OBSERVATIONS ON CERTAIN MECHANICAL PROPERTIES OF THE LIGAMENT OF *PECTEN*

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INTRODUCTION

The hinge ligament of most lamellibranchs is a horny structure situated in the dorsal region of the shell, which causes the opening of the valves when the adductor muscles relax. The morphology, development, nature, and certain aspects of the operation of the hinge ligament have recently been described (Trueman, 1949, 1950, 1951) and the basic structure of the ligament and of the mantle secreting it discussed (Owen, Trueman & Yonge, 1953).

Apart from the paper of Marceau (1909) there is little information on the mechanical properties of the ligament. This is remarkable in view of the attention that has been given to the adductor muscles (e.g. Bayliss, Boyland & Ritchie, 1930) and to the swimming habit in the Lamellibranchia (Yonge, 1936) with particular reference to *Pecten*.

The present paper gives a brief description of the ligament of *P. maximus* and discusses experiments to determine certain mechanical properties related to their form.

THE STRUCTURE OF THE LIGAMENT

The ligament of *P. maximus* is situated between the valves dorsally and extends both in front of and behind the umbo. It consists of two main regions, the outer and inner layers (Fig. 1).

The outer layer, uniting the dorsal margins of the valves, which are elongated in *Pecten* to form the auriculae, is laminated, the laminae lying nearly parallel to its ventral surface. In transverse section the layer is approximately rectangular in shape, the width between the valves being much smaller than its thickness. Apart from the laminations this region of the ligament is undifferentiated, and it may be thus considered as a single layer. This layer may represent either the fusion layer or the true outer layer of the ligament (Owen *et al.* 1953). For convenience of reference it is called herein the outer layer, and a full discussion of its interpretation will be published shortly.

The relatively large, dark brown, inner layer of the ligament is attached to the valves in the ligament pits or resilifers. It is pyramidal in shape, with a base that bulges ventrally particularly when the valves are closed. The inner layer may be divided into three parts, a large non-calcareous central region of rubber-like consistency and two lateral calcified regions attaching the former to the valves (Fig. 2). The lateral parts of the inner layer are rather similar to the entire inner layer of the

ligament of other lamellibranchs, but the central region appears to be a modification characteristic of the Pectinidae. It consists mainly of a tanned protein complex of a somewhat gelatinous appearance. The outer layer is much more fibrous and is generally similar to the outer layer of the ligament of other lamellibranchs, e.g. *Ostrea* and *Tellina* (Trueman, 1951, 1949).
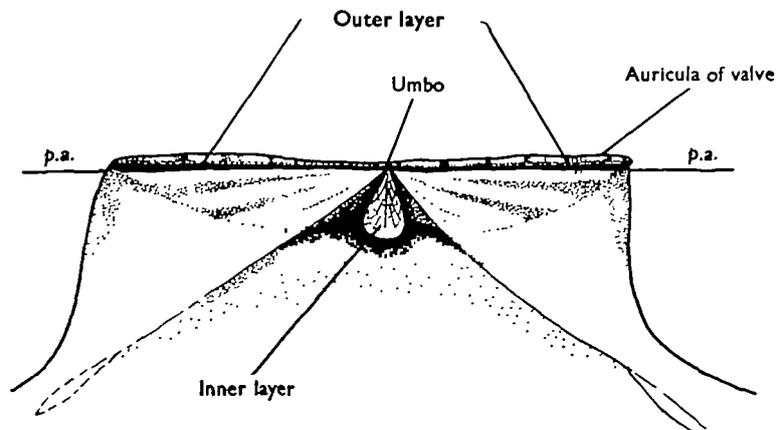

Fig. 1. Interior of the dorsal region of the right valve of *Pecten maximus* with the ligament cut in longitudinal section. The position of the pivotal axis (*p.a.*) is indicated. Approximately natural size.
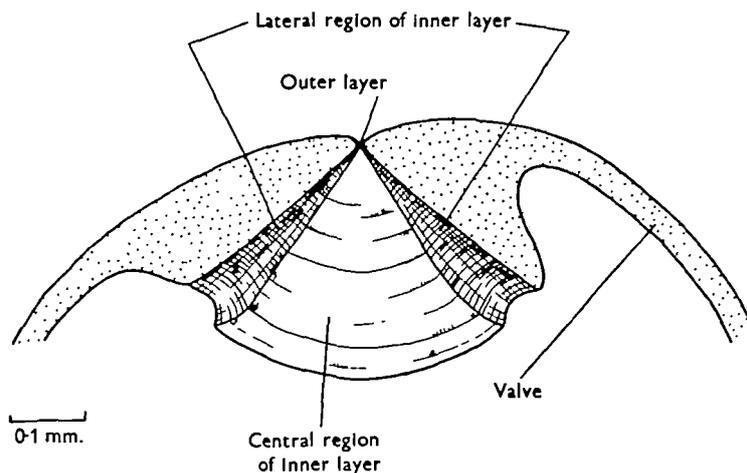

Fig. 2. Diagrammatic transverse section through the ligament of *Chlamys opercularis* showing the outer layer and the central and lateral regions of the inner layer. The outer layer is commonly worn away in this part of the ligament.

