *Callista*. A form in which the directive plane makes a moderate angle ($c. 50^\circ$, Fig. 2f) with the plane of the commissure. Shell form becomes markedly asymmetrical (Fig. 2d); the lunule has a less lanceolate shape (Fig. 2e).

(g-i) *Dosinia*. A form in which the directive plane makes a low angle ($c. 20^\circ$, Fig. 2i) with the plane of the commissure. Shell form is extremely asymmetrical (Fig. 2g); the apparent 'tangential growth component' is very conspicuous; the lunule is heart-shaped (Fig. 2h).

DP, Directive plane; θ , the angle the directive plane makes with the plane of the commissure.

to the anterior of the umbones, it is geometrically in the same position as the lunule in a prosogyrous bivalve.

Function

There has been surprisingly little comment on the possible significance or function of the lunule in the Bivalvia. Wrigley (1948, p. 15) commented 'I have suggested that the escutcheon, like the lunule, is an area of compensatory growth maintaining the valve margins in a plane of junction while the direction of growth is gradually rotated'.

Ansell (1961) suggested that in the Veneridae 'burrowing is possibly assisted by the lunule acting as a pressure plate preventing the animal from moving upwards as the foot is extended'.

It follows from what has been said about structure above that the lunule does not really have a function in the normally accepted sense of the word. It has, however, a nominal 'function' in that it fills in the morphological gap which may arise in front of the beaks in shells with an inclined directive plane.

Implications as to the structure of the mantle edge

Details of the general structure of the mantle edge of the bivalves may be found in Yonge (1957), Beedham (1958a) and Mutvei (1964). There are usually three folds at the edge of the mantle (four in certain venerids) which have different functions. In the vicinity of the mantle isthmus there is usually fusion of the folds.

It is clear that certain modifications of the normal type of mantle edge secretion must be necessary to produce the structures described in this paper. Ansell (1961) has reported that for the British species of venerids, at least, the outer mantle folds remain unfused right up to the umbones on the anterior side of the shell. In these and similar cases, since the lunule is dominantly composed of mesostracum, there must be some modification of the secretory activity of the outer mantle fold. This fold normally secretes the ectostracum on its upper surface at the tip, and the mesostracum with the rest of its upper surface. In the region of the lunule (or escutcheon), there being no ectostracum, the whole of the upper surface of this fold is presumably secreting mesostracum.

In the Crassatellidae there is a thin layer of ectostracum covering the lunule and escutcheon (Fig. 1f and h; a similar situation arises in certain venerids). This ectostracum is sometimes morphologically distinct from, though contiguous with, the extostracum covering the rest of the shell surface. It may represent the secretion of a specialized epithelial zone of the top end of the outer mantle fold.

The exact relation of areas of mantle fusion to these structurally differentiated shell features is a question that needs further careful work.

THE ESCUTCHEON AND CORCELET

History

Escutcheon. For a modern definition I again refer to Moore *et al.* (1952): 'a

depressed plane or curved area along the hinge line behind the beak, corresponding to the posterior part of the cardinal area'. This corresponds to the area termed *vulva* by Linnaeus.

It is perhaps relevant to note here that Valmont de Bomare in his dictionary (1767) does not mention lunule, escutcheon or corcelet with reference to bivalve shells. The term *écusson* is mentioned, but as a part of echinoid tests.

Born (1780) used the term *area antica* or *area* for the differentiated area behind the umbones.

Steinmann (1907) felt that the escutcheon in trigoniids was sufficiently distinct to warrant a special term, the *feldchen*. However, structurally the escutcheon of the trigoniids is exactly comparable to that of other bivalves, and the term is hence unnecessary.

Dodge (1950) proposed to replace 'escutcheon' with the term *vallis*. As with his suggested alternative for lunule, this term has not found general acceptance.

The first usage and definition of escutcheon appear in 1803–04 in the *Nouveau Dictionnaire d'Histoire Naturelle*; 'Escutcheon. On désigne, par ce mot, un espace qui est renfermé dans l'intérieur du corcelet et qui est distingué par un changement de couleur ou par des stries'. Unfortunately there are no genera listed which are said to have an escutcheon.

Corcelet. This term, which does not receive mention by most recent writers in English, is used synonymously with escutcheon in works in which it is mentioned. Franc (1960) says: 'Sur la face dorsale de la coquille existent deux dépressions... l'autre allongée, en arrière d'eux [les sommets], l'écusson ou corcelet dite encore area, au fond de laquelle fait saillie le ligament'.

Even a cursory examination of recent Bivalvia shows that there is more than one structurally differentiated area behind the umbones. This was not recognized by Linnaeus who used the term *vulva* to refer to all differentiated posterior areas, but it was clearly recognized by Lamarck, and other workers of his time, who used the two terms escutcheon and corcelet. Lamarck's (1803–04) definition of corcelet was: 'On entend par ce mot une partie de la face antérieure de quelques coquilles, qui est séparée du disque par une carena saillante, ou par une ligne enfoncée'.

Further, Lamarck (1799) and Poiret (1801) had both previously used the term corcelet, the former citing it in his descriptions of *Crassatella* (... un corcelet enfoncées), *Isocardia* (une dent laterale, isolée, située sous le corcelet), *Cardita* (une longitudinal [tooth] se prolongeant sous le corcelet) and *Unio* (une dent cardinale ... se prolongeant sous le corcelet).

It is clear that the modern terminology of the various differentiated areas behind the umbones is confused and imprecise. Not only are the terms escutcheon and corcelet regarded as synonymous, but the more commonly used of these terms—escutcheon—means different things to different people.

It is desirable to establish, as far as possible, exactly what Lamarck meant by his two terms. Accordingly I have examined typical specimens of the genera quoted by Lamarck as possessing a corcelet (1799): *Isocardia*, *Cardita*, *Unio* and *Crassatella*.

