

THE EVOLUTION OF THE SWIMMING HABIT IN THE LAMELLIBRANCHIA

BY

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1. — INTRODUCTION

The ability to swim is possessed by a wide variety of Mollusca. In the Dibranchiate Cephalopoda, where it is universal, the shell is reduced and internal and the necessary force is supplied by the muscles in the mantle the contraction of which drives out water through the siphon. The direction in which this is pointed controls the direction in which the animal moves. The pelagic squids are most highly adapted for rapid movement, the body being stream-lined with lateral, stabilizing fins. Amongst the Gastropoda, swimming is associated with the reduction or modification of the shell, as in *Carinaria* and the Thecosomatous Pteropoda, or its complete absence, as in *Pterotrachea* and the Gymnosomatous Pteropoda. The motive power is supplied by the foot which is modified to form lateral « wings » in the Pteropoda or a fin in the Heteropoda.

In the Lamellibranchia, on the other hand, the ability to swim has been acquired by only a few species all of which, with the exception of *Solenomya* which may, as Drew (1906) has shown, swim for short distances, are included in the Pectinacea and there confined to the Pectinidae, Amussiidae and Limidae. In these the shell is not reduced, although conditions in the Galeommatidae reveal that this can occur in the Lamellibranchia though only in association with a commensal or parasitic life. Swimming in the Lamellibranchia is carried out by movements of the shell valves and has been made possible by comparatively minor modifications of the mantle, shell and adductor muscle.

It is the aim of this paper to indicate the nature of these modifications and their probable mode of origin. This has involved a study of the literature dealing with conditions in monomyarian genera of the Filibranchia and also of the Sub-Order Ostraeacea and of the Family Aetheriidae of the Eulamellibranchia.

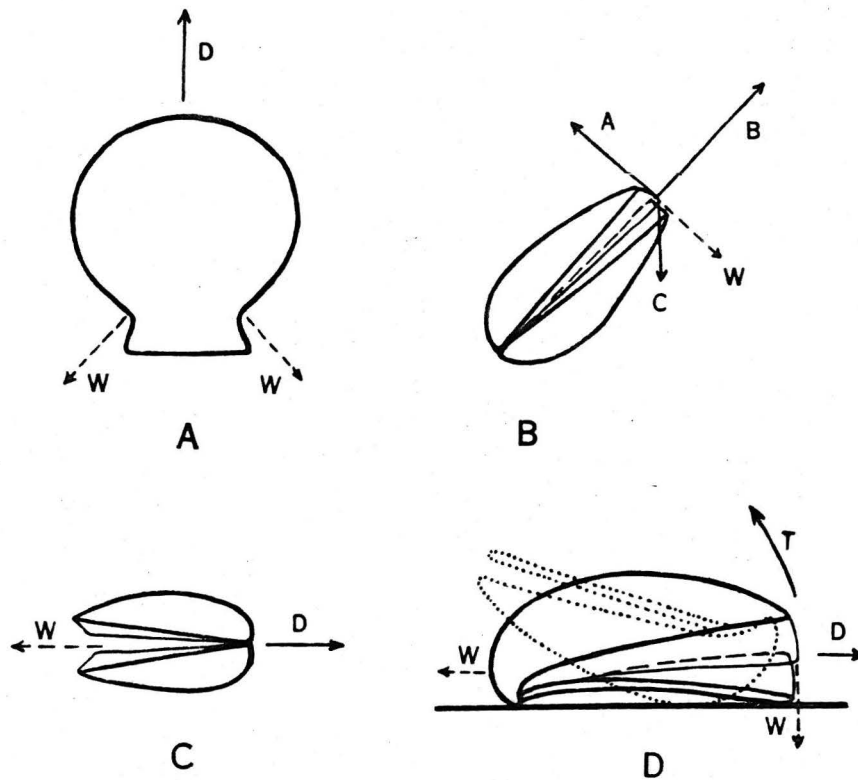
chia. As far as possible actual specimens have also been studied. Material has been obtained from a variety of sources. Specimens of *Pinctada* and *Spondylus* were obtained from the Great Barrier Reef of Australia through the kind offices of Mr. F. W. Moorhouse, a variety of other material was obtained on loan from the British Museum (Natural History) and I have to thank Mr. G. C. Robson for his assistance in this, while other material was purchased from the Plymouth Laboratory. My friend Prof. T. C. Nelson has assisted me out of the wealth of his knowledge and above all by sending me a copy of part of his forthcoming paper (Nelson, 1936). Finally I have to thank Mr. H. F. Steedman, Laboratory Steward in the Department of Zoology of the University of Bristol, for great help in the preparation of sections.

2. — MODE OF SWIMMING

Judging from the shape and delicacy of the shell, *Amussium* is probably the best swimmer amongst the Lamellibranchia. But it is an inhabitant of tropical or deep seas and little is known of its habits. *Pecten* (including *Chlamys*) contains species more specialized for swimming than does *Lima*. The larger species, such as *Pecten maximus* and *P. tenuicostatus*, do not swim so frequently or so efficiently as the smaller species. In *P. maximus* and *P. jacobaeus* the right valve, on which the animal lies, is convex and the left flat. In the giant scallop of America, *P. tenuicostatus*, both valves are convex but the right valve is flatter than the left. In the most active swimmers *P. (Chlamys) opercularis* of European waters and the American *P. irradians*, both of which live in shoals on sandy bottoms at moderate depths and make extensive migrations from time to time, both shell valves are moderately convex. This is also the case in *Amussium* where the convexity is reduced to the minimum. In *Lima* the convexity is greater than in the Pectinidae but the right and left shell valves are almost identical. In the Pectinidae and in *Amussium* the shells are almost circular and are equilateral in the actively swimming species but less so in the fixed species of *Pecten* in which the anterior auricles are enlarged in association with the presence of the byssal gape and the posterior auricles tend to be reduced. In *Lima* the shell is roughly oval in outline and is not equilateral.

The swimming of *Pecten* has been described in most complete detail by Buddenbrock (1911) who has analysed the forces involved. Two swimming movements and one turning movement can be executed. In normal swimming the animal moves with the ventral region foremost, repeatedly flapping its valves and appearing, as Dakin (1909) expresses it, « to take a series of bites out of the water ». At the same time that it moves forward it moves upwards. The water taken in when the shell valves open is prevented from escaping ventrally owing to the greatly enlarged inner folds of the mantle edge or velum. Instead the greater part of it passes out at an oblique angle dorsally at the base of the auricles

on each side as shown in Text-figure 1, A. This causes the forward movement. Owing to the fact that the velum on the left (upper) valve passes down over that on the right valve a certain amount of water is forced downward from the ventral side (see Text-fig. 1, B) which causes an upward movement of the animal which thus progresses obliquely upwards in a series of jerks, falling back a little between each. When suddenly stimulated the animal moves in the opposite direction, executing the « escape » movement. In this case the velum is draw back and so does not obstruct the forward passage of water when the shell valves close and,



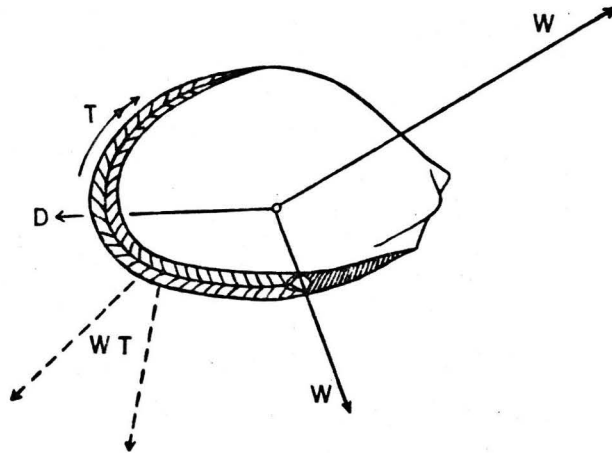
TEXT-FIG. 1. — Movements of *Pecten* (from BUDDENBROCK, 1911).