It may be noted that the ligament of *Chlamys opercularis* is very similar to that of *Pecten maximus*, and that in some experiments it has been used in place of the latter.

A more complete account of the structure and nature of the ligament of *Pecten* will be published shortly.

MECHANICAL PROPERTIES OF THE LIGAMENT OF *PECTEN*

(1) *The closing moment of the ligament*

The ligament of most lamellibranchs consists of two layers, the outer generally situated above, and the inner layer below the neutral axis of the structure. The former layer is subjected to tensile stress and the inner layer to compression when the valves are closed. The force so derived tends to open the valves and has been measured in terms of a moment about the hinge or pivotal axis of the shell (Fig. 1). In many lamellibranchs the pivotal axis lies in the plane of the neutral axis of the ligament. This force is thus referred to as the opening moment of the ligament, while that required to close the valves may be estimated and referred to as the closing moment of the ligament.
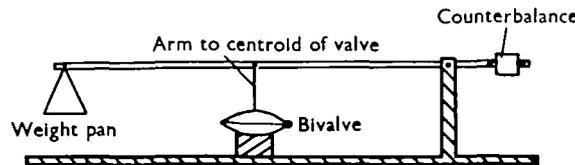

Fig. 3. Diagram of the apparatus used to determine the opening and closing moments of the ligament. A full description is given in the text.

The method used to determine the opening moment of the ligament of the oyster has been briefly described (Trueman, 1951). The equipment consists of a beam, bearing a weight pan and an arm on one side of a pivot, and an adjustable counterbalance weight on the other (Fig. 3). A bivalve shell, from which the tissues have been carefully removed immediately prior to the determination being made, is placed firmly on an adjustable platform with the valves held closed and the counterbalance adjusted so that the arm just rests in a small hole drilled near the centroid of the upper valve. When the valves are released the shell opens and the beam is raised. The weights placed on the pan to close the valves or to hold them in any partly closed position may thus be determined and the effect of their removal observed.

The closing moment of the ligament may be readily determined by means of the equipment described above, measuring the weight required just to close the valves and using the formula

$$\text{closing moment } (M_c) = (2W+v)d \text{ g.mm.},$$

where W = the weight applied (multiplied by 2, since the pan is twice the distance of the arm from the pivot),

v = the weight of the valve, assuming that the point of application of W is close to the centre of gravity of the valve,

d = the distance of the point of application of W from the pivotal axis.

To obtain some basis of comparison for the closing moments of different species it was necessary to take into account the size of the specimen. The closing moment of a number of specimens of the same species, but of different size, was plotted

logarithmically against the length of the shell. This showed that the cube of the length gave the most satisfactory relationship, and accordingly the volume of the shell was taken as a convenient measure of size. Thus the ratio closing moment/shell volume $(M_c/V$ g.mm./c.c.) was determined. The results for the ligament of *P. maximus*, *Chlamys opercularis* and a number of characteristic lamellibranchs are given in Table 1.

These results show a fairly wide range of values for this ratio and it is noteworthy that those of *Pecten* and *Chlamys* are similar and are at the lower end of the range. The ligaments of *Mytilus* and *Cyprina* appear to be amongst the most powerful.