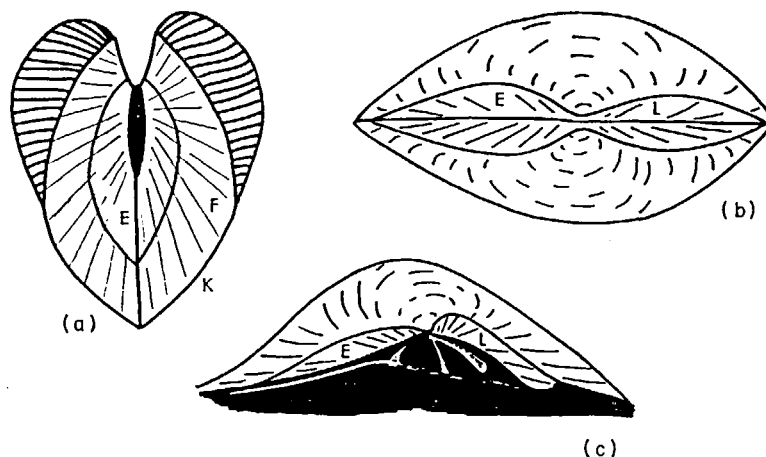


FIG. 3. (a) *Meiocardia* sp., Recent, China; $\times 4/3$. Shell viewed from postero-dorsal aspect. The conspicuous carina delimits the edge of the corcelet, while a faint change in shell opacity marks the edge of the escutcheon.

(b) *Nuculana (Sacella) taphria* Dall, Recent, Central America; (After Keen, 1958) $\times 8/3$. Shell viewed from dorsal aspect. Note the well-developed and sub-equal escutcheon and lunule.

(c) *Crassatella* sp., Eocene, America; $\times 4/3$. An oblique internal view of the left valve to show the well-developed lunule and escutcheon.

E, escutcheon; F, corcelet; K, carina marking the edge of the corcelet; L, lunule.

1. *Glossus* (= *Isocardia*)

G. humanus (L.), the common European species of this genus, has no markedly differentiated posterior area. However, *Meiocardia* (formerly a subgenus of *Glossus*) has a well-marked carina running from the umbo to the postero-ventral border (Fig. 3a, K). The postero-lateral dentition does not reach all the way round the margin to the point where the ridge meets the shell edge. It is possible to recognize, within the area bounded by this ridge and the dorsal border, i.e. within the corcelet, a further discretely differentiated area, corresponding to a slight change in shell opacity, that does coincide with the extent (internally) of the lateral dentition. This is obviously the escutcheon *sensu* Lamarck. Careful examination reveals that the escutcheon represents the track, on the external valve surfaces, of the *growth of the dentition during life*. The dentition itself is an internal structure and, in general, is composed of mesostracum. It is possible to see the escutcheon on *G. humanus* although it is not markedly defined.

2. *Cardita*

Specimens of *C. calyculata* L., the type species, shows no readily recognizable escutcheon, but the corcelet is presumably the area bounded by the marked ridge running from the umbo to the postero-ventral corner, and by the dorsal margin. Again, this area does not correspond entirely with the track of the dentition on the valves.

3. *Unio*

Lamarck cites *Mya margaritifera* L. as type species of *Unio*. However, this species is in reality the type of *Margaritifera* Schumacher, the type of *Unio* being *U. tumidus* Retzius. Accordingly I have examined species of *Margaritifera*. Here again, the differentiated posterior area is due to a ridge running down from the umbo and does not coincide with the track of the dentition, which is confined to that part of the dorsal margin carrying the ligament.

4. *Crassatella*

The shell structure of this group of bivalves (Fig. 1f and h) is different from most other members of the class in that its hinge plates and dentition are built of endostracum and not mesostracum. The incised line bounding the 'corcelet' (Fig. 3c) marks the locus, throughout the growth of the shell, of the junction between the posterior end of the lateral dentition (composed of endostracum) and the shell edge of the main disk (composed of ectostracum and mesostracum). Thus the 'corcelet' represents the track on the valves of the slowly lengthening postero-dorsal hinge edge.

Leaving aside for the moment the case of *Crassatella*, Lamarck consistently used the term corcelet to denote a differentiated area, on the posterior side of the disk, which was bounded antero-ventrally by a carina, and within which it was usually possible to recognize a further differentiated area. This latter area is the escutcheon, and corresponds to the track of the dentition on the external valve surfaces during growth. The escutcheon is always composed of the same shell layer as the dentition, and this may vary from one to another group within the class. Thus the area termed corcelet by Lamarck on *Crassatella* is, in fact, an escutcheon. It should be noted that unless the external ligament is of the same length as the internal hinge plate, the escutcheon bears no direct relation to the ligament, though some writers have used escutcheon for structures associated with the ligament.

Three factors which may be related to differentiated areas of one sort or another on the postero-dorsal part of the shell are :

(1) The opisthodontic ligament. This is essentially an external structure but it is generally inserted into the inside part of the dorsal margin laterally to two calcified ridges termed nymphs. It is certainly not desirable to use the term escutcheon to describe the space (including the nymphs at its centre) that is left between the dorsal valve margins if the entire ligament is eroded away, (see, for example, Plate 35D, E and I). If a name is essential for this feature, I suggest the use of *ligament suture*, a modification of a term first suggested by de Blainville (1825) and subsequently misused by Pictet (1844-46).

(2) The track of the postero-lateral dentition on the valves during life. Any structure on the outside of the shell which is a reflection of this should be termed an escutcheon.

(3) Inhalent and exhalent currents. Most of the structures classed as corcelets are bounded by a carina which may be connected in some way with the presence of siphons, or of inhalent and exhalent current streams.