A, swimming movement, from above; **D**, direction in which animal moves, **W**, direction in which water is expelled. **B**, swimming movement, side view; **A**, **B**, **C**, three components of swimming movement, **A**, being upward movement due to expulsion of water downwards on ventral side, **B**, forward movement due to backward expulsion of water on dorsal side, **C**, downward movement due to gravity and resistance of water. **C**, escape movement, side view; lettering as above. **D**, turning movement of *P. jacobaeus*; **T**, direction of turning movement, other lettering as above.

as a result, the animal makes a sudden darting movement with the hinge foremost, as shown in Text-figure 1, C. All swimming species of *Pecten* lie on the right valve and when turned over on to the left valve they invariably right themselves by a characteristic turning movement. This is most clearly seen in species such as *P. maximus* or *P. jacobaeus* where the valves are different.

Turning is brought about by forcing water downward, the extended velum on the right (temporarily upper) side being arranged over that on the left side, and also dorsally as in the normal swimming movement, so that the animal moves upward and slightly forward, turning over as a result of this. The hinges acts to some extent as a fulcrum in this turning movement which is illustrated diagrammatically in Text-figure 1, D. Rotating and « scuttling » movements have also been observed (see Gutsell [1931] for references to these and other observations on the movements of American species of *Pecten*).

In *Lima hians*, which has been studied by Studnitz (1931), swimming movements are neither so frequent nor so complex as in *Pecten*. This animal has a well-developed foot and is capable of crawling with the aid of this. In the



TEXT-FIG. 2. — Movements of *Lima hians* (from STUDNITZ, 1931).

D, direction of movement when swimming; T, turning movement from horizontal to vertical position preliminary to swimming; W, direction in which water expelled when swimming; WT, direction in which water expelled in the turning movement.

swimming process the animal is arranged as it is in crawling, namely with the shell valves vertical, instead of horizontal as in *Pecten*, and with the anterior side uppermost, as shown in Text-figure 2. Only one swimming movement is executed, with the ventral side foremost, and this corresponds in every way with the normal swimming movement of *Pecten* except that the upward movement (impossible owing to the orientation of the valves) is absent. As a result the animal sinks to the bottom again at the end of each movement, while these are less frequent than those of *Pecten*. The animal may also turn from a horizontal position to the vertical position assumed when swimming by forcing out water near the ventral end of the anterior margin of the shell as shown in Text-figure 2 (WT).

3. — FACTORS INVOLVED IN SWIMMING

Four sets of organs are involved in swimming. First there is the shell which tends to become more equilateral and flatter (hence better stream-lined) with increased capacity for swimming, i. e. in the series *Lima-Pecten-Amussium*. It also tends to become thinner, though not with the same regularity. Thus the shell of *Amussium* is thinner than that of *P. opercularis* which in turn is thinner than that of *P. maximus* but the shell of *Lima hians* is thinner than that of either of these species of *Pecten* although the animal is not so efficient a swimmer. Second, all swimmers are monomyarian and the solitary adductor (posterior) is divided into two regions, a larger portion composed of striated fibres and a smaller one composed of smooth fibres. In functional association with this, although actually concerned with the shell, are the absence of hinge teeth and the presence of a powerful internal cartilaginous ligament. Third, the inner lobe of the mantle edges has been greatly developed, especially on the ventral side, to form the velum⁽¹⁾ which controls the direction in which water is expelled when swimming. Fourth, there is a notable development of sense organs which may assist swimming by orientating the movements. These consist of eyes and tentacles on the pallial margins and statocysts.

The evolution of the swimming habit has also been accompanied by the reduction in the foot which, though still an organ of locomotion in *Lima hians*, has lost this power in *Pecten* and *Amussium*.

It is now necessary to consider the probable reasons for these modifications.

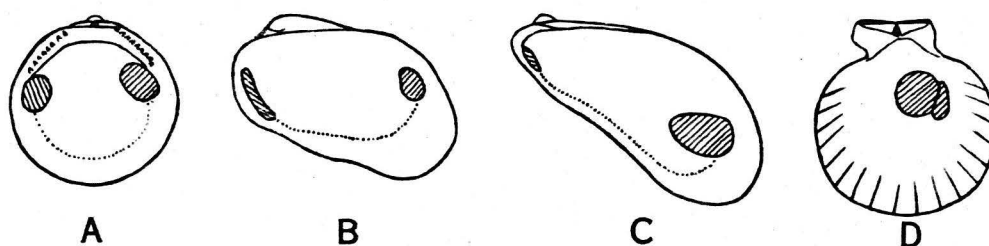
4. — CHANGE IN SHAPE OF THE SHELL

The change in the shape of the shell was undoubtedly due originally to the assumption of a fixed habit, in the first place by means of a byssus, the acquisition of the power of swimming being, it is here maintained, secondary. This change in the shell involves, as Pelseneer (1906) has shown, a shortening of the antero-posterior axis and a proportional increase in the dorso-ventral axis. The process is well shown by a comparison between the shells of different filibranchs, ranging from the Arcacea by way of the Mytilacea to the Pectinacea, and exemplified by *Glycimeris* (sand burrower, never attached), then *Modiolaria* and *Modiola* (both attached by a byssus) and finally *Pecten* (of which some species, such as *P. (Chlamys) varius* and *P. (Chlamys) pusio*, are attached by a byssus and others swim). It is clear from the outline drawings of these shells shown in Text-figure 3 that the tissues must be swinging round anteriorly because there is a

⁽¹⁾ Prof. T. C. Nelson informs me that he proposes to introduce the term « pallial curtains » in place of velum (Nelson, 1936). I am entirely in favour of this.

progressive movement toward the umbo and an accompanying reduction in the size of the anterior adductor muscle which ultimately, in *Pecten*, disappears. In the words of Drew (1906) « a large part of the body of *Pecten* is to be considered morphologically posterior ».

This process is revealed more clearly in development, for instance in that of *Ostrea* which has been most thoroughly studied. Stafford (1913) states that at the time of fixation the two adductors of *O. virginica* are of nearly equal size, the anterior being, if anything, slightly larger. But as the organs of the adult are formed the anterior adductor becomes smaller and moves upwards and backwards owing to the general rotation of the tissues until, when the spat is about 0.5 mm. long, it disappears altogether. The process is indicated in Text-figure 4. At the same time the posterior adductor becomes larger and more central in position. This change in position is the result primarily of the turning movement of the tissues but may have been accentuated, as Pelseener (1906) has



TEXT-FIG. 3. — Right valves of **A**, *Glycimeris*, **B**, *Modiolaria*, **C**, *Modiola*, **D**, *Pecten*, showing stages in the change in shape of the shell and consequent reduction and final loss of the anterior adductor resulting in the monomyarian condition.