(2) *The loading and unloading cycle and the opening moment of the ligament*

If a load-extension curve is drawn for the loading and unloading of an elastic material the form of the curve is a loop, the 'hysteresis loop'. It is possible to draw
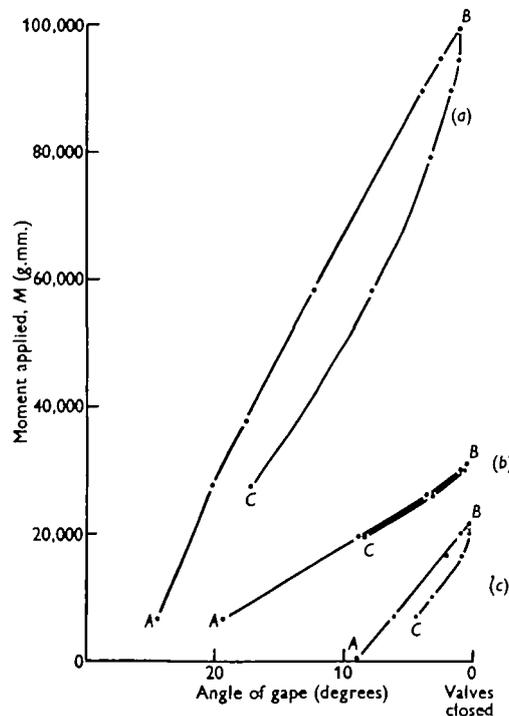

Fig. 4. Graph showing the relation between the load applied to the valve, expressed as a moment '*M*' about the pivotal axis, and the angle of gape for the loading (*AB*) and unloading (*BC*) of the ligament of (*a*) *Cyprina islandica*, (*b*) *Pecten maximus*, (*c*) *Mytilus edulis*.

a similar curve for the ligament (Fig. 4), the load being represented by the weight applied to the valve, expressed in terms of a moment about the pivotal axis of the ligament, and the extension by the angle of gape of the valves. Clearly the state of maximum stress of the ligament is in the closed position of the valves, so that in plotting such a curve it is convenient to show the position of maximum gape

(corresponding to minimum stress) on the left of the graph. The loading curve (Fig. 4, *AB*) corresponds with the closure of the shell and the unloading curve to its opening (Fig. 4, *BC*).

The loading curve of the ligament of many species of lamellibranchs (thirty-five species investigated), e.g. *Pecten maximus, Chlamys opercularis, Cyprina islandica* and *Mytilus edulis*, is a near linear relationship between the force tending to close the valves and their angle of gape. This curve indicates the conditions through which the adductor muscles contract when closing the shell, and shows that the force required is fairly constant per degree of gape over the entire range of gape of the valves.

A consideration of the unloading curve (Fig. 4, *BC*) of the ligament is important, for it is upon the upper part of this curve that the ligament operates in causing the valves to open. When the weight, *W*, which just closes the shell, is reduced slightly the valves do not immediately open. They commence to gape only when the thrust of the ligament exceeds the pressure on the valves. This thrust of the ligament may be measured as the opening moment (M_o), and it is convenient to determine this and the opening moment per degree of gape of the valves from the unloading curves. The latter are best drawn with the load expressed as the ratio M_o/V in a similar manner to that described for the closing moment. Such curves are shown in Fig. 5 and the results of the determination of the opening moment in Table 1.

Table 1. *Results of the determination of the opening and closing moments of the ligament of a number of typical lamellibranchs*

(The mean closing moment (M_c), the estimated mean opening moment (M_o), and the opening moment per degree of gape (θ) have been expressed in relation to the volume (V) of the shell.)

Species	Number of specimens	$M_o/V \pm$ s.e. (g.mm./c.c.)	M_o/V	$M_o/V/\theta$ (g.mm./ c.c./degree)
Mytilacea: *Mytilus edulis*	30	780 ± 48	660	65
Pectinacea: *Pecten maximus*	7	167 ± 16	160	5
Chlamys *opercularis*	29	148 ± 3·8	142	5
Ostreacea: *Ostrea edulis*	6	425 ± 24	370	40
Cyprinacea: *Cyprina islandica*	2	610	550	25
Cardiacea: *Cardium edule*	35	140 ± 10	114	5
Mactracea: *Lutraria lutraria*	8	285 ± 5·3	265	20
Tellinacea: *Tellina crassa*	29	370 ± 13	320	9

Examination of the hysteresis loops drawn for different ligaments in Figs. 4 and 5 shows that the difference between the loading and unloading curves is at a minimum in the case of *Pecten maximus* and *Chlamys opercularis*. Similarly, from Table 1 it may be observed that these species show least difference between the closing and opening moments. The difference between these moments is some measure of the internal resistance of the structure. It is approximately 4 % of the closing moment in *Pecten*, but values of between 10 and 20 % are commonly encountered in other bivalves. The relatively low internal resistance of the ligaments of *Pecten* and *Chlamys*, and their correspondingly low 'work-loss', suggests that these structures

are more efficient for the frequent opening and closing of the valves than are those of the other species examined.