STROPHIC AND NON-STROPHIC BIVALVIA

Rudwick (1959) has suggested that the Brachiopoda might be divided into two major, and mutually exclusive, morphological groups. These two groups were termed strophic or non-strophic depending on whether their members had 'some arc of the growing edge of each valve . . . exactly in the line of the hinge axis' or not. By virtue of the inequivalve nature of brachiopods, the groups may also be distinguished by their possession of identical, or non-identical growing edges in the two valves.

In the bivalves, there is a dichotomy into the same morphological groups that Rudwick has established for the brachiopods. As the terms strophic and non-strophic were proposed in an exclusively morphological sense, there should be no objection to using them to describe similar features in the Bivalvia.

However, by virtue of the equivalve nature of the bivalves, the two valves have identical growing edges, and so the sole criterion for deciding whether a form is strophic or not devolves on whether it possesses some arc of the growing edge of the shell exactly in the line of the hinge axis or not.

Strophic bivalves (Fig. 4a and d) include the Arcacea, Isognomonidae, and some genera from the Pteriacea (*Pteria*, *Pinctada*, *Pterinea* and similar genera), Spondylidae (*S. princeps* Broderip), Pernidae (*Gervillia* and similar forms) and Myalinidae (*Liebea*). This list does not pretend to be comprehensive.

Within these various groups of strophic forms the Arcacea themselves form a distinct subgroup. This is in accord with the report (Trueman, 1957) that their epithelial mantle surface is unique in its possession of very numerous mucous glands: Owen (1959) has clearly realized the difficulty of explaining shell secretion of the arcids in terms of the usual bivalve model and has tentatively suggested that the mantle is sundered into two lobes.

The majority of 'typical' equivalve bivalves are non-strophic (Fig. 4b).

Certain bivalves, such as *Pinna* (Fig. 4c) and most *Pecten* have a long and straight dorsal margin. These forms are mechanically 'strophic', in that this straight dorsal margin is coincident with the hinge axis during the opening of the valves, but they do not possess any type of interumbonal area—the ligament fully filling laterally the gap between the two valves. In terms of a strophic shell, as originally defined by Rudwick, these forms do not possess an arc of the growing edge of either valve in the line of the hinge. I suggest that these forms be termed *pseudo-strophic*. A pseudo-strophic shell is recognized by its possession of a linear dorsal border coinciding with the hinge axis of the shell, but does not have an interumbonal area. It is possible that, amongst the brachiopods, certain productids are pseudo-strophic.

In the definitions of lunule and escutcheon cited earlier from Moore *et al.* (1952), it was suggested that the lunule and escutcheon were geometrically equivalent to the area. This was first suggested by Zittel (1913) and is certainly so. In addition, the interarea in strophic brachiopods is geometrically homologous to the ligamental area of strophic bivalves; and the lunule and escutcheon of non-strophic bivalves are geometrically homologous to the palintropes of non-strophic brachiopods. This

homology does not extend to the structural composition of these various areas. In both strophic and non-strophic brachiopods, palintropes and area are composed of both major shell layers; on the other hand, in bivalves of the *Arca* type, the area is comprised of mes-ectostracum, or even of mesostracum alone. And in the non-strophic forms such as the venerids, the lunule and escutcheon are composed of mesostracum alone.

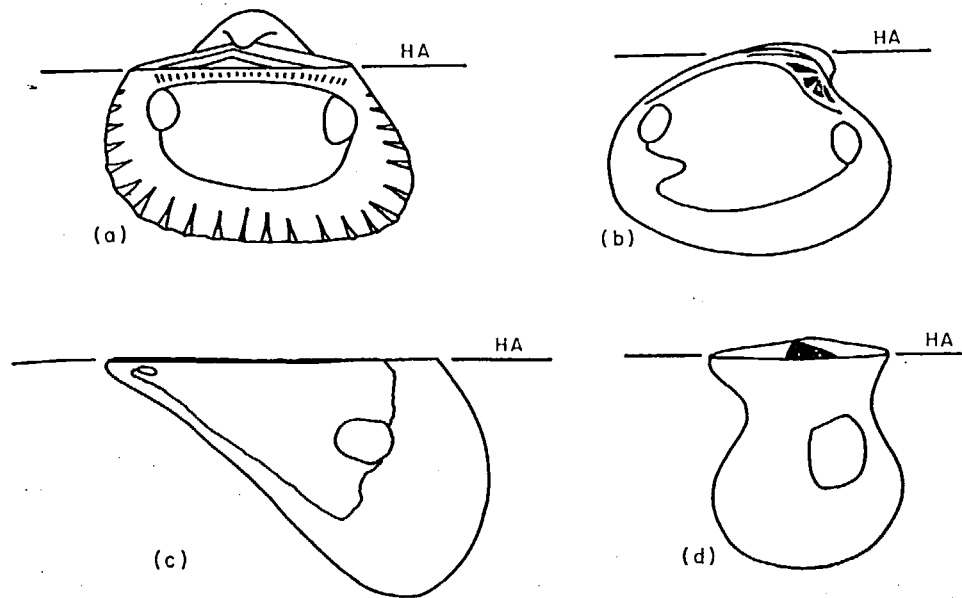


FIG. 4. Diagram to illustrate the use of the terms strophic, non-strophic and pseudo-strophic.

(a) A typical strophic bivalve of the Arcacea. Note the straight dorsal margin, which is coincident with the hinge axis, and the well developed ligamental area. (b) A typical non-strophic bivalve of the Veneridae. (c) A pseudo-strophic bivalve, *Pinna*. Note the straight dorsal margin, which is coincident with the ligament and the hinge axis, but the lack of any ligamental area. (d) A strophic bivalve of the extinct genus *Aviculopecten*.

HA, Hinge axis.

