# The Ligament of the Lucinacea (Eulamellibranchia)

*By* J. A. ALLEN

*(From the Dove Marine Laboratory, Cullercoats)*

## SUMMARY

The basic structure of the opisthodetic ligament of the Lucinacea consists primarily of inner layer, anterior and posterior outer layers, and periostracum. This is secondarily extended by fused periostracum and fusion layer. Fused periostracum extends as far as the posterior adductor muscle and, except in the Ungulinidae, to the anterior adductor. The fusion layer covers the posterior outer layer and a little beyond. Only in *Loripes lucinalis* is the fusion layer to be found anteriorly. Below the umbos the inner layer, posterior outer layer, and overlying fusion layer are split. This split can be explained in terms of the growth and form of the shell. The anterior outer layer fills the split and extends to the anterior limit of the lunule. The ligament, external in the Ungulinidae, becomes progressively more internal. At the same time the posterior limit of the outer layer becomes modified as a result of the elongation of the outer surface of the outer mantle fold between the pallial lobes in the depth of the posterior mantle embayment. The Lucinidae are most specialized in this respect where, in *L. lucinalis*, a tongue of tissue divides much of the ligament horizontally. The Thyasiridae, the remaining family of the group, occupies an intermediate stage in this specialization.

## INTRODUCTION

RECENT studies by Owen, Trueman, and Yonge (1953), Trueman (1953, 1954), Owen (1953, 1958, 1959), and Yonge (1953, 1957) on a wide range of species of Bivalvia make clear the basic form of the adult ligament and the mantle secreting it. Primarily the ligament is composed of an inner layer covered by anterior and posterior outer layers and the periostracum (fig. 7, p. 35). The inner layer is secreted by the epithelium of the mantle isthmus, the outer layers are secreted by the outer surface of the outer mantle fold within the depths of the mantle embayments at either end of the mantle isthmus, and the periostracum is secreted by the inner surface of the outer mantle fold. This primary ligament may be secondarily extended anteriorly and/or posteriorly by fusion of the mantle margins and may involve (1) extension by periostracum, where the inner surfaces of the outer mantle folds fuse to form a single periostracal secreting surface, or (2) extension by fusion layer, where the outer surfaces of the outer mantle lobes are united.

Yonge (1957) suggests that 'each natural group of lamellibranchs has a characteristic pattern of mantle fusion involving the ventral margins, the siphons and the ligament'. In a recent investigation into the basic form of the Lucinacea the ligament was examined to see whether its structure was comparable to that of other ligaments described by the above workers and whether it showed characteristics peculiar to the group. In addition to providing answers to these queries this study indicates a pattern of evolution of the ligament that is similar to and probably associated with other evolutionary

[Quarterly Journal of Microscopical Science, Vol. 101, part 1, pp. 25–36, March 1960.]

