Observations on the Ligament of *Mytilus edulis*

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**Summary**

1. The ligament of *Mytilus edulis* is situated between the valves of the shell immediately below the dorsal margin and may be divided into two main layers, the inner and the outer, the principal features of which appear to correspond with those of other bivalves.

2. The outer layer is subjected to a tensile strain transverse to the longitudinal plane of the shell, which is imposed by the addition of the inner layer. This strain is increased when the valves are closed. At the same time the inner layer is compressed. It is significant, however, that the birefringence of the main outer layer is much smaller than in *Tellina*.

3. The prodissoconch has a small internal ligament which is replaced by the normal adult structure as the posterior dorsal margin of the young mussel is extended.

4. The axis about which the valves open is situated along a line drawn between the two main layers. Anteriorly the adult ligament becomes split and ceases to function. Possible explanations are suggested.

**Introduction**

In recent years little work has been carried out on the ligament of bivalves and that which has been done is largely the work of palaeontologists (e.g. Newell, 1937 and 1942). Among earlier works reference should be made to the important description of some features of the morphology of the ligament of *Mytilus edulis* by Villepoix (1892), to the account of Reis (1902), and to the more recent descriptions of Field (1922), White (1937), and Werner (1939). Other workers such as Jackson (1890), Dall (1889 and 1895), and Bernard (1895-7) discussed the ligament in general terms, the latter with some reference to development. The author has previously published observations on the ligament of *Tellina tenuis*, which is wholly external and parivincular (Trueman, 1942 and 1949).

This paper contains a brief account of the structure of the adult ligament of *Mytilus edulis* in which some new features are described, together with observations on its operation, development, and possible homologies. Results of work on the nature of the horny material, *conchiolin*, of the shell and ligament, will be published later. The term conchiolin is used in this paper in the most general sense to indicate the non-calcareous material of the shell and ligament.

The methods used in this investigation are similar to those previously described (Trueman, 1949). Descriptions and drawings of the ligament have been made from serial sections cut in ester wax and stained in Mallory’s triple
stain. The specimens used ranged from 0·25 mm. to 13 mm. in length. Comparison was made with larger mussels which are inconveniently long for serial sections.

**General Description**

The ligament, which extends along the dorsal margin of the valves for just less than half of the length of the shell (Text-fig. 1), is situated between the valves and does not project above them. In transverse section it is nearly rectangular (Text-fig. 3), in marked contrast to the shape of a wholly external ligament (e.g. *Tellina*). Like such a ligament, however, it consists of two main layers, comparable with the outer (1) and the inner (2) layers respectively of the *Tellina* type of ligament. In *Mytilus edulis* the outer may be subdivided into layers 1a and 1b. These layers show many features similar to those of the corresponding parts of the ligament of *Tellina tenuis* (Trueman, 1949).

Layer 1a is formed at the posterior end of the ligament near the fusion of the mantle lobes and extends forwards first as a 'posterior cover' (Trueman, 1949), then as the dorsal and outermost layer of the ligament (Text-fig. 2). This layer is laminated, the laminae being most clearly seen in the posterior region of the ligament (Text-fig. 2). The outer part of layer 1a is referred to in this paper as layer 1a1 and it is probably equivalent to layer 1a1 of the ligament of *Tellina*. The periostracum of each valve is attached to the lateral margin of this layer (Text-figs. 2 and 3). In the ligament of the mussel but not in that of *Tellina*, layer 1a1 becomes split in the mid-line above the posterior part of layer 2. The remainder of layer 1a is thus exposed along the dorsal surface of the ligament (Text-fig. 3).

Layer 1b forms the main part of the outer layer (1), extending from the umbo to near the posterior margin of the ligament. The shape and general relationships of this layer may be best understood from Text-figs. 1, 2, and 3, 1b. This layer is sharply marked off from the shell laterally and there seems to be little adhesion of the valves to the ligament except by means of layer 1a and the periostracum.
Layer 2 is situated below all but the posterior part of layer 1b (Text-figs. 1 and 3). In sections it has a fine fibrous appearance with the fibres running perpendicular to the ventral surface (Text-figs. 1 and 3). Lines nearly parallel to the latter indicate growth stages. As layer 2 is secreted a calcareous (White, 1937) or ligament ridge is deposited along each valve. These structures tend to prevent the ligament from moving in a ventral direction. They are nacreous and vacuolated (see Villepoix, 1892). The inner layer (2) is attached laterally to the ligament ridge upon a flat surface, termed the nympha (Text-fig. 3).