THE LUNULE, ESCUTCHEON AND CORCELET IN SOME MAJOR BIVALVE FAMILIES

Veneridae

It is in this family that the lunule is most typically developed, particularly in the subfamilies Venerinae (*Venus*), Circinae (*Circe* and *Gafrarium*), Dosiniinae (*Dosinia*, Plate 36E) and Chioniinae (*Chione*, Plate 35F and G; *Tawera*, *Placamen* and *Gircomphalus*, Plate 36C).

In other subfamilies such as Meretricinae (*Meretrix* and *Tivela*, Plate 36J), Pitarinae (*Pitar* and *Callista*, Plate 35C) and Cyclininae, the disk ornament is generally not marked, if present at all, and the lunule is accordingly less conspicuous

and sometimes not bounded by an incised line. However, it is still clearly recognizable by a change in colour or a discrete change in the appearance of the valve surface.

The structure of the lunule in this family is described above. Suffice it to say here that this family may well be considered the 'type' for the lunule, since the structure is generally conspicuous, well developed, and obviously corresponds to the structure that Lamarck had in mind when he introduced the term.

The corcelet and escutcheon are variously and well developed in the different groups of venerids. In most forms with a marked escutcheon (e.g. *Circomphalus plicata* (Gmelin), Plate 36I; *Chione* (*Chionopsis*) *gnidia* (Brow & Sow.), Plate 35D), the posterior end of the escutcheon in the left valve acts as an additional lateral tooth and fits snugly under the posterior end of the escutcheon in the right valve. In some cases (*Periglypta puerpura* (L.), Plate 35E) this is so marked that there is virtually no escutcheon in the right valve but a wide one in the left. In *Sunetta* (Plate 36F) the escutcheon is deeply sunk below the dorsal border in a fashion somewhat analogous to the escutcheon in the Crassatellidae. Many forms, in addition to having a well-marked escutcheon, have also a carina or ridge of some sort marking the edge of the corcelet (Plate 36I). This ridge may carry spines (*Hysteroconcha*).

Lucinidae

There is generally no escutcheon as the ligament is sunk along the sharp straight edge of the postero-dorsal part of the valve and usually stretches as far as the underlying dentition (Plate 35I). In some cases (e.g. certain specimens only of *Phacoides borealis* (L.)) there may be a very small flattened area posterior to the ligament which corresponds to an escutcheon.

The lunule is generally well marked and sunken; it may be slightly asymmetrical. Outside the lunule is a further anterior differentiated area, especially marked on the left valve by a groove. This structure appears to be somehow related to the growth, or migration, of the anterior adductor during ontogeny. A similar feature, only even more pronounced, is present on the venerid *Placamen*.

The posterior differentiated area of the lucinids—here termed a corcelet—is obviously different from the similarly located structure in the venerids. In general it is bounded by a groove running from the umbo to the postero-ventral border, rather than a carina. Allen (1958, p. 427) has suggested that this is due to the line of attachment of the gill. If this be so, it is strange that there is little indication of the structure on the inside of the valves, whereas externally it is very marked. It terminates at the ventral border in the form of a sharp re-entrant in the valve edge. It is the perpetuation of this nick throughout ontogeny that produces the groove on the valve surface. This, coupled with the observation that the structure lines up with the inside of the posterior adductor, lead me to tentatively suggest that it may be in some way connected with the growth of this muscle.

Donaciidae

In the common British species *Donax vittatus* (da Costa), there is a small and very elongate lunule in front of the beak and a larger and better defined corcelet behind

it. In the striking genus *Hecuba* there is more conspicuous lunule (Plate 35A). The ornament of the anterior part of the main disk is in the form of raised, frilled, concentric ridges, and these are sharply terminated at the lunule edge. The lunule itself only carries fine growth lines. There is a large corcelet.

Macridae

In this family the structures on either side of the umbones are often somewhat obscure. However, forms such as *Macra violacea* Gmelin (Plate 35J) show a clear and well-defined lunule (Plate 35B) corresponding to the extent of the dentition anteriorly, and an equally well-defined escutcheon posteriorly. There is also a corcelet. In the common *M. glauca* of Normandy coasts, these same structures are all recognizable, though less well defined, and are marked mainly by discrete changes in the colour of the periostracum. Spectacular tropical forms such as *M. (Macrinula) plicataria* (L.) have very marked corcelets within which it is generally possible to recognize an escutcheon. They also possess a lunule.

Carditidae

There is always a small, though marked, lunule (Plate 36G), generally a broad carina marking the extent of the corcelet, and sometimes a small escutcheon. Owing to the somewhat specialized nature of the hinge in this family, the lunule is different in detail from that of the venerids. In the left valve it comprises the anterior wall of the socket receiving the most anterior tooth of the right valve; and in the right valve it comprises the anterior wall of the socket receiving the major cardinal tooth of the left valve. In addition, in the right valve its ventral end may be produced into the most anterior tooth of that valve. As the valve ornament consists of strong radial ribs, the cessation of these at the lunule edge is very striking—the lunule itself being smooth apart from growth striae.

Tellinidae

The lunule is usually asymmetrical, being more elongated in the left valve and having its anterior end produced into a lateral tooth. If there is an escutcheon (*Strigilla*) it is small, only developed in the left valve, and has its posterior end produced into lateral tooth. In *Arcopagia* (Plate 36A) the lunule has been completely lost in the right valve, but its 'half' in the left valve has grown across the median plane of contact of the two valves to fill the gap. The whole inside edge of the lunule in this case acts as a lateral tooth.

This case is closely analogous to the general case described by Rudwick for non-strophic brachiopods. In the vicinity of the palintropes in the latter group there is usually a 'localized anomaly in the vertical component growth rate on the ventral growing edge; but . . . there is no correspondingly anomaly in the dorsal growing edge' (Rudwick, 1959, p. 20). The term *non-strophic deflection* was suggested to describe this feature. In *Acropagia*, the non-strophic deflection is in the left valve. In the right valve there is no growth between the 'nick point' (Rudwick, 1959), at the anterior end of the lunule, and the umbo. Of course the primary difference

between this case and that of the brachiopods is that in the brachiopods there is a non-strophic deflection symmetrically disposed on either side of the umbones, whereas in *Arcopagia*, by virtue of bilateral asymmetry, there is only a single deflection in front of the umbones.