Only in a few lamellibranchs do the valves open to the maximum gape, the ligament normally operating over the top portion of the curves shown in Fig. 5. The experimental loading and unloading of the valves was arranged, in a number of species, so that a curve could be drawn representing loading from a position of maximum gape, partial unloading and the subsequent reloading of the ligament.
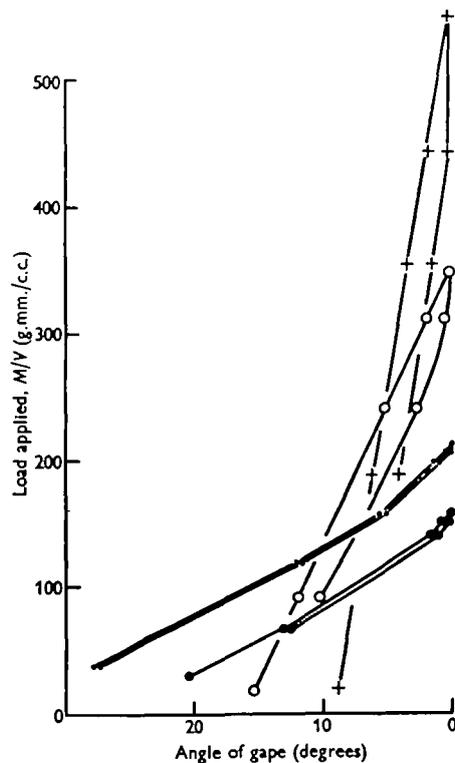

Fig. 5. Graph showing the relation between the load applied to the valve, expressed as a ratio between the moment 'M' and the shell volume 'V' (M/V), and the angle of gape for the following species: +———+, *Mytilus edulis*; O———O, *Lutraria lutraria*; •———•, *Pecten maximus*; ●———●, *Chlamys opercularis*.

Such curves are shown in Fig. 6 for the ligaments of *Mya*, *Anodonta* and *Chlamys*, the operation being carried out in a period of 10 min. From this figure it may be observed that the second loading curve is commonly to the right of the initial loading curve. Successive unloading curves however remain relatively constant.

Repeated experimental opening and closing of the valves, e.g. 100 times in 1 min. in *Chlamys opercularis*, 100 times in 2 min. in *Pecten maximus* or 160 times in 4 min. in *Anodonta cygnea*, through an angle of gape restricted to about 10 degrees, showed practically no variation in the unloading-loading cycle. From these observations

it may be concluded that there is little change in the elastic properties of the ligament of these species due to the repeated opening and closure of the valves over relatively short periods. A comparison of the area enclosed in such loops as these
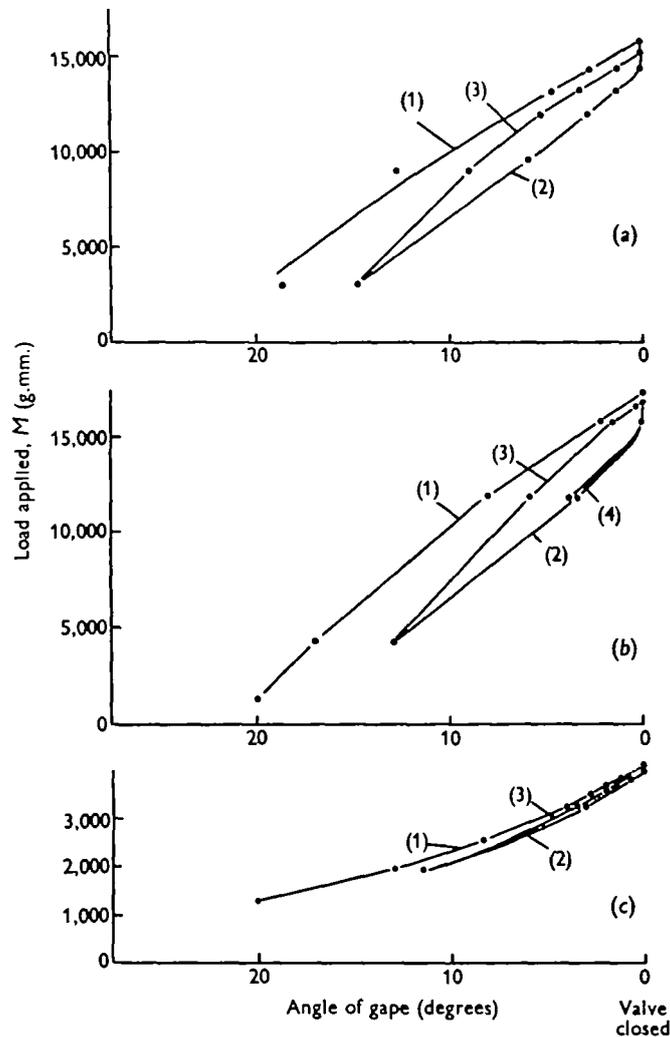