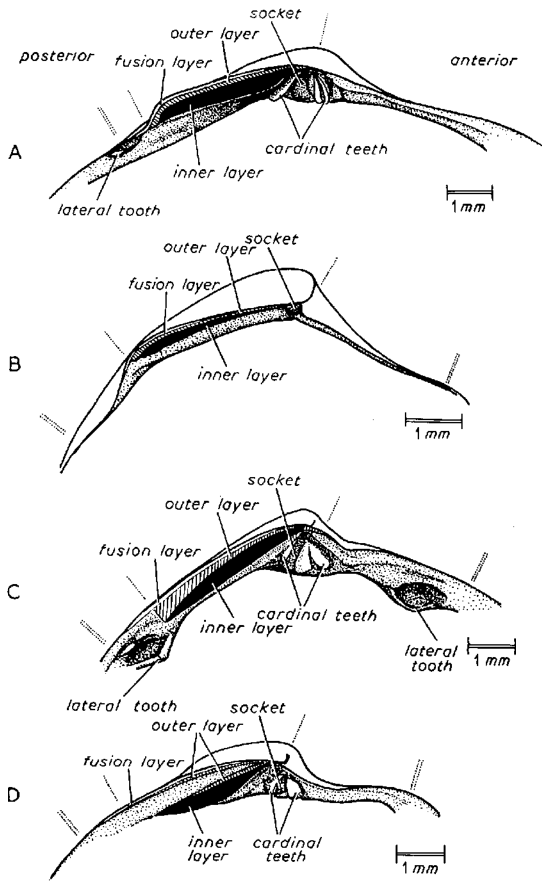


FIG. 1. Lateral views of the hinge structure of the left valves of A, *Diplodonta punctata*; B, *Thyasira flexuosa*; C, *Codakia costata*; and D, *Loripes lucinalis*. Dotted single lines mark the limits of the primary ligament and dotted double lines mark the limits of the secondary extensions of the ligament. The differentiation of the outer layer into anterior and posterior parts is shown in figs. 2 to 5.

trends in this group (Allen, 1958). It also provides information concerning the evolution of the ligament of lamellibranchs generally. The nomenclature proposed by Owen, Trueman, and Yonge (1953) has been followed.

## The Hinge Structure of the Lucinacea

Three families, the Ungulinidae, the Thyasiridae, and the Lucinidae, are grouped together and form the Lucinacea. They show an evolutionary sequence in the development of characteristic morphological features and habits, the Ungulinidae the least and the Lucinidae the most modified (Allen, 1958). Although 13 species were examined (Allen, 1958, p. 421), for clarity and conciseness reference will be largely restricted to *Diplodonta punctata* Say (Ungulinidae), *Thyasira flexuosa* (Montagu) (Thyasiridae), and *Codakia costata* d'Orbigny and *Loripes lucinalis* Turton (Lucinidae).

The hinge teeth of most species examined are poorly developed. The Ungulinidae and Lucinidae have two cardinal teeth below the umbo of each valve. The larger (anterior in the left valve, posterior in the right) is wedge-shaped and may be medially grooved (fig. 1). The larger tooth of the right valve fits behind that of the left. The second smaller cardinal tooth is reduced to a slight ridge and forms one wall of the socket into which the larger tooth of the opposite valve fits; i.e. the posterior wall on the left valve and the anterior wall on the right valve. A very poorly developed posterior lateral tooth may be present in the Ungulinidae. Both anterior and posterior lateral teeth may be present in the Lucinidae. The anterior tooth is usually better developed than the posterior (*Phacoides*, *Lucina*, *Divaricella*). Lateral teeth are most prominent in species of *Codakia* and absent in *Lucina* (*Loripinus*) *chrysostoma* and *Loripes lucinalis*. *Thyasira flexuosa* (Thyasiridae) bears a very small tooth below the umbo of the right valve. The left valve is toothless.

The ligament, in contrast with the hinge teeth, is well developed in the Lucinacea. The primary ligament extends from the anterior end of the lunule to a point approximately two-thirds of the way to the posterior adductor muscle. It is an opisthodetic ligament. The secondary ligament may extend as far as the anterior and posterior adductor muscles (figs. 1–5). The basic form and structure of the ligament closely resemble that of *Tellina tenuis* (Trueman 1949) and of *Glauconome rugosa* recently described by Owen (1959). Owen (1959) points out that the structure of the ligament is dependent on the degree of pallial fusion while the form is dependent on the growth pattern of the shell. Each shell increment is laid down as an open coaxial figure (gnomon). The ligament of the Lucinacea, being opisthodetic, has a single point of minimal growth near the anterior end.

*Ungulinidae.* The structure of the ligament of *D. punctata* and of this genus generally is shown in fig. 2. Posteriorly, between the limit of the outer layer and the anterior margin of the posterior adductor, there is a short extension of the primary ligament by fusion layer and fused periostracum. The ligament is external and, in transverse section, the periostracum, fusion layer, and