The lunule in the Fimbriidae (*Fimbria*, Plate 36B) has a similar structure to that of the tellinids.

Cardiidae

The structures in this group are neither well defined nor, in general, easily seen. *Discors* is one of the genera in which lunular and escutcheonal structures are reasonably clear.

The lunule is asymmetrical. Immediately anterior to the umbones the margins of the lunule are generally deflected dorsally in order to accommodate interlocking of the underlying cardinal teeth. The escutcheon is somewhat swollen and, almost invariably, the posterior end of the escutcheon in the right overlaps and interlocks with the posterior end of the escutcheon in the left valve. In *Discors* both lunule and escutcheon are differentiated from the main disk by their deeper red colouration. In the figured example (*Fragum*, Plate 35H) the lunule is slightly longer in the left valve and is the area without tubercular ornament.

Nearly all cardiids possess a marked corcelet, bounded either by a sharp carina or by a marked change in ornament. The ornament on the corcelet is often of tubercular nature (e.g. *Nemocardium*).

Crassatellidae

In this family the lunule and escutcheon are not only marked off from the rest of the shell by a slight step, they form an acute angle with the main disk, this serving to emphasize their structural distinctness. The dentition is primarily composed of endostracum (Fig. 1f and h). Where the main disk has a marked ornament it is cut out sharply at the lunule and escutcheon edge (*C. sulcata* (Solander) from the Barton Beds Eocene).

Nuculacea

The ligament is internal in this superfamily. When a lunule or escutcheon is developed, as in many nuculanids, it can clearly be seen to be the result of successive positions of the dentition during growth. In most nuculanids the escutcheon is well developed and bordered by a sharp ridge; the lunule is generally small but may be large and conspicuous (*N. (Sacella) taphria* Dall, from the tropical Americas).

In *Nucula* there is rarely a pronounced lunule though there is often a somewhat ill-marked escutcheon. It is interesting to note that, because of the opisthogyrous nature of the shell in this genus, the escutcheon has very much the nature of the lunule in the normal prosogyrous forms. This fact serves to emphasize that these differentiated areas on either side of the umbones are of a purely structural nature.

Unionidae

The ligament is generally as long as, or longer, than the posterior lateral dentition.

Consequently there is no escutcheon. However, in certain genera—especially *Tritogonia* and *Arcidens* (Fig. 5) there is a sunken lunule-like structure immediately anterior and below the beak. In these genera there is no antero-lateral dentition. The lunule in this case is due to the track of the cardinal dentition of the valves, which explains its comparatively central position.

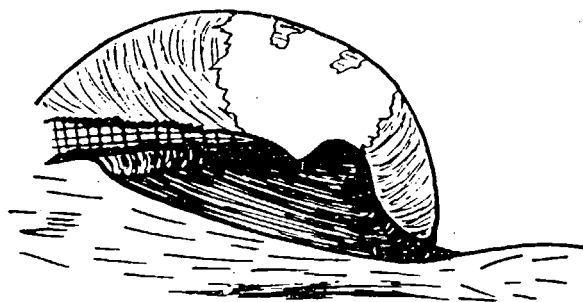


FIG. 5. *Arcidens* sp. Showing well-developed lunule situated almost directly under the umbo. It corresponds to the track during growth of part of the dorsal hinge edge.

Mytilidae

Due to the coextensive nature of the postero-lateral dentition and the ligament there is no escutcheon in this group. There may be, however, a clearly differentiated area in front of the beak which appears to be a lunule.

SUMMARY

The history of usage of the terms lunule, escutcheon and corcelet is reviewed. The term lunule has been applied with consistency since its introduction by Lamarck. However, there has been confusion over the meanings of corcelet and escutcheon and, in order to clarify their meanings, a brief description is presented of the genera to which Lamarck gave reference when introducing these terms. The terms lunule, escutcheon and ligamental suture are defined. The structure and possible function of these differentiated areas is discussed; it is suggested that their shape is dependent on the angle the directive plane makes with the plane of the commissure of the shell. A dichotomy of bivalves into strophic and non-strophic groups, as suggested for the brachiopods by Rudwick (1959), is outlined. The term pseudo-strophic is introduced. The distribution of the lunule, escutcheon and corcelet in some major families of bivalves is discussed.