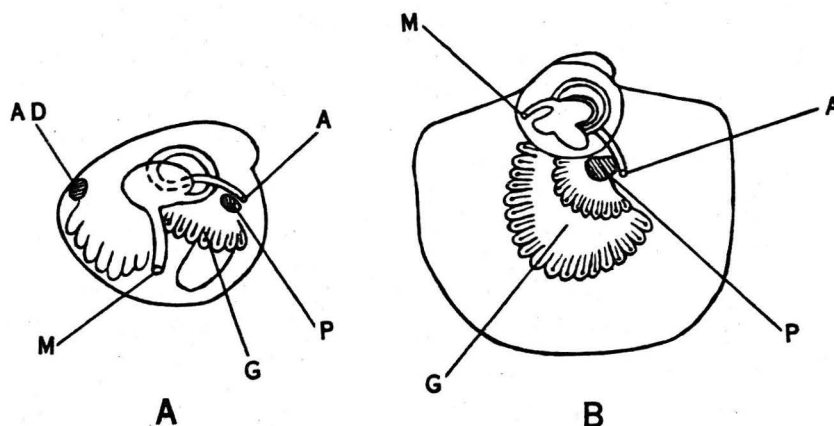
(Modified from PELSENEER 1906.)

observed, for the attainment of greater mechanical efficiency which is certainly the reason for its increase in size. The course of development in the Pectinacea is very similar, as shown by Gutsell (1931) for *P. irradians*.

Douvillé (1912) has put forward a very interesting suggestion as to the cause of these changes. This can most suitably be presented in his own words. « Dans les eaux agitées, ces filaments s'allongent et la coquille est ballottée par les courants; leur action est plus forte sur la partie postérieure plus développée comme nous venons de le voir, et elle est dirigée à peu près suivant la ligne médiane du profil latéral de la coquille. Le byssus tend alors à se placer sur le prolongement de cette ligne et du côté opposé à la poussée, et par suite à se rapprocher du côté antérieur. Dans ce mouvement il entraîne le pied auquel il adhère et celui-ci presse sur le muscle antérieur qui fait obstacle à ce mouvement; cette pression du pied gêne le développement du muscle qui s'atrophie de plus en plus; de là l'inégalité des deux muscles (le postérieur étant toujours le plus développé) qui caractérise les Anisomyaires de Neumayr. L'atrophie du muscle antérieur peut même aboutir à sa disparition complète, comme on le voit dans les Monomyaires.

Le pied occupant toujours la partie moyenne du corps de l'animal, son déplacement du côté antérieur entraîne non seulement l'atrophie du muscle correspondant, mais encore celle de toute la partie antérieure de l'animal; de là, la grande inégalité des deux côtés de la coquille dans les *Avicules* et dans les *Pecten*; chez ces derniers, le côté antérieur n'est plus représenté que par l'aile comprise entre la charnière et l'échancrure byssale. »

Whatever be the cause, the end result of this turning movement is that the foot (except in *Plicatula*, *Ostrea* and *Mulleria* where this later atrophies) comes to lie just anterior to the umbo instead of being mid-ventral. Moreover the mantle lobes remain either entirely free from one another, as in the Anomiacea and most Pectinacea, or else attached at one point only, separating the inhalent and exhalent cavities, as in the Ostracea. As a result the animals attach them-



TEXT-FIG. 4. — Stages in the postlarval development of *Ostrea virginica* showing changes in the shape of the shell and body and loss of the anterior adductor. (Modified from STAFFORD, 1913.) **A**, late free-swimming larva; **B**, settled spat of 1 mm length. A, anus; AD, anterior adductor; G, gills; M, mouth; P, posterior adductor.

selves permanently near the umbo with a byssus (cementation in *Spondylus*, *Plicatula*, *Ostrea* and the Aetheriidae is secondary) and so are able to draw in water with contained food particles over a wide surface. The velum controls the areas through which water enters and leaves the mantle cavity. The mantle edges may be widely separated as they are usually in *Ostrea virginica* (Nelson, 1921) or a more limited inhalent aperture be formed by their apposition, as also shown by Hopkins (1933) for *O. gigas*, except in the mid-ventral area as in *O. edulis* (Text-fig. 5, C), but in all species the mantle edges are continually altering their position (Hopkins, 1933; Nelson, 1936) thereby controlling the amount of water which at any time enters. In *Pecten tenuicostatus* the inhalent aperture may vary in position (Drew, 1906), but Orton (1912) states that in *P. maximus* the separation of the inner mantle folds permits of an ingoing current in the mid-ventral region and another near the base of the anterior

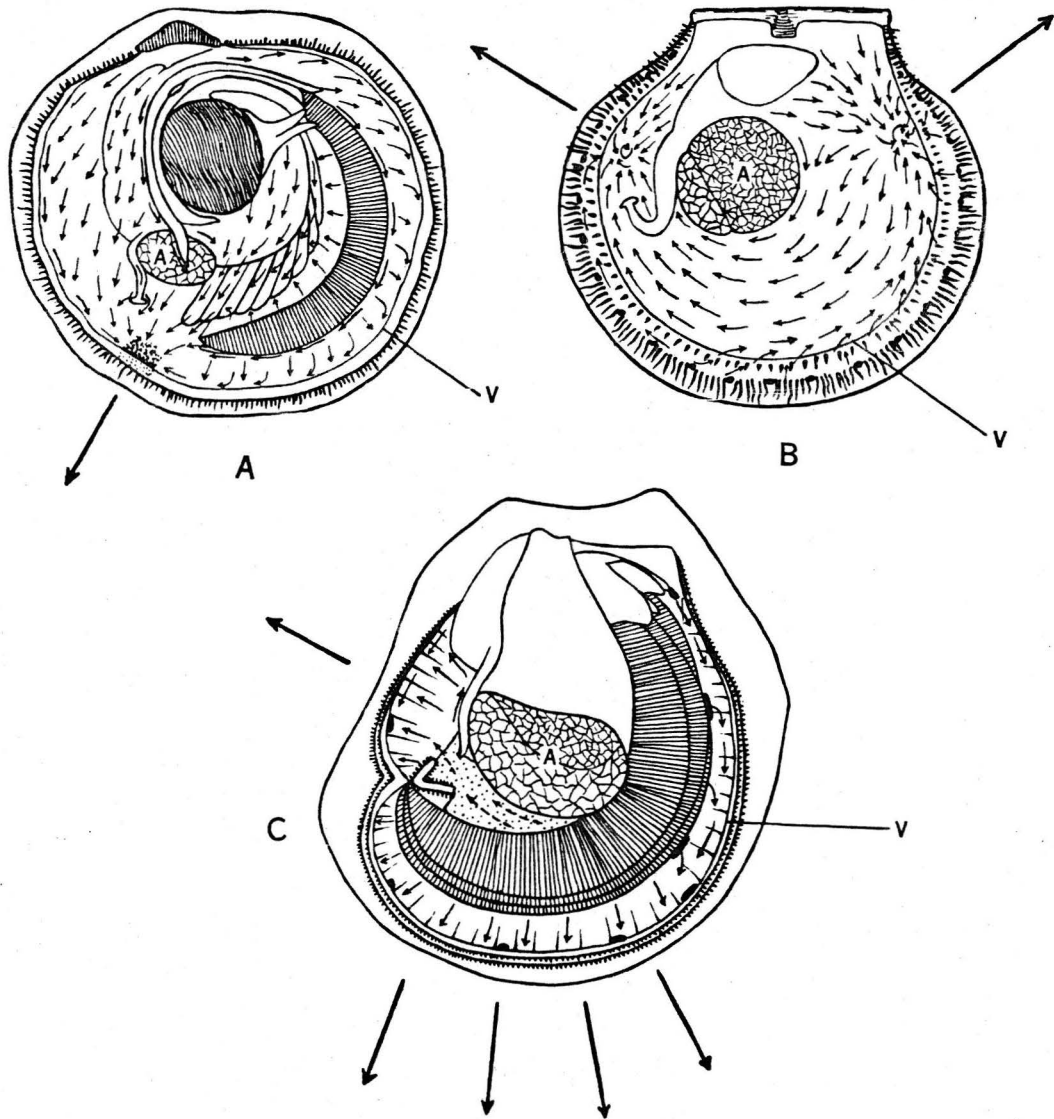
auricles of the shell. In *Ostrea* the mantle edges are withdrawn in the exhalent chamber to allow the passage of the exhalent current, in *P. maximus* this passes out near the base of the posterior auricles of the shell.