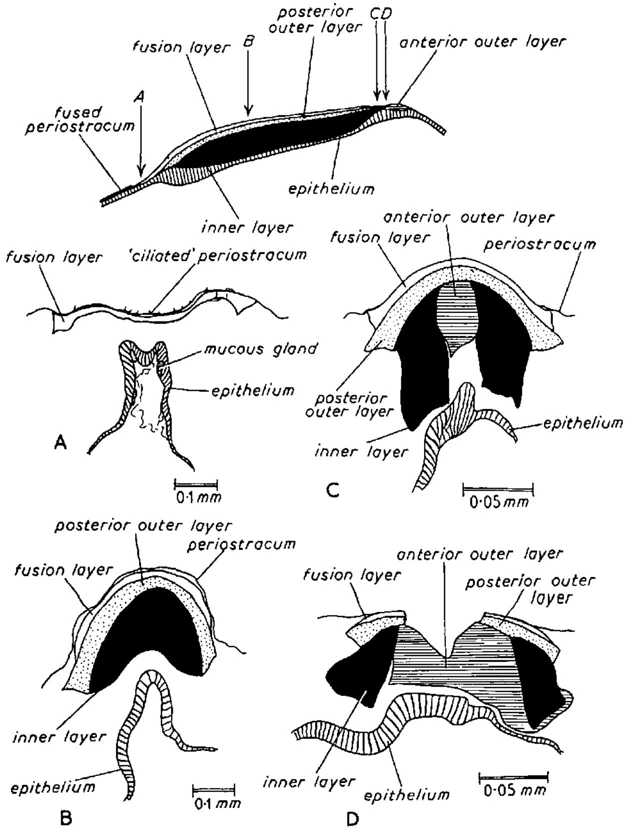


FIG. 2. Semi-diagrammatic representation of transverse sections through the ligament and dorsal margin of the mantle of *Diplodonta punctata*. The levels from which the sections were taken are indicated by arrows over a sagittal section of the same ligament viewed from the right side.

posterior outer layer form an inverted U, the centre of the U being filled with inner layer. Anteriorly below the umbos the ligament is split and bifurcated in the sagittal plane. The extent of the split is slight, approximately 200$\mu$. Sections show that posteriorly only the inner layer is split, while further forward the posterior outer layer, fusion layer, and periostracum are divided (fig. 2, C, D). The anterior outer layer (previously termed the cardinal ligament by Trueman, 1949) fills the split and extends beyond to the anterior limit of the lunule. In section the anterior outer layer and the fusion layer are so similar in appearance as to cast some doubt as to the identity of this layer (see p. 34). However, the anterior outer layer is secreted by the outer surface of the outer fold of the mantle within the depths of the anterior mantle embayment and sections show that there are no mucous glands present in this secreting epithelium. Mucous glands are present under the fusion layer and periostracum. There is no secondary anterior extension to the ligament in the Ungulinidae.

The secretory epithelia of the different layers of the ligament indicated in figs. 2 to 5 are similar to those described by Yonge (1953) for *Pinna carnea*. The cells secreting the outer layer are taller than those secreting the inner layer. The former are particularly well developed posteriorly at the point of maximum growth. The cells secreting the inner layer are cuboid, thus differing somewhat from those in *Pinna*. No mucous glands are present in the epithelia underlying the primary ligament. The cells secreting the fusion layer, although columnar, are not as tall as those secreting the outer layers, and their cytoplasm is not as granular as that of the cells below the primary ligament. Mucous glands are present in the epithelium-secreting fusion layer and fused periostracum. As Yonge (1953) observed in *Pinna*, there is no sharp demarcation between the various epithelia.

*Thyasiridae.* The ligament of *Thyasira flexuosa* differs little from that described above for the Ungulinidae. In cross-section the posterior outer layer and fusion layer no longer form an inverted U (fig. 3) and little is seen of the ligament externally. Posteriorly the fusion layer extends somewhat further than in the Ungulinidae and is, relatively, a much thinner layer. The posterior outer layer is thicker than that in *D. punctata* and forms a sharp posterior boundary instead of merging gradually to the fusion layer. The abrupt termination is reflected in the secreting epithelium, where the tall granular cells form a compact group with an indentation that coincides with the junction of inner and outer layers (fig. 3). The anterior outer layer differs little from that in the Ungulinidae, but there is secondary extension by fused periostracum as far as the anterior adductor. The anterior bifurcation of the primary ligament is more pronounced than that in the Ungulinidae, but, as in the latter family, the split is bridged by the anterior outer layer (fig. 3, F). The sagittal split is continued posteriorly as a cavity between the inner and posterior outer layer (fig. 3, D). This cavity is lozenge-shaped in cross-section and lined with anterior outer layer secreted by a tongue of epithelium. In *T. flexuosa*, at the tips of the bifurcation, the inner layer is lateral to the posterior outer layer and not ventral (compare figs. 3, D, F, and 2, D).