With Mallory’s triple stain layers 1b and 2 are readily differentiated, the former staining red and the latter blue. This is comparable with the staining reactions in *T. tenuis* previously described (Trueman, 1949) and those of the ligaments of certain other bivalves which have been examined, e.g. species of *Cardium, Sphaerium, Anodonta, Ostrea,* and *Nucula.* The epithelium of the pallial suture concerned with the secretion of the layers of the ligament is similar in *Tellina* and *Mytilus* (Text-figs. 1, 2, and 3).

In shells of more than 5 mm. length the anterior end of the ligament becomes progressively divided down the mid-line into two halves. This phenomenon is shown in Text-fig. 4 in a series of transverse sections of a specimen 13 mm. long; a is the most posterior section and d the most anterior. The stages shown in this figure are equivalent to those through which any part of a ligament passes when becoming split. The fissure first occurs in the inner layer (Text-fig. 4a) and extends to the outer layer as the ligament is pulled apart. Into the gap thus formed the epithelium of the pallial suture secretes a fold of conchiolin (Text-fig. 4, b, c, and d) which is similar to the outermost layer (1a). Immediately posterior to the split portion of the ligament the inner layer (2) is secreted. The reasons for this change in the nature of the secretion are of interest. They are probably related to the physical and chemical properties of
the layers concerned. Layers similar to layer 1a appear to be characteristic of
the outer surfaces of the bivalve. Those similar to layer 2 are typically internal.

After the fissure has developed the calcareous shell is deposited around each
half of the ligament which becomes deeply embedded in the valve (Text-fig. 4, c and d). The fold of conchiolin is extended and eventually separates the

![Text-fig. 4](image)

**Text-fig. 4.** A series of sections of the anterior end of the ligament of a specimen of *Mytilus* to show stages in the formation of the split in the ligament. a is the most posterior section and shows the fissure beginning in layer 2. b, 0.23 mm. in front of a, shows the split well developed with a fold of conchiolin extending between the two halves. In c and d these have become more separated and the inner calcareous layer of the shell is secreted between them. Section c is 0.1 mm. in front of b, and d 0.1 mm. in front of c.

hinge teeth. Similar features are found in *Modiolus modiolus*. Their possible interpretation is discussed below.

In larval stages (0.25 mm. long) the ligament is not divisible into the two
characteristic main layers (1 and 2). The valves are joined together by the
periostracum and by a layer of about 2μ in thickness, situated below the
former, which appears to be similar to the outer layer (1b) of the adult shell.
The inner layer (2) was first observed in young specimens of length 0.5–1
mm. (i.e. immediately after spatfall). The position of the early ligament has
been described by Bernard (1895–7) who made the important observation
that it is invariably internal when it appears in the young pelecypod. The
primary ligament of the young mussel (Text-fig. 5) is a small internal struc-
ture and clearly consists of outer and inner layers, which correspond with
those of the adult ligament. It is situated immediately below the umbones, and
hinge teeth or crénelures (Bernard, 1896) can be observed both in front of and behind this primary ligament, somewhat resembling a form of taxodont dentition. The adult ligament is secreted in a shallow pit situated in the region of the posterior hinge teeth. In mussels 0.5–2 mm. long the outer layer extends between the valves in a similar manner to the posterior cover of Tellina (Trueman, 1949). The primary ligament consists of this outer layer, slightly thickened, and a wedge of inner layer (2). The latter is not continuous with the corresponding part of the main ligament (Text-fig. 5b). In the fully grown mussel the primary ligament is surrounded by the shell and is non-functional.

![Text-fig. 5. Transverse (a) and longitudinal (b) sections of the primary ligament showing its relationship with the adult ligament and the hinge teeth.](image)

**THE GROWTH OF THE LIGAMENT**

As in the case of Tellina deposition of the outer layer extends forwards from its posterior margin to the posterior end of the inner layer. The rapid increase in thickness between these two points is clearly shown in Text-fig. 6. The outer layer is extended posteriorly as the mussel grows, whereas the inner is also increased in thickness along most of its length.