The absence of siphons and the wide area over which food material is drawn into the inhalent cavity exposes lamellibranchs of this type to great danger from the amount of sediment which will accumulate within the mantle cavity should the water be turbid, and which would quickly clog the feeding and respiratory mechanisms were it not promptly removed. In siphonate lamellibranchs where this danger is not so great because they can control and to some measure select the water which enters the mantle cavity, waste material accumulates at the base of the inhalent siphon and is expelled through this from time to time by contractions of the adductor muscles (see Kellogg [1915] and Yonge [1928a] for a general review of this subject). In the monomyarian lamellibranchs under consideration special mechanisms have been evolved for overcoming this danger. In the first place the ciliation on the gills, associated with the muscular activity of these, is such that large masses of material are passed directly to the mantle surface and not to the palps. Such mechanisms, varying in details but with the same effect, have been described in Anomiacea (*Monia machrochisma*, Kellogg, 1915) Pectinacea (*Pecten irradians* and *P. tenuicostatus*, Kellogg, 1915) and Ostreaacea (*Ostrea edulis*, Yonge, 1926; *O. edulis*, *O. (Gryphea) angulata*, *O. virginica*, Nelson, 1936). The waste matter which accumulates on the mantle surface, directly from the inhalent current or after rejection by the gills or palps, is carried away by ciliated tracts on this. In *Monia* (Text-fig. 5, A) Kellogg has shown that waste material accumulates in one large mass in the mid-ventral region and is « thrown out by a sudden contraction of the adductor muscle which closes the valves ». In *P. irradians* (Text-fig. 5, B) and *P. tenuicostatus* it is carried for later expulsion to the base of the auricles on both sides, i. e. to both inhalent and exhalent regions. In *O. edulis* (Yonge, 1926) it is carried to the inner side of the ventral mantle edges (Text-fig. 5, C) where it accumulates and is expelled by frequent contractions of the adductor; in *O. virginica*, where the shell is more elongated, material is carried to the anterior side for expulsion (Kellogg, 1915, Nelson, 1921). It is of great significance that, as indicated by the large arrows in Text-figure 5, only in *Pecten* is material expelled from the dorsal regions of the shell, i. e. where expulsion will produce water currents which induce ventrally directed movements in the free animal. Free specimens of *Ostrea* occasionally execute dorsally directed « escape » movements⁽¹⁾ but only in *Pecten* (and other swimmers) is movement in the opposite direction possible — owing to the different regions where waste material collects and is expelled.

The sudden closure of the valves during this cleansing operation forces

(¹) The swimming movements of *Solenomya* are of the same character.

water against the gills. Ruptures are avoided because, as Ridewood (1903) noted, the upper edges of the ascending lamellae in the filibranchs are almost invariably free. In the Ostraeacea, out of five species of *Pinna* examined by Ridewood the



TEXT-FIG. 5. — Distribution of ciliary currents concerned with the ejection of excess material from the mantle cavity of **A**, *Monia machrochisma* (KELLOGG, 1915); **B**, *Pecten tenuicostatus* (KELLOGG, 1915); **C**, *Ostrea edulis* (YONGE, 1926). A, adductor; V, velum. Small arrows indicate direction of ciliary currents in the mantle cavity, large arrows the direction in which material accumulated by these currents is expelled by the contraction of the adductor muscles.

lamellae are free in all but *P. nobilis*. In *Ostrea* alone are they always fused. Here the larger size of the exhalant cavity added to the stouter character of the Eulamellibranch gill may account for the fusion.

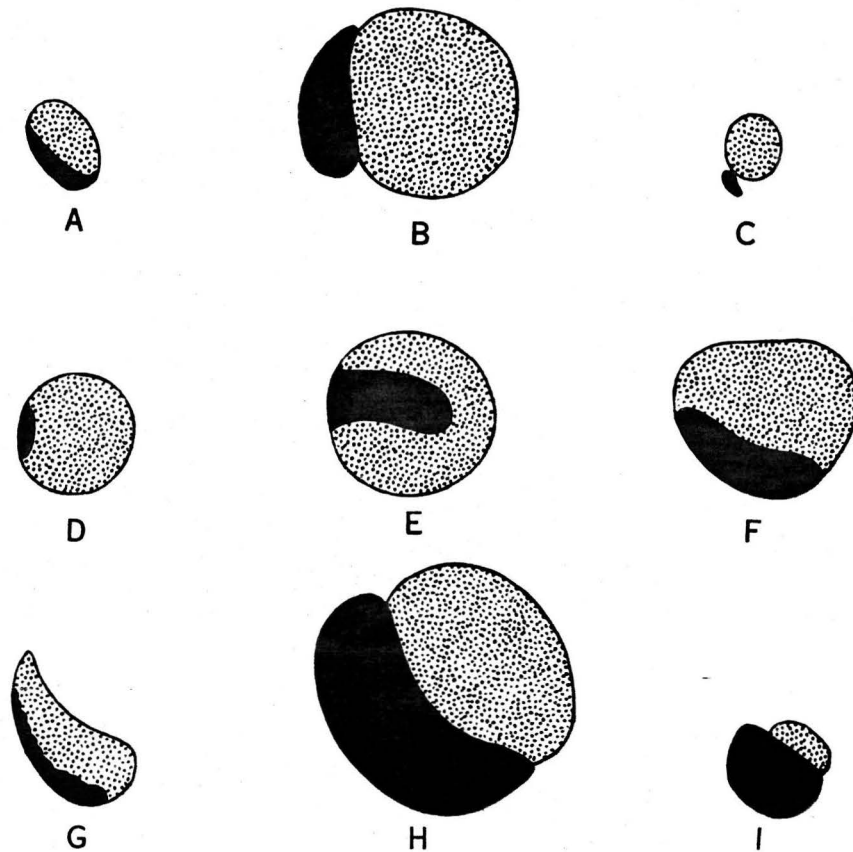
5. — MODIFICATION OF THE ADDUCTOR MUSCLE

The reasons for the disappearance of the anterior adductor muscle have already been considered. There remains for discussion the exceptionally well-marked division of the remaining (posterior) adductor into two regions composed in *Pecten*, where they have been most thoroughly studied, one of smooth and the other of striated fibres. The functions of these have long been known, full references to previous literature being given by Bayliss, Boyland and Ritchie (1930) who have made the most recent and detailed study of the physiology of the adductor muscle in *Pecten*. The smooth or « catch » muscle is responsible for the slow but often long-continued closure of the shell, the striated or « quick » muscle for the rapid movements used in swimming but primarily, as will be shown, for the ejection of waste matter from the mantle cavity.