Fig. 6. Graphs showing the effect of loading (1), partial unloading (2), and subsequent reloading (3) and unloading (4) of the ligament of the following species: (*a*) *Mya arenaria*, (*b*) *Anodonta cygnea*, (*c*) *Chlamys opercularis*. The load applied to the valve expressed as a moment (M) is plotted against the angle of gape.

latter (Fig. 6) is possibly a better means of measuring the efficiency of the various ligaments than consideration of the complete loading-unloading cycle. The relatively small loop of the ligament of *Chlamys* is again apparent.

(3) Thermoelastic properties

Study of the thermoelastic properties of natural high polymers has been most useful in obtaining insight into the shape and properties of their molecules. The presence of long folded flexible chain molecules is responsible for the high reversible extensibility shown by many substances such as rubber, muscle and collagen. Stretching is considered to produce the straightening of such flexible chains, and when the deforming force is removed, thermal agitation leads the chains to return to a more folded condition. If such a rubber-like substance is stretched and the length kept constant the elastic force increases as the temperature rises and decreases as the temperature falls. This is in marked contrast to the behaviour of a normal solid, stretched to a constant length, in which the elastic force diminishes on warming.
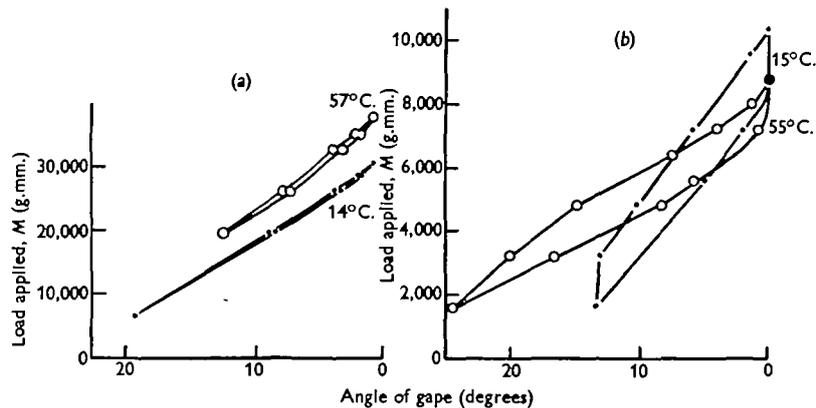

Fig. 7. Graph plotted similarly to Figs. 4 and 6 showing the effect of raising the temperature on the ligaments of (a) *Pecten maximus* and (b) *Anodonta cygnea*. The temperatures used are indicated on the graph.

In considering the effect of change of temperature on the ligament of lamellibranchs it should be noted that only the outer layer is subjected to tensile stress. Experiments carried out to determine the effect of temperature change on the compression of the isolated inner layer of the ligament of *Pecten*, using the method described on p. 463, showed no change of moment when the temperature was raised from 15 to 50° C. In specimens of *Chlamys opercularis* and *Pecten maximus* the effect of raising the temperature on the loading cycle is to produce an increased moment at all angles of gape (Fig. 7 a). When the temperature is raised from 15 to 55° C., the ligaments of *Anodonta cygnea* and *Mytilus edulis* show little change at low angles of gape, but at wider angles, i.e. conditions of little stress, the opening moment is increased (Fig. 7 b). When such specimens are returned to the lower temperature, the loading-unloading cycle generally reverts to normal. Since the temperature change does not appear to affect the inner layer of the ligament the increased moment may be attributed to the contraction of the outer layer as the temperature is raised.

At all stresses normally encountered in the ligaments of *Chlamys* and *Pecten* the temperature coefficient is positive, and the outer layer of the ligament behaves as if composed of long flexible chain molecules. This also occurs at low stresses in the ligaments of *Mytilus* and *Anodonta*. When the valves of the latter are closed the stress is much greater and the temperature change has no positive effect.