Measurements of the thickness of the outermost layer (ia) show a considerable reduction after deposition of the inner layers (ib and 2). The latter probably cause a tensile strain in layer ia, which thus behaves similarly to and is homologous with the posterior cover and layer ia of Tellina (Trueman, 1949. See fig. 13). Layer ib shows little modification after secretion. As described above the outermost layer (ia1) of the ligament of Mytilus becomes split in the mid-line above the posterior margin of the inner layer (2) (Text-figs. 2 and 3). This is probably due to the increase of tensile strain in the transverse plane of the ligament as the inner layers (ib and 2) are secreted. The splitting of layer ia1 does not occur in the ligament of Tellina.

The distance across the dorsal surface of the ligament (Text-fig. 7, AB) or the width of the ligament has been measured in different specimens at various distances from the umbones. The maximum occurs not at the posterior end of the ligament (where layer ia is thickest) but more anteriorly (Text-fig. 6), the distance thus being increased during deposition of the inner layer. The dorsal margin of the ligament appears to be stretched in a direction normal to the median plane of the shell.

As the outermost layer ia is stretched it becomes anisotropic in a similar way to that observed in Tellina. Layer ib is anisotropic only when the inner
layer is secreted on its ventral surface. The birefringence of layer 1b in *Tellina* is considerably greater than that of the same layer of *Mytilus*, the maximum value determined in transverse section being 0.005, as compared with 0.022 in *Tellina* (Trueman, 1949).

It may be concluded that post-depositional stretching of the outer layers (1a and 1b) takes place in the ligament of *M. edulis*. It occurs more markedly

![Graph showing the relationship of the thickness of the main layers (1 and 2) and of the width of the upper surface (Text-fig. 7, AB) of the ligament to each other and to the other features indicated.](image)

in the external parivincular type of ligament, e.g. *Cardium* or *Tellina*. The higher value of birefringence in the latter is possibly associated with the greater amount of stretching of their outer layers.

**Some Observations on the Operation of the Ligament**

Observations were made of the operation of the ligament by use of transverse sections of whole specimens in which all muscle attachments had been cut so that the opening of the valves could be controlled. The outer layer (Text-fig. 7, AB) was measured in both the closed and the normal feeding position of the valves. When the valves are closed from the latter position the upper surface of the ligament is visibly stretched in the transverse plane, the width being increased by about one-eighth (measured on a section of a ligament 25 mm. behind the umbo of a mussel 70 mm. long). Simultaneously the width of cross-section of the ventral edge of the inner layer (Text-fig. 7, EF) is reduced by approximately the same amount. Where layers 1 and 2 are of equal thickness the transverse measurement along their common boundary (Text-fig. 7, CD) remains constant when the valves are opened and closed. From these and other observations it is probable that the pivotal axis of the ligament, about which the valves open, lies between layers 1 and 2 in the midline (Text-fig. 7), as in *T. tenuis*. 
About two-thirds of the ligament of an adult mussel is effective in causing the opening of the valves. There are two non-functional regions, one at each end of the ligament. Anteriorly the split portion together with the ligament immediately behind it no longer operates the valves; posteriorly layer 1 does not open the shell prior to deposition of the inner layer (2). From such observations as have been made the presence of both the outer and the inner layers seems to be necessary in ligaments of most bivalves.

Dall (1895) pointed out that all hinge ligaments must be arranged along a straight axis, as no bivalve ligament can function around a curve. Thus most external hinge ligaments are situated along the straight dorsal margin of the shell, and many bivalves without this characteristic feature possess an internal ligament.

The location of the pivotal axis in the mid-line between the two main layers (1B and 2) (Text-fig. 7) accounts for certain of their characteristics. The outer layer is subjected to tensile stresses when the valves are closed; at the same time the inner layer undergoes compression. The latter is weak to tensile stresses, splitting easily parallel to the fibres (Text-fig. 3). But since this layer (2) is situated below the pivotal axis, it is normally only subjected to compression when the valves are closed.

In any consideration of the development of the ligament it is essential to take note of the progressive increase of the angle (Text-fig. 8, APA1) between the early parts of the valves, which is caused by the secretion of the shell along the ventral margin (Text-fig. 8, AD or A1D). An attempt has been made to measure the rate of increase of this angle in various genera. A transverse section was cut through the shell in the umbonal region and projected so that an enlarged outline of the valves could be drawn. Measurements were then made of the height of the shell (Text-fig. 8, PA, PB, PC, and PD) and of the corresponding increase of angle of gape at the pivotal axis, represented in Text-fig. 8 by angles APB + A1PB1, APC + A1PC1, and APA1. The amount of angular separation undergone by the valves of a shell in growing from a height of 10 mm. to various subsequent stages was thus determined. Owing to the
obliquity of the shell of *M. edulis* measurements were made on sections cut perpendicular to the ligament at the distance from the umbones equivalent to the ligament length of a young mussel of 10 mm. height. With more equilateral bivalves such as *Cardium* the heights can be measured directly from the projected section, but with *Mytilus* it is more convenient to convert this dimension into the true height of the shell.