Probably because species of *Pecten* have almost exclusively been used for the investigation of these muscles, it has too often been assumed that this division of the adductor is largely confined to swimming species and is a modification concerned exclusively with the swimming habit. Thus Dakin (1928a) appears to regard the division of the adductor in *Spondylus* as additional evidence that this genus is descended from swimming ancestors (as it may have done, but the presence of a quick muscle is no evidence of this). Actually this division of the adductors is widespread, as shown by Marceau (1909). It is especially well-marked in the great majority of monomyrians, including not only all Pectinacea but also all Anomiacea, all Ostracea including the Pinnidae where a small anterior adductor is present. It is also of frequent occurrence in dimyrians, affecting both adductors as in *Anodonta* which has been investigated in great detail by Brück (1914).

The division of the adductors in the dimyrians has been most thoroughly investigated by Marceau (1909). Pelseneer (1911) has made an important generalization on this matter. He states that « La portion striée (à contractions rapides) des adducteurs est de plus en plus développée dans les formes largement ouvertes, et, en général, de plus en plus réduite dans les formes « enfermées » ». The significance of this lies in the fact that the more widely open the mantle the greater is the need for frequent closures of the shell for the removal of the large amounts of waste matter which enter. This accounts for the great development of the quick muscle in the monomyrians which have evolved as a result of the processes outlined above and in which the mantle is widely open. In the Tridacnidae, as demonstrated on morphological grounds by Lacaze-Duthiers (1902) and on functional grounds by Yonge (1936), the monomyrian condition has been attained in a different way, namely by a twisting of the mantle and shell round the visceral mass. As a result the mantle remains closed to a large extent. Owing to this, and also to the fact that these animals invariably establish themselves on or in rocks near the surface of coral reefs owing to the

light requirements of zooxanthellae contained in the exposed mantle edges (Yonge, 1936), thereby living in water with little contained sediment, there is little need for frequent expulsions of waste matter. This is probably the reason why the quick muscle in the adductor in this family is so poorly developed. According to Woodward (1898) the adductor in *Mulleria Dalyi* is not divided. This monomyarian Eulamellibranch lives in fresh water and it is probable that, as it is cemented to rocks, it lives in clear water.



TEXT-FIG. 6. — Relative sizes of the catch muscle (shown black) and the quick muscle (stippled) in the adductor of various monomyarians. Magnification varies. **A**, *Lima hians* (PELSENEER, 1911); **B**, *Pecten maximus* (DAKIN, 1909); **C**, *Amussium electrum* (PELSENEER, 1911); **D**, *Monia patelliformis* (original); **E**, *Placuna placenta* (HORNELL, 1909); **F**, *Pteria radiata* (original); **G**, *Pinctada (Margaritifera) vulgaris* (HERDMAN, 1904); **H**, *Spondylus gaederopus* (DAKIN, 1928a); **I**, *Plicatula australis* (WATSON, 1930).

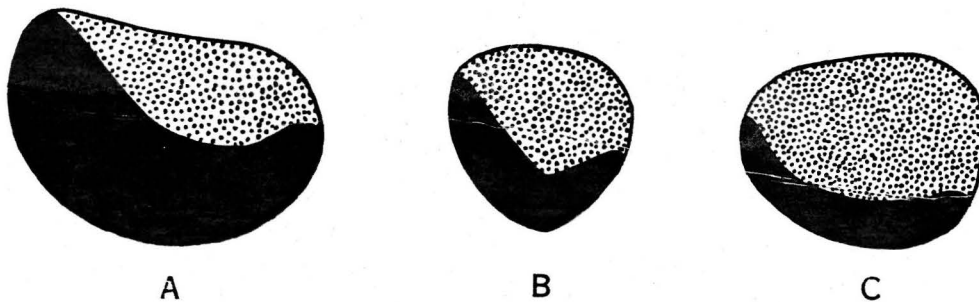
The relative size of the two portions of the adductor varies greatly in different monomyarians as shown in Text-figure 6. The quick muscle is naturally well-developed in all swimmers, progressively so relative to the catch muscle in the series *Lima* (A)-*Pecten* (B)-*Amussium* (C). But examination of a representative series of fixed genera (excluding *Ostrea* considered below) shows

that the quick muscle may be equally well developed in these, although conditions vary, most probably owing to the different habitats of the animals. In the six examples figured, in two only—*Spondylus* (H) and *Plicatula* (I)—is the catch muscle larger than the quick muscle. In *Monia* (D) the quick muscle is as large, in relation to the catch muscle, as in *Amussium*. Jackson (1890) and Marceau have shown that the place of the adductor has in part been taken in *Anomia* by the pedal muscles attached to the calcified byssus; these largely take the place of the catch muscle. But the Anomiidae have a wide vertical range and, owing to their close application to rocks, will be greatly exposed to sediment. It is therefore not unreasonable to correlate the large size of the quick muscle with the need for efficient cleansing. In the allied *Placuna* (E) the quick muscle is also very large. This animal is unattached but lives on muddy bottoms where sediment is very heavy. *Pteria* (F) and *Pinctada* (G) are both of them attached by a byssus but frequently extend to fair depths in muddy areas; they both have well-developed quick muscles. *Spondylus* (H) and *Plicatula* (I) are both cemented to rocks but, certainly in *Spondylus* and possibly in *Plicatula* about the habitat of which no definite statements have been found, nearer to the surface and so in clearer water. Moreover the presence of prominent hinge teeth (the nature of which will be discussed later) in both will render frequent movements of the valves more difficult.

A point of great interest emerges when the adductors of various species of oysters are compared, namely *Ostrea edulis*, *O. (Gryphea) angulata* and *O. virginica* (Text-fig. 7). The quick muscle is notably larger in *O. angulata* and *O. virginica* than it is in *O. edulis* where it is smaller than the catch muscle, although in the others it is almost double the size of this. These differences are almost certainly correlated with the habitat of these species. Nelson (1936) has shown from a detailed study of the ciliary feeding mechanisms on the gills and palps that *O. angulata* and *O. virginica* are fitted for life in water of much greater turbidity than is *O. edulis*. They will need, therefore, to eject excess material more frequently and this is reflected in the greater development of the quick muscle in these.

Another factor has to be considered in this connection; the greater development of the catch muscle in species, and actually in individuals of a species, which are exposed for long periods on the shore when they need to keep the shell closed. Hopkins (1930) has shown that in *O. virginica* the ratio by weight of quick muscle to catch muscle in the adductors of eighteen animals living near the upper level of growth was 1.26 ± 0.09 , whereas in seventeen oysters taken from a level $2 \frac{1}{2}$ feet lower down where they were submerged for a correspondingly longer period the ratio was 2.51 ± 0.09 . But even when allowance is made for this increase in the size of the catch muscle in individuals which live between tide marks, the large *specific* difference between the relative sizes of the two parts of the adductor in *O. edulis* on the one hand and *O. angulata* and *O. virginica* on the other hand, remains as a significant fact.