A similar but very much greater bifurcation occurs in *Glossus* (Owen, 1953). In this case Owen relates the progressive anterior splitting to a large tangential component of growth. There is no anterior secondary extension of the ligament in *Glossus*. There is little doubt that the bifurcation of the ligament in the Lucinacea is a result of the tangential component of growth. While this component is very large in *Glossus* it is small in the Lucinacea and

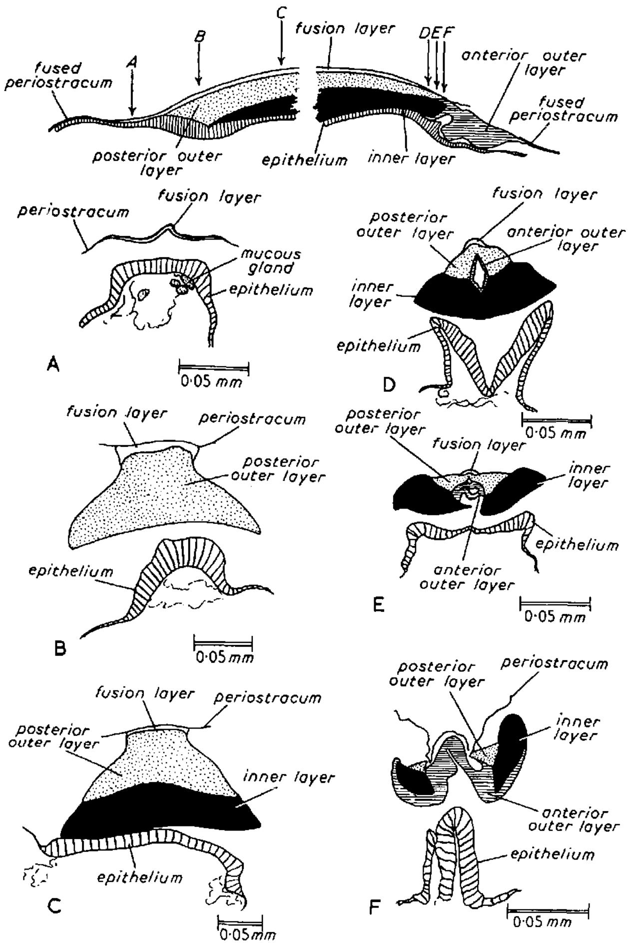


FIG. 3. Semi-diagrammatic representation of transverse sections through the ligament and dorsal margin of the mantle of *Thyasira flexuosa*. The levels from which the sections were taken are indicated by arrows over a sagittal section of the same ligament viewed from the right side.