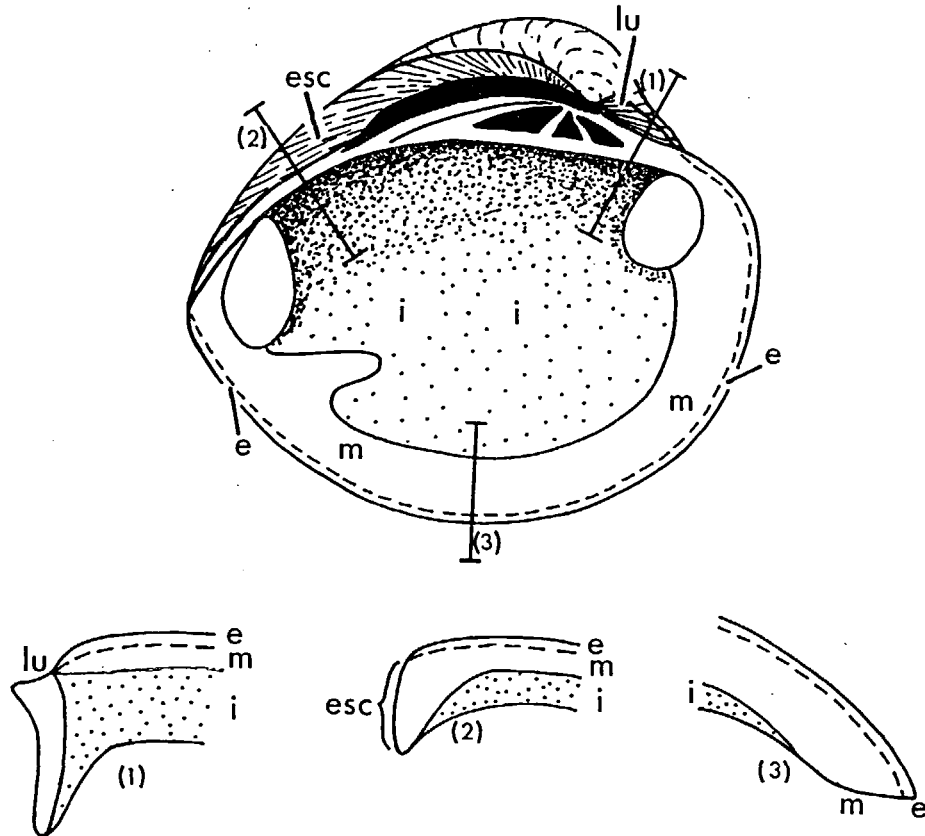


FIG. 6. A diagrammatic generalized venerid type shell to illustrate the use of the terms lunule and escutcheon. (1), (2) and (3) are sections through the shell at the indicated points. esc, Escutcheon; lu, lunule; e, ectostracum; m, mesostracum; i, endostracum.

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APPENDIX

Definition of terms (see Fig. 6).

Lunule, Lamarck (= anus, Linnaeus; slopes, declivitas, da Costa; sigilla, Dodge).

A generally cordate-shaped differentiated area situated anterior to the umbones. It represents the track on the external surface of the valve of the ever lengthening antero-dorsal hinge edge during the growth of the shell.

Escutcheon, Lamarck (= vulva, Linnaeus; slopes, declivitas, da Costa; area antica, Born; feldchen, Steinmann; vallis, Dodge).

A differentiated area of varying shape situated posterior to the umbones. It represents the track on the external surface of the valve of the ever lengthening postero-dorsal hinge edge during the growth of the shell.

Corcelet, Lamarck.

A further differentiated area posterior to the umbones, outside of the escutcheon. In the absence of knowledge of its exact significance it is not possible, or desirable, to give a precise definition to the term. It was originally proposed to describe the area enclosed between the general posterior carinae of various bivalves. It might be used as a concise general term for such little understood differentiated areas outside the escutcheon in varied groups of bivalves. In this case it would be essentially synonymous with terms such as posterior flank, posterior area, etc. Its use should ultimately be restricted to features that can be shown to be homologous with the corcelet in the four genera for which the term was first used (i.e. *Unio*, *Cardita*, *Isocardia* and *Crassatella*).

REFERENCES

- ALLEN, J. A., 1958. On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). *Phil. Trans. B* **241**, 421-484.
- ALLEN, J. A., 1960. The ligament of the Lucinacea (Eulamellibranchia). *Q. Jl microsc. Sci.* **101**, 25-36.
- ANSELL, A. D., 1961. Functional morphology of British Veneracea (Eulamellibranchia). *J. mar. biol. Ass. U.K.* **41**, 489-517.
- BEEDHAM, G. E., 1958a. Observations on the mantle of the Lamellibranchia. *Q. Jl microsc. Sci.* **99**, 181-197.
- BEEDHAM, G. E., 1958b. Observations on the non-calcareous component of the Shell of the Lamellibranchia. *Q. Jl microsc. Sci.* **99**, 341-357.
- BORN, I. E., 1780. *Testacea Musaei Caesarai Vindobonensis*. Vienna.
- DA COSTA, E. M., 1776. *Elements of Conchology*. London.
- DE BLAINVILLE, H. M. D., 1825. *Manuel de Malacologie*. Paris.
- DODGE, H., 1950. Suggested substitutes for the terms 'lunule' and 'escutcheon' in Pelecypoda. *J. Pal.* **24**, 500-501.
- FRANC, A., 1960. In: *Traité de Zoologie* (Ed. by P. P. Grassé) Vol. 5, pp. 1845-2019. Masson, Paris.
- KEEN, A. M., 1958. *Sea Shells of Tropical West America*. Stanford University Press, California.
- LAMARCK, J. P. B. A. DE M., 1799. Prodrome d'une nouvelle classification des coquilles. *Mém. Soc. d'Hist. nat., Paris* **7**, 85 et seq.
- LAMARCK, J. P. B. A. DE M., 1801. *Système des Animaux sans Vertébrés*. Paris.
- LAMARCK, J. P. B. A. DE M., 1803-4. *Nouveau Dictionnaire d'Histoire Naturelle*. Paris.
- LINNAEUS, C., 1758. *Systema Naturae*, 10th edn.