(4) ·The role of the outer layer of the ligament

The method used for the determination of the closing moment of the ligament may be utilized in the assessment of the function of different regions of the ligament. Parts of the outer layer of the ligament of *Pecten* or *Chlamys* may be easily removed, because of its location along the auriculae of the valves (Fig. 1), and the
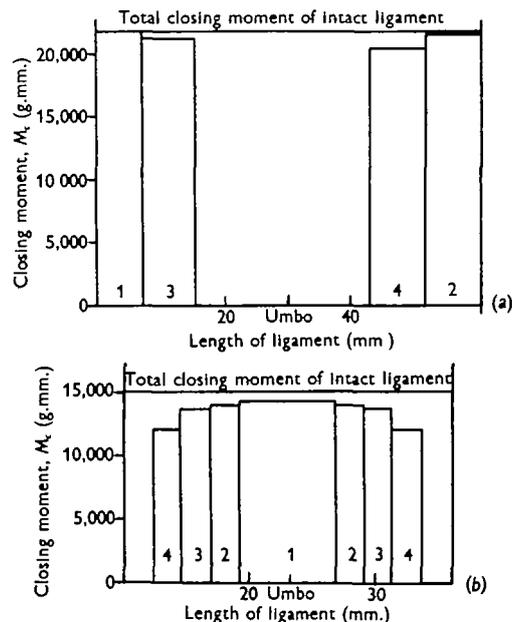

Fig. 8. Graphs showing the effect of removing the outer layer of the ligament on the closing moment (M_o). The columns numbered 1 to 4 indicate the successive parts of the ligament removed (a) centripetally, and (b) centrifugally. The height of each represents the closing moment of the ligament with that portion of the ligament removed.

effect on the closing moment of the ligament observed. The outer layer of the ligament of *Pecten maximus* was removed in some specimens, first from the anterior and posterior margins of the auriculae, successively cutting away more central portions (Fig. 8a), and in other specimens first from the region close to the inner layer, then progressing centrifugally (Fig. 8b). Very little, if any, functional outer layer was left above the inner layer of the ligament in the latter procedure.

It may be observed from Fig. 8a that the lateral parts of the outer layer can be removed with little effect upon the total closing moment of the ligament, but that the amount that can be cut away is limited. Below this limit the stress applied to the reduced outer layer, when the valves are closed, causes the tearing of this layer and the fracturing of the inner layer. Removal of the central part of the outer layer

(Fig. 8b) shows that a considerable portion may be taken away with little effect, e.g. with only about one-third of the outer layer functional the closing moment is not greatly effected. Complete removal of the outer layer either from in front of or from behind the umbo leads to the fracturing of the inner layer. This is presumably caused by the then asymmetry of the arrangement of the ligament.

These experiments show that considerable parts of the outer layer of the ligament of *Pecten* may be removed without any great effect on the strength of the ligament and possibly indicate that no part of the outer layer is normally subjected to extreme stress. This may be related to its considerable relative length. This view is supported by the small width of the outer layer between the valves (Fig. 2), by its faint birefringence when seen in transverse section and by the similarity of the properties of the isolated inner layer to those of the inner layer of the intact ligament, as discussed in the following section. The outer layer produces a long fairly rigid hinge line near the pivotal axis of the opening of the valves, and is probably of importance in preventing any rotation of the valves on each other, particularly when they are gaping. The association of a single adductor muscle with a relatively long, straight and symmetrical hinge should be noted.
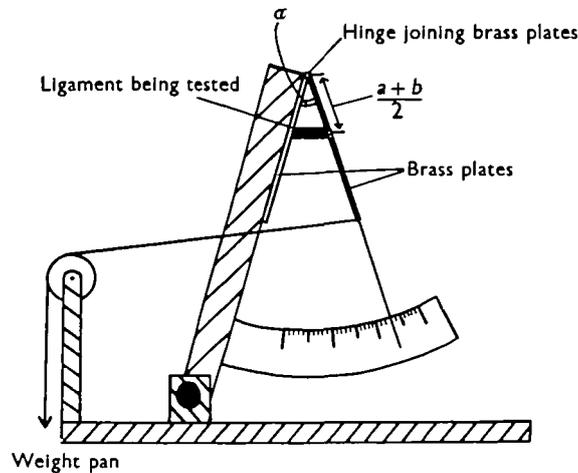

Fig. 9. Diagram of the apparatus used to investigate the compression of the isolated inner layer of the ligament. For further explanation see the text.

(5) The properties of the isolated inner layer

The results of the experiments described above indicate the importance of the inner layer of the ligament of *Pecten*. To enable the properties of this layer of the ligament to be investigated under conditions as similar as possible to those found in life, but without the complication of the presence of the outer layer, the following equipment was used.

Two brass plates were firmly hinged together, one attached to a wooden arm and the other hanging free with a pointer extending to a scale on which the angle (α, Fig. 9) could be read off. Pieces of ligament cut from the inner layer were

placed between the plates, orientated the same way as between the valves, and subjected to compression by means of weights attached to the end of the free plate using the pulley wheel shown in Fig. 9. The main arm was adjustable, allowing the free plate to be moved into a vertical position so that its weight need not affect the calculations.