The supreme importance of the quick muscle in the ejection of waste matter from the mantle cavity — and so in the continued survival of the animals — has been experimentally demonstrated in a very striking manner by Nelson (1921). He made kymograph records of the shell movements of *O. virginica* when the animal was living under natural conditions. He found, as shown in Text-figure 8, that there is a direct correlation between the number of contractions and the degree of sediment in the water. In the course of one hour an oyster made 8 complete or almost complete contractions of the adductor when the turbidity of the water corresponded to a content of about 0.1 grams of dry material per litre (Text-fig. 8, A), but when the turbidity was approximately doubled the same individual made 27 complete and many more smaller contrac-

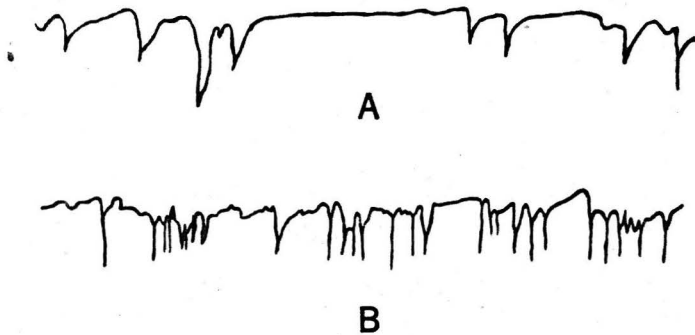


TEXT-FIG. 7. — Relative sizes of the catch muscle (shown black) and the quick muscle (stippled) in the adductor of **A**, *Ostrea edulis*; **B**, *O. (Gryphea) angulata*; **C**, *O. virginica*. (Original.)

tions (Text-fig. 8, B). He has more recently greatly extended these observations and experiments (Nelson, 1936).

The quick muscle of *Pecten*, *Lima* and *Spondylus* is striated (Marceau) and there are certain records of the nature of the quick muscle in other monomyarians which do not swim. Herdman (1904) speaks of the quick muscle of *Margaritifera* (= *Pinctada*) *vulgaris* as having « an appearance which has been described as striation, but is by no means distinct ». Hornell (1909) states that the fibres of the quick muscle in *Placuna placenta* are finer than those of the catch muscle but he saw no striation. Marceau (1909) found transverse striation in *Anomia*. Dakin (1928a) speaks of the quick muscle of *Spondylus gaederopus* as though it had the same microscopic structure as that of *Pecten maximus*. Brück (1914) studied the histological structure of the two parts of the adductors of *Anodonta cellensis* in great detail and showed that the catch muscle is composed of fibres which are larger than those of the quick muscle and contain longitudinal striations, the fibrillae being arranged in concentric rings. The fibres of the quick muscle, on the other hand, he found contain heterogeneous fibrillae in that they possess light-refractile elements. Moreover these fibrillae tend to be accumulated in bundles and to be arranged peripherally in the form of spirals. These run in both directions and the two series cross repeatedly (see also Marceau [1909]).

In the hope of obtaining further evidence on the nature of the striation in the quick muscle of swimmers and other monomyarian species, sections were cut of the adductors of the following : *Monia* (*Anomia*) *patelliformis*, *Pinctada margaritifera*, *Pecten opercularis*, *Spondylus* sp., *Lima hians*, *Ostrea virginica* and *Pinna fragilis*. All sections were stained with Heidenhain's haematoxylin. No essential difference was found in any case between the structure of the catch muscle fibres and that described by Marceau and Brück. With the exceptions of *Monia*, *Pecten*, *Spondylus* and *Lima*, the fibres of the quick muscle, so far as can be determined, have the same spiral striations as the quick muscle of *Anodonta*. They certainly do not exhibit transverse striations. In *Monia* the fibres of the quick muscle have a peculiar appearance owing to the presence of



TEXT-FIG. 8. — Kymograph tracings of movements of shell valves of *Ostrea virginica* in water of varying turbidity. **A**, in water of turbidity approximating to 0.1 grams dry matter per litre ; **B**, in water approximating to 0.2 grams of dry matter per litre (after NELSON, 1921).

very thick, rounded striations which are arranged somewhat obliquely although there is no evidence of a true spiral formation. In *Lima* the fibres are striated transversely, individual striations being thick and single. In *Pecten* transverse striation is better developed than in *Lima*, delicate staining showing that striations are double. In *Spondylus* transverse striation is clear but less well-marked than in *Pecten* or *Lima*, while the individual striations are much thinner than those of *Monia*. These observations confirm those of Marceau.

These facts, as noted by Anthony (1918), are of interest. It is generally accepted that the difference between smooth and striated muscle is one of degree and not of kind. Smooth muscle appears first in the animal kingdom and is replaced by striated muscle when quick and frequent movements are needed. Thus in the Coelenterata striated muscle is confined to the pulsating bell of Scyphozoa. In the Mollusca, where quick movement is infrequent, striated muscle is correspondingly rare. Pelseneer (1906) states that in Gastropoda it occurs in the buccal mass of certain species, in the heart, in the fins of Pteropods

and Heteropods (swimmers) and in the columellar muscle of the larvae of certain Nudibranchs, while in the Cephalopoda it appears in the siphon (again in association with swimming). In Lamellibranchia, apart from species here considered, transversely striated muscle has been described in the adductors of *Teredo* (Miller, 1924) and in the septum of *Cuspidaria* (Grobben, 1892; Yonge, 1928a) both of them muscles which are called upon to make continuous movements throughout life.

It would appear that the development of striations in muscle is preceded by a reduction in the thickness of the fibres. Brück states that the spirally striated fibres of *Anodonta* arise from fibres with homogeneous fibrillae. As stated by Anthony the initial development of striation apparently results in the spiral condition. Further demands on the quick contractibility of the muscle — corresponding to the difference between the demands made on the quick muscle in *Pinctada* and *Ostrea* on the one hand and in swimmers such as *Lima* and *Pecten* on the other — lead to the appearance of much more pronounced striations⁽¹⁾ which become transverse instead of spiral. Moreover this striation is better developed in *Pecten* than in *Lima* corresponding to the greater powers of swimming possessed by the former. The condition in *Monia*, however, reveals that the appearance of transverse striation is not necessarily an exclusive characteristic of swimming species. The great size of the quick muscle in *Monia* has been discussed above and correlated with the great danger from sediment to which species of this genus are exposed. It is for this reason, it may not unreasonably be assumed, that the muscle fibres have developed horizontal striations although of a more primitive character than those of *Lima* which in turn are less well-developed than those of *Pecten*.