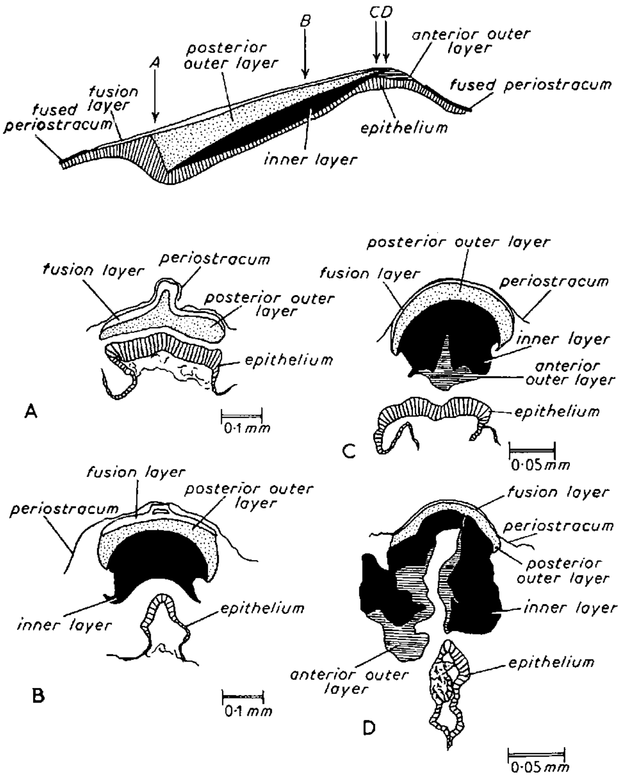


FIG. 4. Semi-diagrammatic representation of transverse sections through the ligament and dorsal margin of the mantle of *Codakia costata*. The levels from which the sections were taken are indicated by arrows over a sagittal section of the same ligament viewed from the right side.

the resulting split is considerably shorter. Unlike *Glossus* the outer lobes of the mantle anterior to the primary ligament are fused with the consequent extension by periostracum and, in the case of *L. lucinalis* (p. 34), by fusion layer. Unlike *Glossus* (Owen, 1953, fig. 3, E–H), the split does not involve the anterior outer layer. Sections, and observations on the intact ligament of the Lucinacea, suggest that the anterior outer layer is laid down in a more fluid form than the other layers. It appears to function as a cement or filling repairing the split ligament. Anterior outer layer is also present ventral to the inner layer and occasionally dorsal to the posterior outer layer, forming a small convoluted 'knob' at the anterior end of the primary ligament. Trueman (1949) describes a similar condition for *Tellina tenuis*. There is no sign of successive layers of conchyolin as is seen in the other layers of the ligament.

The greater part of the region of bifurcation in fully grown animals corresponds to the entire ligament of the larvae and early post-larvae. The split also coincides with the region of minimum growth in the older shells. As successive shell increments are laid down, the two regions representing the valves of the early post-larva are carried farther apart beyond the limit of normal maximum gape (fig. 6). This, as Trueman (1950) postulates for *Mytilus edulis*, may in itself be responsible for the split and reinforces the effect of the tangential component of growth. The divergence of the two halves of the split will be due to the effect of the tangential component alone. The lateral position of the inner layer at the tips of the bifurcation as seen in *Thyasira flexuosa* is a result of a large constant angle of growth (Thompson, 1942).

*Lucinidae*. All species of the Lucinidae examined, except *L. lucinalis*, have a ligament that is similar to that described for the Thyasiridae. The characteristic, sharply defined posterior limit of the outer layer is even more pronounced, ending abruptly at right angles to the fusion layer. Similarly, the corresponding indentation of the epithelial layer is much more pronounced than in *T. flexuosa* (fig. 4). The extent of the anterior split is similar to that described for *Diplodonta*. The split initially affects the internal surface of the inner layer (fig. 4, c). The anterior outer layer is secreted between the split and extends to the limit of the lunule. Secondary extension of the ligament is similar to that of *Thyasira*. Anteriorly fused periostracum extends as far as the anterior adductor muscle. Posteriorly the fusion layer extends almost to the posterior adductor muscle. The short distance between the limit of the fusion layer and the muscle is roofed by fused periostracum.

In *L. lucinalis* (fig. 5) modification of the posterior limit of the primary ligament is extreme. A tongue of epithelium reaches anteriorly almost as far as the umbo and divides much of the ligament horizontally into a long, narrow, external portion and a shorter, broad, scoop-shaped internal portion. This epithelium secretes posterior outer layer dorsally and ventrally, and shell laterally. The external part of the ligament is composed of fused periostracum, fusion layer, and a comparatively thick posterior outer layer, while the internal part is composed of inner layer and a thin outer layer, probably comparable to layer 1*c* described by Trueman (1949) for *Tellina tenuis*. The outer layers of each part are joined together at the umbos (fig. 5). The form of this ligament is correlated with the elongation and folding of the outer surface of the outer mantle fold between the pallial lobes in the depth of the posterior mantle embayment. This is not an isolated example, for elongation of the mantle epitheleum occurs in the Semelidae (Trueman, 1953). In the Semelidae there is a similar horizontal division of an opisthodetic ligament but here inner layer is present at each side of the external part.