Using this equipment portions of the inner layer of the ligament can be subjected to compression and the angular change recorded. From these figures the modulus of elasticity under compression can be determined and stress-strain (or load-compression) curves may be drawn.

Young's modulus of elasticity in compression may be determined from the formula

$$E = \frac{2M\alpha}{\theta s (a+b)},$$

where E = the modulus of elasticity in compression,

M = the force applied, estimated as a moment about the hinge,

$\frac{a+b}{2}$ = the mean distance from the hinge to the material tested,

s = the cross-sectional area of the material used,

α = initial angle subtended by the arms (in radians),

θ = change in angle subtended by the arms (in radians).

Where possible these symbols are indicated in Fig. 9. The stress-strain curves for the material tested may be drawn, plotting the forces applied per unit cross-sectional area (g./mm.^{2}) against the percentage compression estimated from the angular change.

This procedure was applied to portions of the inner layer of the ligament of *Pecten maximus*, *Ostrea edulis* and *Lutraria lutraria*, and the results are given in Table 2 and Fig. 10.

The mean modulus of elasticity in compression of the inner layer of the ligament of *Pecten* is 320 g./mm.^{2}. This figure is much lower than the values obtained for *Ostrea* (2170 g./mm.^{2}) or *Lutraria* (2240 g./mm.^{2}) and indicates that the inner layer of the ligament of *Pecten* is much less resistant to forces closing the valves than that of the latter two bivalves. The variations in the results obtained for *Ostrea* and to a lesser extent those of *Lutraria* are probably due to the small size of the portions of the ligament obtainable, which consequently had to be placed as near the hinge as possible.

The stress-strain curves (Fig. 10) show that the load necessary to produce 20 % compression of the inner layer of the ligament of *Pecten* is approximately one-fifth of that required similarly to compress that of *Ostrea*. The percentage compression undergone by the inner layer of the ligament *in situ* between the valves when the shell closes is about 45 % in *Pecten*, 30 % in *Ostrea* and 40 % in *Lutraria*. Stress-strain curves have also been drawn for the isolated inner layer when subjected to these amounts of compression, with similar results.

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The curves shown in Fig. 10 are in the form of the hysteresis loop, and the area of this for *Pecten* is much smaller than that of the other species. This corresponds to the observations on the complete ligament. This, together with the conclusions reached regarding the role of the outer layer of the ligament of *Pecten*, emphasizes the importance of the inner layer of this type of ligament in the determination of its characteristic properties.
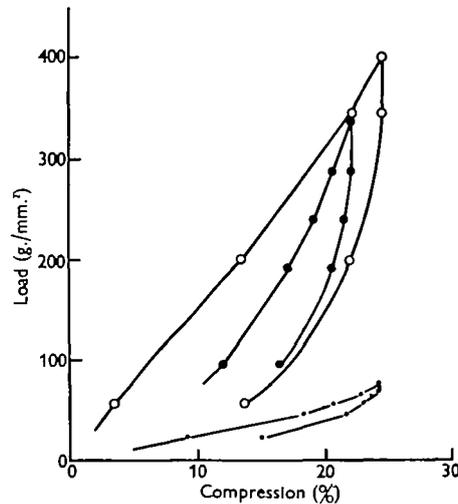

Fig. 10. Stress-strain curves for the inner layer of the ligaments of *Ostrea edulis* (O———O), *Lutraria lutraria* (●———●) and *Pecten maximus* (•———•) when tested in the equipment shown in Fig. 9. The stress is represented by the load applied per mm.² of cross-sectional area under test and the strain by the percentage compression estimated from the angular change.

Table 2. *Results of the determination of Young's modulus of elasticity (E) in compression of the inner layer of the ligament of certain lamellibranchs*

Species	Number of specimens	$E \pm$ s.e. (g./mm.²)
Pecten maximus	8	320 ± 16
Ostrea edulis	5	2170 ± 395
Lutraria lutraria	6	2240 ± 92

DISCUSSION

While the ligament of *Pecten maximus* is structurally and functionally comparable to that of other lamellibranchs, it shows two important differences: first the elongated fusion or outer layer, and secondly the presence of an unusual central region of the inner layer. These modifications are found in other genera of the Pectinidae, e.g. *Chlamys, Amussium* and *Hinnites*.