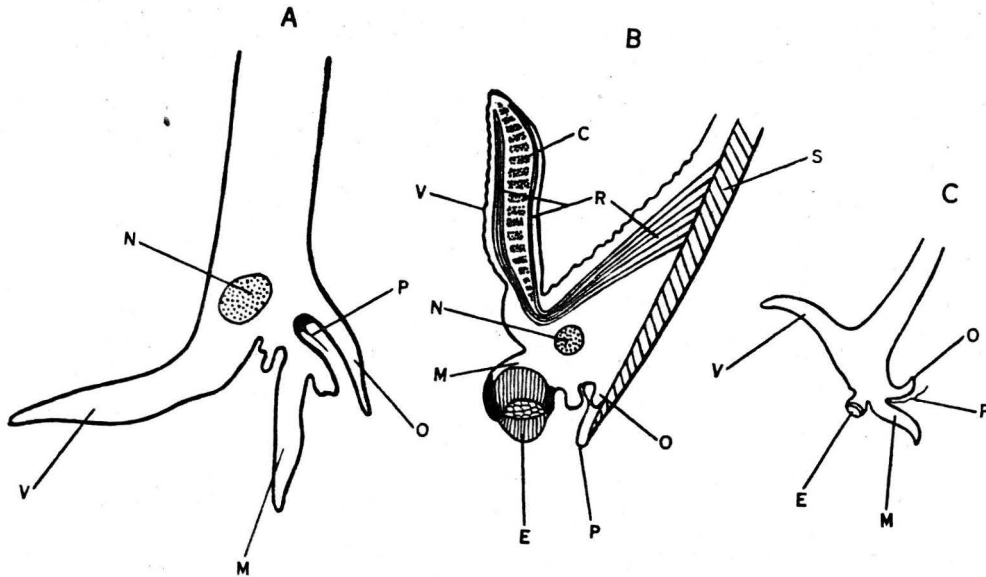
In functional association with the greater development of the quick muscle are the reduction or absence of hinge teeth (except in *Spondylus* and *Plicatula*). The presence of the internal ligament characteristic of all of these Filibranchia and of all Ostracea provides a mechanically more efficient and quicker opening mechanism than would an external ligament.

The swimming species differ from their fixed relatives in the greater length of the adductor and also in the oblique arrangement of the quick muscle as shown in *Amussium* by Pelseneer (1911). This permits of a wider gape and so of the entrance of a greater volume of water with correspondingly greater movement when it is expelled. The adductor in swimming species is also arranged more centrally than in allied fixed genera, that of *Plicatula* being notably excentric (Watson, 1930). Moreover the elastic ligament of the shell is condensed into a massive pad which causes the shell valves to spring widely open as soon as the adductor relaxes. This is very notable in the Pectinidae and in *Amussium* where the ligament is triangular in cross section. In *Lima* it is crescent-shaped.

(1) These persist in a less pronounced form in *Spondylus*.

6. — THE VELUM

In the words of Pelseneer (1906) the margins of the mantle in the Lamellibranchia « normally present reduplications, generally three in number, and in the Pectinidae the most internal of these is turned in to form the « velum » ». This inwardly directed « pallial curtain » is essential to all lamellibranchs in which the pallial margins are not fused because it is of vital importance, as shown above, in the formation of the temporary inhalent and exhalent apertures by means of which the amount of water which enters the mantle cavity is



TEXT-FIG. 9. — Transverse sections of mantle edges of **A**, *Placuna placenta* (HORNELL, 1909); **B**, *Pecten* sp. (BUDDENBROCK, 1911); **C**, *Spondylus gaederopus* (DAKIN, 1928, a). C, circular muscle in velum; E, eye in middle fold; M, middle fold of mantle edge; N, nerve; O, outer, secretory, fold of mantle edge; P, periostracum; R, radial muscles of velum; S, shell; V, velum or inner fold of mantle edge.

controlled. This has been clearly shown by Hopkins (1933), see Text-figure 10. It is present in all the genera considered in this paper, being only *relatively larger* in the swimming species owing to the greater gape in these.

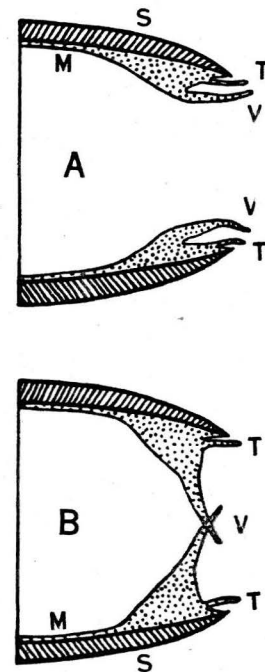
In the Anomiacea, as exemplified by *Anomia* and *Placuna*, the mantle edges are divided into three folds. The condition in *Placuna* is shown in Text-figure 9, A, in *Anomia* the velum is relatively a little smaller. The same conditions prevail in the Pectinacea, such as *Pinctada*, *Pteria*, *Pecten* (Text-fig. 9, B), *Spondylus* (Text-fig. 9, C), *Plicatula* and *Lima*. In *Plicatula*, Watson (1930) states that the velum is confined to a small ridge. This is clearly correlated with the small size of the quick muscle indicating that this animal probably lives in water largely free from sediment. In *Spondylus* there is a well-developed velum

but the middle fold is only slightly developed. Dakin (1928a) states that it is absent and that the outer fold is subdivided and bears eyes and tentacles on the inner side. It seems more probable, however, judging from conditions in allied genera, that the eyes and tentacles in *Spondylus* represent the middle fold. Dakin's figure (reproduced in Text-fig. 9, C) bears out this impression. Amongst the Ostraeacea, both *Ostrea* and *Pinna* have three folds. In *Ostrea* the middle one is small and the velum, though of the greatest functional importance, is not so large as in the Pectinidae. In *Pinna* the two outer folds are small but the velum is very large, especially in the posterior region where the gape is widest and the inhalent current is drawn in. In association with the peculiar habits of this animal, which lives with the anterior end downward almost buried in mud, there are two additional folds in the inhalent chamber. These are situated some distance within the velum with which they merge in the region of the foot anteriorly and of the intermantele septum posteriorly. They enclose a groove in which, as Stenta (1903) and Grave (1909) have shown, waste matter is carried upwards for eventual ejection.

In all cases the outer fold is secretory in function. It produces the shell, the periostracum (Text-fig. 9, P) being formed at the base of the groove on its inner side. The middle fold is usually sensory. It bears eyes (E) in the Pectinidae and in *Spondylus* and also sensory tentacles (except in *Pinna*). Tactacles may also occur on the edge of the velum as in the Pectinidae and in *Ostrea* (Text-fig. 10, T), while in *Pinna* they are confined to the velum and there only in the posterior region.

The innermost fold constitutes the velum. This is highly muscular, a necessity in view of the frequent and extensive movements it performs. Radial muscles (Text-fig. 9, B, R) attached to the shell at the pallial line, extend up both inner and outer sides of the velum, while between these are circular muscles (Text-fig. 9, B, C). Contraction or relaxation of these three sets of muscles, in conjunction with the forcing in of blood to cause distension, are responsible for the movements executed by the velum (Text-fig. 10).

Although an essential part of the swimming mechanism, the velum, as already noted, has certainly arisen in the first place as a part of the feeding and cleansing mechanism in lamellibranchs of this type. Dakin (1928a), states that in *Spondylus*, although the animal is cemented, the velum is almost as well developed as it is in *Pecten*. It is interesting in this connection to note that in



TEXT-FIG. 10.

Diagrammatic cross-sections through edge of open shell of *Ostrea gigas*. **A**, velum drawn back to permit free flow of water; **B**, velum extended and so closing aperture. M, mantle; S, shell; T, tentacles on middle fold of mantle edges; V, velum with tentacles (after HOPKINS, 1933).