In *L. lucinalis* the growth pattern of the inner layer is clearly seen. Each lamina or growth increment is thick posteriorly but thin ventrally (fig. 5), so

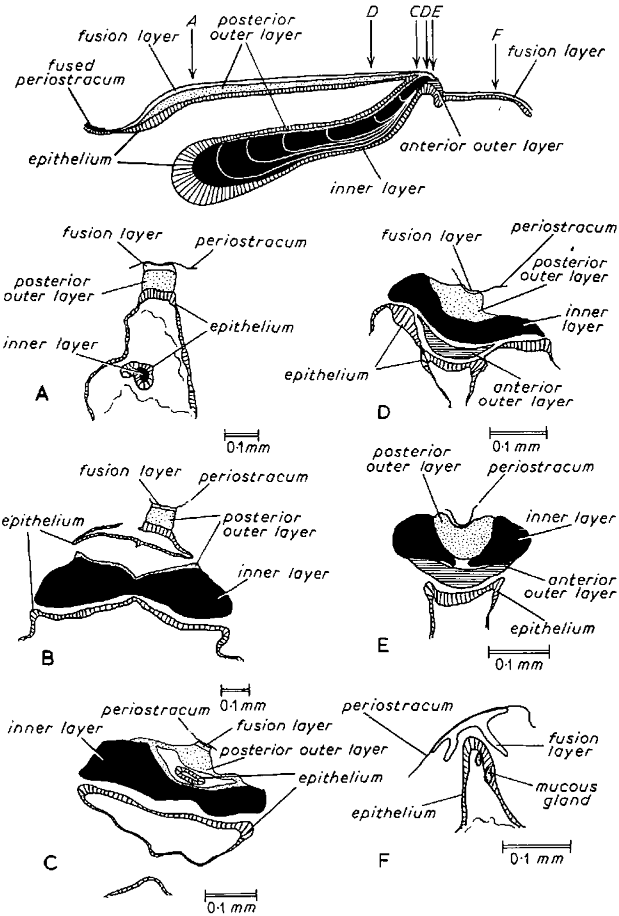


FIG. 5. Semi-diagrammatic representation of transverse sections through the ligament and dorsal margin of the mantle of *Loripes lucinalis*. The levels from which the sections were taken are indicated by arrows over a sagittal section of the same ligament viewed from the right side.

that in transverse sections other than at the extreme posterior part it appears that there are two zones, the upper with vertical and the lower with horizontal layering. In trichrome staining the lower zone stains blue while the upper is pale pink or colourless.

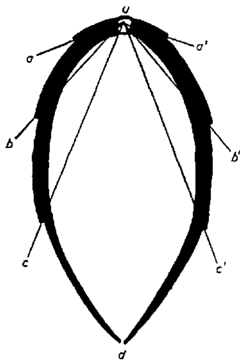


FIG. 6. Transverse section through the shell of a four-year-old bivalve. *ua*, *ab*, *bc*, *cd* represent annual increments of growth, while the angles *aua'*, *bub'*, *cuc'* represent the present gape of what were the valves of one-, two- and three-year-old shells.

The ligament is split anteriorly in much the same way as other members of the Lucinidae. Anterior outer layer cements the split and extends to the anterior limit of the lunule. The ligament is secondarily extended as far as the anterior adductor muscle. Fusion layer and fused periostracum are both involved. There is no fused periostracum anterior to the fusion layer. The fusion layer and anterior outer layer are so similar in staining and refractive properties that it is difficult to distinguish the junction between them. In *L. lucinalis* the fusion layer forms two long parallel ridges adjoining the valves of the shell, the ridges being connected by a thin dorsal covering (fig. 5, F). Posterior secondary extension of the external portion of the ligament is similar to that in other Lucinidae.