The function of different parts of the ligament of *Pecten* has been referred to above, the outer layer being subjected to tensile stress and the inner to compression when the valves are closed. The outer layer probably behaves as a fairly rigid hinge structure, and the peculiar characteristics of this ligament may be attributed very

largely to the central region of the inner layer. The relatively small area enclosed in the hysteresis loops drawn for the ligaments of *Pecten* and *Chlamys* (Figs. 4 and 5), the correspondingly low work-loss and the similarity of the opening and closing moments (Table 1) are features of this type of ligament. Furthermore, it should be noted that the ligament of *Pecten* opens the valves to a wide angle (approximately 30 degrees) as compared with 10 degrees for *Mytilus edulis* or *Ostrea edulis*. Accordingly, the opening moment per degree of gape is relatively low for *Pecten* (Table 1). Another characteristic of the ligament of *Pecten* is the rapidity of change of angle of gape with variation of the load on the valve. The change is effected almost instantaneously in *Pecten*, but in bivalves such as *Mytilus* or *Anodonta* there is both an instantaneous effect and a subsequent movement lasting over several minutes. Allowance was made for this when measuring the closing moment of such lamellibranchs. Thus the inertia of the ligament of *Pecten* appears to be lower than that of other ligaments. These properties may be largely attributed to the central region of the inner layer of the ligament.

It is significant that this region is markedly different in composition from the inner layer of the ligament of other lamellibranchs. The lack of calcification of the inner layer, except for the lateral parts, is the main difference between this layer in the ligament of *Pecten* and that of other lamellibranchs, e.g. *Lutraria* or *Ostrea*. It may be considered that the effect of calcification is to increase the resistance of the inner layer to compression. This would account for the higher modulus of elasticity in compression of the inner layer of the ligament of *Ostrea* and *Lutraria* (Table 2). It is probable also that calcification increases the internal resistance of the material of the ligament, so that the relative efficiency is decreased at the same time as the modulus is increased. It may be noted that the increase in the modulus of the inner layer corresponds with the rather more substantial outer layer of the ligament of *Lutraria* and *Ostrea*, and a greater opening moment than that of *Pecten*.

It is noteworthy that the ligament of *Pecten maximus*, which is representative of the small number of lamellibranchs that are free-swimming, is a more efficient structure for the opening and closing of the valves than that of *Ostrea* or *Lutraria*.

The evolution of the swimming habit has been discussed by Yonge (1936), who points out that with the exception of the functional asymmetry of the statocyst in *Pecten*, the adaptations present in swimming Lamellibranchia are no more than further developments of those originally acquired for the efficient cleansing of the mantle cavity. The opening and closing of the shell of *Ostrea* for the purpose of cleansing the mantle cavity is fairly frequent, especially in water where the rate of sedimentation is high (Nelson, 1921). But the ligament of *Pecten* has certain characteristics, such as the wide angle of gape, and its relatively high efficiency, which would seem to be advantageous for swimming. It is possible that they were initially related to the cleansing of the mantle cavity but they would certainly be an asset in the adoption of the swimming habit.

SUMMARY

The ligament of *Pecten maximus* consists of two layers, the outer extending along the dorsal margin of the valves, and the inner situated between the valves in the region of the umbo. The former appears fibrous and is somewhat similar to the outer layer of other ligaments. The inner layer consists of three parts, a large central non-calcified structure and two lateral calcified regions attaching the former to the valves. The central region is characteristic of the ligament of *P. maximus* and associated species, this layer being uniformly calcified in the ligament of most bivalves.

When the valves are closed the outer layer is subjected to tensile stress and the inner to compression, and the force so derived tends to open the valves. This force and that required just to close the shell are expressed as the opening and closing moments of the ligament respectively, and these have been determined for various lamellibranchs.

The exact conditions of the opening and closing of the valves have been observed by drawing the stress-strain curves for the intact ligament, plotting the applied moment against the angle of gape. The loading and unloading curves so produced describe a hysteresis loop. The area enclosed in that of *Pecten* (or *Chlamys*) is markedly less than that of other lamellibranchs and indicates the greater efficiency of the ligament of the former.

The mechanical properties of the isolated central region of the inner layer of the ligament of *Pecten* were investigated and showed similar properties to those of the intact ligament. The modulus of elasticity in compression of this region of the ligament of *Pecten* is approximately one-seventh of that of the inner layer of *Ostrea* or *Lutraria*, which are calcified structures. The ligament of the latter two bivalves has a greater opening moment but lower efficiency than that of *Pecten*. The characteristics of the ligament of *Pecten* are probably due to the central non-calcified region of the inner layer. The significance of these properties in regard to the swimming habit of *Pecten* is briefly discussed.

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