![Diagram](image)

**Text-fig. 8.** Diagrammatic transverse section of a bivalve showing the effect of the secretion of the shell at the ventral margin. In the young bivalve points A and A₁ were together and have been separated by the deposition of AD (and A₁D), so that the valves now have a permanent gape of the angle APA₁. Some intermediate stages have been indicated.

The cross-section of a valve of most lamellibranchs corresponds to an equiangular spiral, though a reduction of spiral angle in the later stages of growth is not uncommon. *Cardium edule* and *Barbatia lactea*, for example, have a comparatively large spiral angle, and deposition at the margin of the valves causes a large increase of the angle between the early valves. Those shells with a lower spiral angle, such as *Chlamys opercularis*, have relatively a much lower rate of increase of angle at their pivotal axis. When the stages in the increase in the angle of gape of some young part of a shell (e.g. representing the stage of 10 mm. height) are plotted against the corresponding heights of the shell, e.g. with *Cardium*, the curve produced is similar to that obtained from comparable measurements made on an equiangular spiral (Thompson, 1942, p. 749). The curve resulting from these measurements in *Cardium edule* corresponds approximately with one based on a logarithmic spiral of 55° spiral angle (Text-fig. 9).
The corresponding curve based on similar measurements in *Mytilus edulis* is more complex, showing a marked change in the rate of increase in the gape of an early stage in the shell. This results from the fact that the section of the young shell of *Mytilus* approximates to a spiral angle of about 35° which is reduced relatively suddenly in large shells (Text-fig. 9). This implies that, in adult stages, the rate of increase of the gape of an early stage of *Mytilus* is markedly slower than in many lamellibranchs.

**DISCUSSION**

It may be observed that the ligament of *Mytilus* has a very significant split even though the rate of opening of the valves, especially during later growth, is relatively low. The whole of the original ligament of a shell 16 mm. long becomes split when the bivalve has grown to a length of 70 mm. While this growth is taking place the valves have increased their angle of gape by 120°. The ligament of a specimen of *Cardium edule*, 12 mm. long, becomes entirely split when the valves have opened during growth to an angle of about 200°. Such a split only affects the inner layer (2) of the ligament. It appears that the progressively increasing gape of a growing shell affects differently the different types of ligaments.
The dorsal surface of the ligament of *M. edulis* is slightly arched at the anterior end when viewed in the plane of a sagittal section. As the gape of the early valves increases the umbones move away from each other. The anterior part of the ligament is completely below the pivotal axis (owing to the slight arching) and upon the opening of the shell both layers (1 and 2) of the ligament tend to be pulled apart. If the ligament were not arched at the anterior end, then the opening of the valves, during growth of the shell, would be about the normal pivotal axis of the ligament. Layer 2 would thus be subjected to an increasing tensile strain as the valves open and layer 1 would probably be only little affected. The latter seems likely to be the conditions found in *C. edule*. As observed above, the ligament of the mussel becomes deeply embedded in each valve after it has split. This is a process which progresses as the shell grows and gives rise to the much thickened sub-umbonal region of the shell.

It may be deduced that the ligament of the mussel splits because of its slight dorsal arching coupled with the increasing gape of the valves. The comparatively long ligament of *M. edulis* must be related to the development of the mytiliform shell with a long posterior end. The length of the ligament may to some extent be accounted for by its internal situation. Because of this it is probably less efficient than the external parivincular type of ligament of *Tellina* or *Cardium*.

The ligament of an adult mussel begins to develop at about the time of spatfall, as the posterior dorsal border of the shell extends. The internal, primary ligament appears to function only when the shell is small and circular. If the shell had remained more or less equilateral in shape it might possibly have persisted as an 'internal' type of ligament situated in the umbonal region only, such as, for example, that of *Ostrea*. A full discussion of the problem of the relationship of ligament form and efficiency to the shell shape and to the influence of the environment will be published later.

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