## DISCUSSION

Of the Lucinacea, the ligament of the Ungulinidae is the least modified and may be said to represent the basic form of the group. There is no secondary extension anterior, and little posterior, to the limits of the primary ligament. Modification in the Thyasiridae and Lucinidae includes secondary extension by fused periostracum as far as the anterior and posterior adductor muscles. Fusion layer extends beyond the posterior limit of the posterior outer layer but never as far as the posterior adductor muscle. Only in *L. lucinalis* is fusion layer present anterior to the ligament. Further modification includes the elongation of the outer surface of the outer mantle fold in the depth of the posterior embayment. At its maximum, in *L. lucinalis*, a tongue of tissue divides the ligament horizontally into internal and external portions. An evolutionary sequence can be postulated (fig. 7).

The anterior end of the ligament is split at the point of minimum growth and involves inner layer, posterior outer layer, and fusion layer. The extent of the split varies with the tangential component of growth and the constant angle of the valves. The split is filled with anterior outer layer, which acts both as cement and as a protection to the thinnest part of the ligament. Observations suggest that this layer is secreted in a more fluid form than other layers. The anterior outer layer probably has protective function in all opisthodetic ligaments at the point of minimum growth.

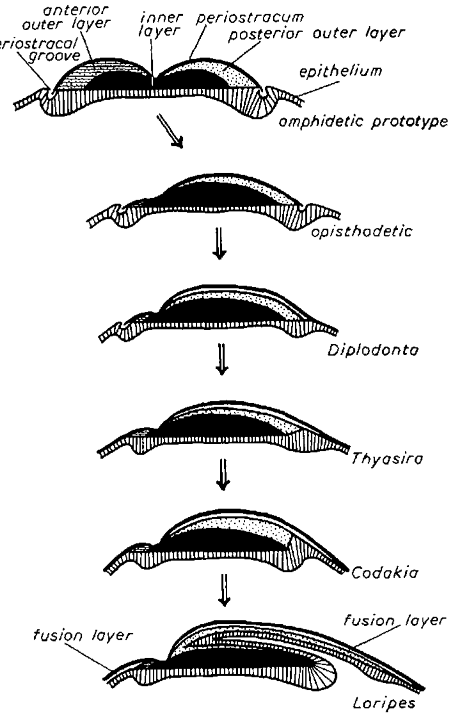


FIG. 7. The possible course of evolution of the ligament of the Lucinacea. Diagrammatic sagittal sections, seen from the left side. The various layers of the ligament correspond to those labelled in figs. 2 to 5.

I wish to thank Professor C. M. Yonge, C.B.E., F.R.S., for his advice and encouragement and Dr. G. Owen for his criticism of the manuscript. I am also indebted to the John Murray Committee of the Royal Society for a grant that made this work possible.

## REFERENCES

ALLEN, J. A., 1958. 'The basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia).' Phil. Trans. B, **241**, 421.

OWEN, G., 1953. 'On the biology of *Glossus humanus* (L.) (*Isocardia cor* Lam.).' J. mar. biol. Ass. U.K., **32**, 85.

—— 1958. 'Shell form, pallial attachment and the ligament in the Bivalvia.' Proc. zool. Soc. Lond., **131**, 637.

—— 1959. 'Observations on the Solenacea with reasons for excluding the family Glaucomyidae.' Phil. Trans. B, **242**, 59.

OWEN, G., TRUEMAN, E. R., and YONGE, C. M., 1953. 'The ligament in the Lamellibranchia.' Nature, **171**, 73.

THOMPSON, D'ARCY W., 1942. *On growth and form.* Cambridge (University Press).

TRUEMAN, E. R., 1949. 'The ligament of *Tellina tenuis*.' Proc. zool. Soc. Lond., **119**, 717.

—— 1950. 'Observations on the ligament of *Mytilus edulis*.' Quart. J. micr. Sci., **91**, 225.

—— 1953. 'The structure of the ligament of the Semelidae.' Proc. malacol. Soc. Lond., **30**, 30.

—— 1954. 'The structure of the ligament of *Pedalion*.' Ibid., **30**, 160.

YONGE, C. M., 1953. 'Form and habit in *Pinna carnea* Gmelin.' Phil. Trans. B, **237**, 335.

—— 1957. 'Mantle fusion in the Lamellibranchia.' Pubbl. Staz. Zool. Napoli, **29**, 151.