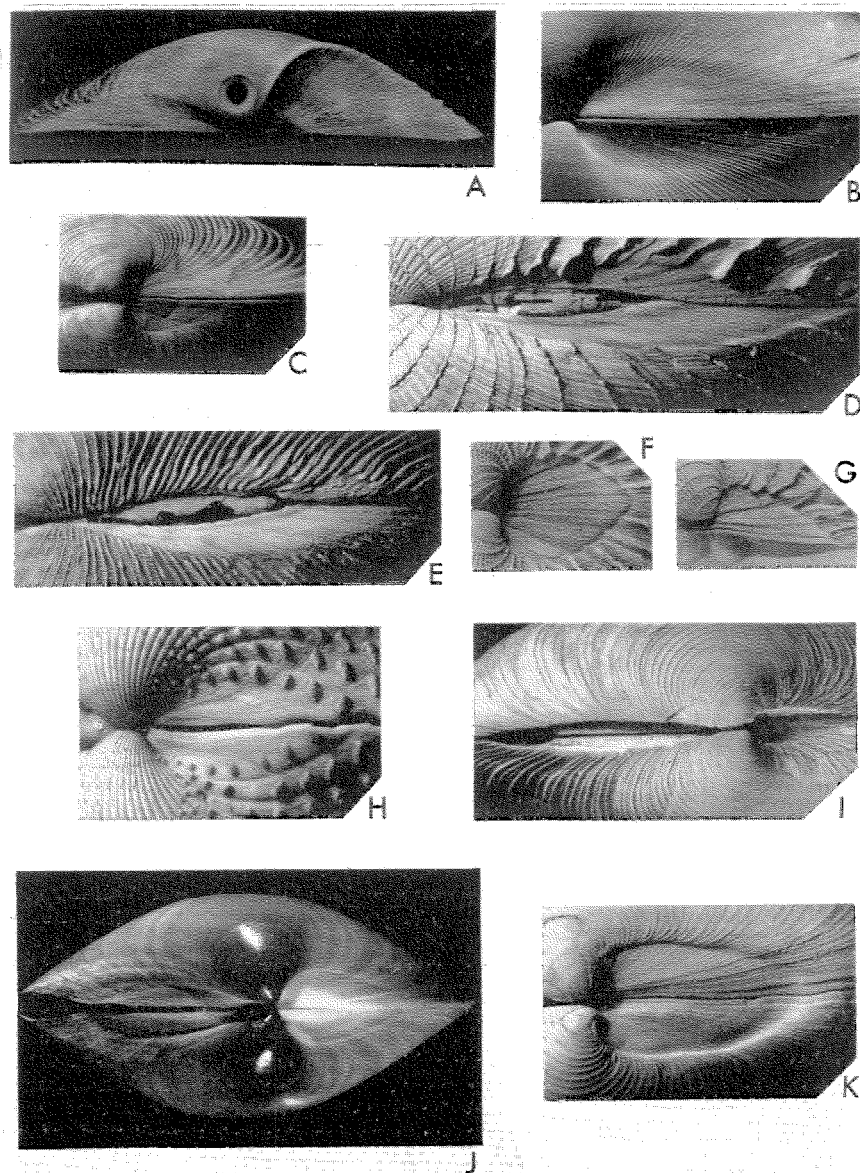
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- LISON, L., 1949. Recherches sur la forme et la mécanique de développement des coquilles des lamelli-branches. *Mem. Inst. r. Sci. nat. Belg.* 2nd series, fasc. 34, 3-87.
- MOORE, R. C., LALICKER, C. G. and FISCHER, A. G., 1952. *Invertebrate Fossils*. McGraw-Hill, New York.
- MOQUIN-TANDON, A., 1855. *Histoire Naturelle des Mollusques de France*. Paris.
- MUTVEI, H., 1964. On the shells of *Nautilus* and *Spirula* with notes on the shell secretion in non-cephalopod molluscs. *Ark. Zool.* 16, 221-278.
- OBERLING, J. J., 1955. Shell structure of West American Pelecypoda. *J. Wash. Acad. Sci.* 45, 128-130.
- OBERLING, J. J., 1964. Observations on some structural features of the pelecypod shell. *Mitt. naturf. Ges. Bern*, n.s. 20, 1-63.
- OWEN, G., 1953. The shell in the Lamellibranchia. *Q. Jl microsc. Sci.* 94, 57-70.
- OWEN, G., 1959. The ligament and digestive system in the taxodont Bivalves. *Proc. malac. Soc. Lond.* 33, 215-223.
- PICTET, F. J., 1844-46. *Traité Élémentaire de Paléontologie*. Paris.
- POIRET, J. L. M., 1801. *Coquilles fluviatiles et Terrestres Observées dans le Département de l'Aisne et aux Environs de Paris*. Paris.
- RUDWICK, M. J. S., 1959. The growth and form of brachiopod shells. *Geol. Mag.* 96, 1-24.
- STASEK, C. R., 1963. Geometrical form and gnomonic growth in the bivalved Mollusca. *J. Morph.* 112, 215-229.
- STEINMANN, G., 1907. *Einführung in die Paläontologie*, 2nd edn. Leipzig.
- STOLICZKA, F., 1871. The Pelecypoda, with a review of all known genera of this class, fossil and recent. In: *Cretaceous Fauna of Southern India*, Vol. III. Pal. Indica.
- TRUEMAN, E. R., 1957. Mucous gland cells of the outer mantle epithelium of *Arca noae*. *Nature (Lond.)* 180, 1492.
- VALMONT DE BOMARE, J. C., 1767-68. *Dictionnaire Raisonné Universel d'Histoire Naturelle*, 6 volumes. Paris.
- WRIGLEY, A., 1948. Observations on the structure of lamellibranch shells. *Proc. malac. Soc. Lond.* 27, 7-19.
- YONGE, C. M., 1957. Mantle fusion in the Lamellibranchia. *Pubbl. Staz. zool. Napoli* 29, 151-171.
- ZITTEL, K. A., 1913. *Text Book of Palaeontology*, 2nd edn (Ed. by C. R. Eastman). McMillan, London.

EXPLANATION OF PLATES

PLATE 35

- A. *Donax (Hecuba)* sp., Recent; $\times 1$. There is a well-developed lunule and escutcheon, both of which correspond to the lateral extent of the dentition internally.
- B. *Mactra violacea* Gmelin, Recent, Tranquebar; $\times 2$. Lunule well defined by a subtle change in shell texture.
- C. *Callista erycina* (L.), Recent; $\times 1$. A typical venerid lunule.
- D. *Chione (Chionopsis) gnidia* (Broderip & Sowerby), Recent, America; $\times 1$. A view of the escutcheon and ligament. Note the sharp cessation of the raised ectostracal ornament at the escutcheon edge, and the greater width of the escutcheon in the left valve, due to the posterior end of the escutcheon in this valve fitting under the escutcheon of the right valve.
- E. *Periglypta puerpura* (L.), Recent; $\times 1$. A view of the escutcheon and ligament. The escutcheon in the right valve has here become almost totally repressed, and there is marked interlocking of the valve margins at the posterior end of the escutcheon.
- F. and G. *Chione (Chionopsis) gnidia* (Broderip & Sowerby); $\times 1$: Two views of the lunule. Note especially the end of the hinge plate in G coinciding with the nick in the dorsal valve edge.
- H. *Fragum unedo* (L.), Recent; $\times 2$. A view of the lunular sector of the valves.
- I. *Phacoides borealis* (L.), Recent, U.K.; $\times 1$. There is no escutcheon due to the ligament occupying the whole length of the hinge plate. The well-marked lunule is characteristic and typical of the lucinids.
- J. *Mactra violacea* Gmelin, Recent, Tranquebar; $\times 1$. There is a well-defined lunule, a marked escutcheon (the inner of the two differentiated posterior areas) and a similarly marked corcelet.
- K. *Lucina pensylvanica* L., Recent; $\times 1$. A particularly large lunule for this family.



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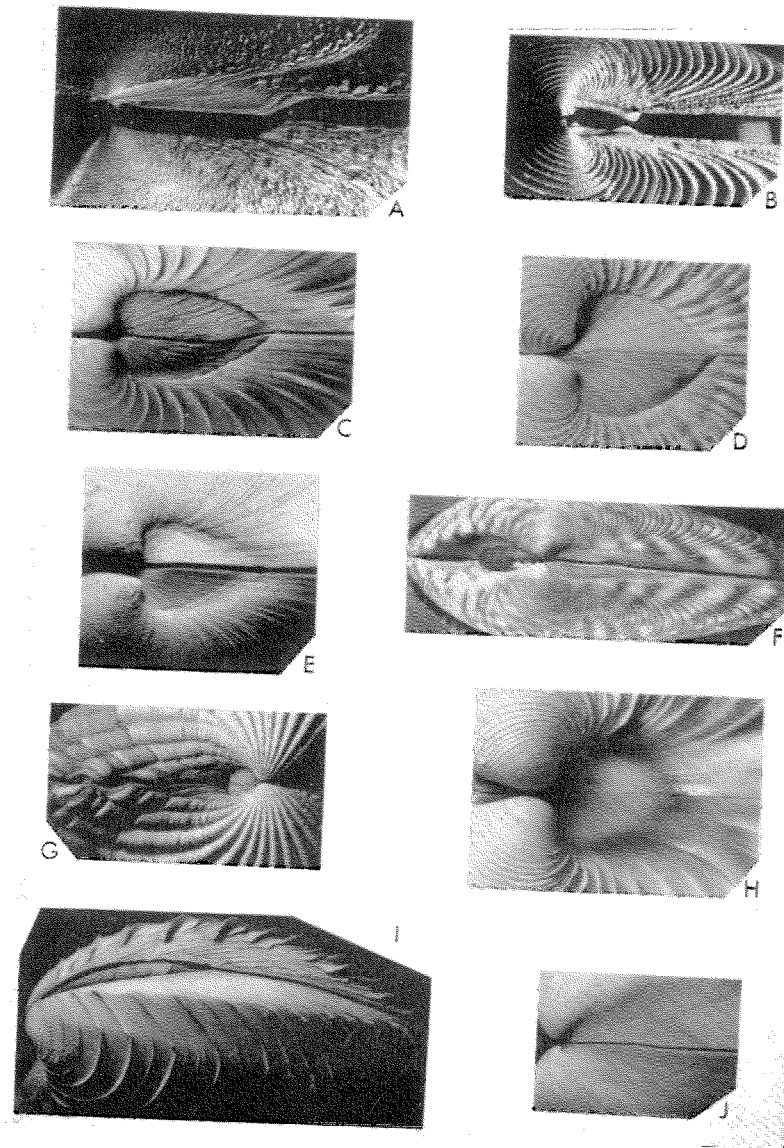


PLATE 36

A. *Arcopagia* (*Scutarcopagia*) *scobinata* (L.), Recent; $\times 2$. An unusual lunule in that it is totally comprised of the projecting edge of the left valve which fills a space in dorsal margin of the opposing valve. The valves are separated slightly for clarity.

B. *Fimbria* sp., Recent; $\times 2$. Note the asymmetrical nature of the lunule and the extension of its postero-ventral edge into teeth.

C. *Circumphalus plicata* (Gmelin), Recent; $\times 2$. A characteristic venerid lunule.

D. *Venus verrucosa* L., Recent, U.K.; $\times 2$. This genus has a large lunule. Note that there is a small part of the lunule posterior to the umbones.

E. *Dosinia concentrica* Born, Recent; $\times 2$. A typical dosiniid lunule.

F. *Sunetta meroe* (L.), Recent; $\times 2$. Note the elongated lunule and the very characteristic sunken escutcheon.

G. *Venericardia incrassata* (Sow.), Recent, Australia; $\times 2$. A small but marked lunule as is typical of the family.

H. *Hysteroconcha* sp., Recent; $\times 2$. The lunule here is bounded by a gently incised line, a colour stain, and the cessation of the raised lamellae of the main disk.

I. *Circumphalus plicata* (Gmelin); $\times 1$. A view of the well-developed escutcheon (note the edge of the left valve fitting under the edge of the right valve) inside the carina marking the edge of the corcelet. The ligament is at the centre of the escutcheon.

J. *Tivela* sp., Recent; $\times 2$. An inconspicuous lunule such as is commonly found in the subfamily Meretricinae.