Tridacna (Yonge, 1936) the mantle edges are also divided into three well-defined horizontal folds, of which the innermost is developed to a remarkable extent, in this case for harbouring zooxanthellae. The mantle edges are amongst the many structures exploited in the course of adaptation by the Lamellibranchia.

7. — SENSE ORGANS

Three types of sense organs are associated with the swimming habit, eyes and tentacles on the mantle edges, and the statocyst. Tentacles and statocysts are present in all cases, well-developed eyes occur in all species of the Pectinidae and *Amussium*, except those from abyssal seas (Pelseneer, 1888), also in *Spondylus*, and comparatively poorly developed in *Lima excavata* and *L. squamosa* but absent in *L. inflata* and *L. hians* (see Dakin [1928b] for a review of this subject and for literature). In other monomyarian Filibranchs and in the Ostracea eyes are absent.

It is necessary to consider whether these sense organs have arisen as a result of the swimming habit and, if not, to what extent they have been further developed as a result of new needs imposed by this habit. Tentacles are present around the inhalent opening in all lamellibranchs, they possess clusters of sense cells or definite receptor organs, with nerves running from them. These presumably receive tactile or chemical stimuli. The tentacles which surround the mantle edges of the monomyarian genera under consideration represent the extension around the mantle of the more localized tentacles in the siphonate genera. They are actually most highly developed in *Lima*. Their primary function there appears to be the direction of the food currents. This is certainly true of *L. hians* when the animal is expanded within its nest (personal observation).

The presence of extremely well-developed eyes in all swimming lamellibranchs with the exception of *Lima hians* might be considered the direct result of this habit. Dakin (1928b) considers that their presence in *Spondylus* is due to the probable descent of this genus from *Pecten*. But against this we have the fact that *Lima excavata*, which does not swim, possesses eyes, while *L. hians* does not. Moreover pallial eyes are present in a variety of genera which do not swim and the ancestors of which did not swim, for instance in *Arca*, *Glycimeris* and *Cardium*, while in *Tridacna* (Yonge, 1936) the inner mantle lobes possess hyaline organs which serve to illuminate the inner mantle tissues for the benefit of the zooxanthellae and which have a similar structure, and possibly a similar origin, to the lens of the pallial eyes in other genera. Other genera again possess pigment spots which may have a certain capacity for the reception of the stimulus of light. There is no reason for thinking that pallial eyes arose in direct association with the assumption of the swimming habit.

The tactile and light receptive powers of the tentacles and eyes are possibly of value in the initiation of reflex movements concerned with swimming, notably those of the velum. Dakin (1928*b*), however, doubts whether a reduction in the pallial eyes of *Pecten* would lead to unfitness for swimming. He considers that their development is the result of orthogenesis. This, he further holds, would account for their retention without loss of elaboration in *Spondylus*. In the absence of experimental evidence as to the value of these eyes it is difficult to take any definite standpoint on this matter.

Statocysts are present in all lamellibranchs though poorly developed in fixed genera, such as *Ostrea*. They can seldom be of such value as they are in the swimming species. The statocysts in *Pecten*, as Buddenbrock (1911, 1915) has shown, are unique amongst those of bilaterally symmetrical animals, owing to the fact that the posture of *Pecten* when swimming is horizontal. Although two statocysts are present Buddenbrock has shown that the nerves from both mantle lobes communicate exclusively with the left statocyst, all reflex movements associated with movement and orientation being initiated by this one receptor. Studnitz (1931) states that in *Lima*, where the posture when swimming is vertical, there is no such asymmetry.

8. — DISCUSSION

Evidence has been put forward in this paper in support of the view that the power of swimming possessed by certain Lamellibranchia is secondary, all the modifications which have made it possible having been evolved in the first place in response to the needs of monomyarians originally attached by the byssus. It was not until this idea had been developed independently that it was found that it had already been put forward by Drew (1906). Referring to the water currents produced for cleansing purposes he states that as this « is primarily of service in cleansing the mantle chamber and is used habitually for locomotion by only a few forms, it seems quite possible that those forms that do use it for locomotion may have simply perfected an already existing mechanism primarily designed for another purpose ». Drew did not, however, develop this suggestion.

It has been shown that the necessary change in shape of the shell with the accompanying loss of the anterior adductor was due to the assumption of a fixed habit, attachment by a byssus. Possible causal influences have been suggested by Douvillé. This was accompanied by retention of the open mantle which afforded the animal a wider surface for feeding which may have had selective value. This led to a greater danger from sediment, the supreme danger to which all sedentary animals with ciliary feeding mechanisms are exposed. This was met by greater elaboration of cleansing mechanisms. This involved ciliary mechanisms on the gills, palps and especially on the mantle by means of which excess material was collected and accumulated in definite regions. It also involved

the adductor and velum, responsible respectively for the force with which and the direction in which these accumulations were expelled. The great development of the velum was also of primary importance by permitting the formation of local inhalent and exhalent apertures.

It would appear that waste material was originally always ejected ventrally and that only in certain specialized cases was this process transferred to the dorsal side. This appears to have been associated with the extension of the gills posteriorly. This process, which finds final expression in all swimmers and their immediate allies, is indicated in *Pinctada* where, as shown by Herdman (1904), waste matter is carried along the mantle to the posterior extremity of the gills which are situated some distance posterior to the mid-ventral line. The further extension of the site of ejection to the posterior side of the auricles, as shown in *Pecten* (see Text-fig. 5, B), would appear to have resulted, owing to the great distance that material had to be carried if transported from the extreme anterior end, to the appearance of a second site of ejection at the anterior side of the auricles. The advantage to fixed animals of cleansing ejection in these regions is clear. It enabled them to remove waste matter without greatly disturbing the water ventrally from which the feeding currents are drawn. Instead of water entering and being ejected in the same regions it passed through the mantle cavity, in ventrally and out dorsally⁽¹⁾. In all such animals the capacity for ventrally-directed movements, i. e. the true swimming movements of Lamelli-branchia, was latent; others could at best execute no more than escape movements. The various adaptations possessed by these swimmers are, as already shown, no more than further elaborations of those already developed for the purpose of cleansing, the solitary exception being the functional asymmetry of the statocysts in *Pecten*.

The phylogenetic relationships of these monomyarians has been discussed at great length by Jackson (1890). Further consideration of this matter lies beyond the scope of this paper but a few comments on the *functional aspect* of these changes may not be out of place.

The original ancestors of all of these animals were undoubtedly dimyarians attached by a byssus. The change in shape of the shell and the gradual assumption of the monomyarian condition with the foot and byssus at the extreme anterior end followed, possibly as a result of the agencies suggested by Douvillé. It seems more than probable that these changes took place in *clear water free from sediment*, i. e. near the summit of rocks or reefs, probably in the surf region. This view fits in well with that of Douvillé who postulates moving water as responsible to a large extent for the change in form of the body. Certainly

⁽¹⁾ The evolution of this type of cleansing mechanism possibly explains the great success and wide distribution of the Pectinidae.

the final attachment at the anterior end enables the animals to be moved about freely with little risk of damage.

The descent into deeper and more sediment-laden waters must have been accompanied by the evolution of more efficient cleansing mechanisms involving modifications of the ciliary mechanisms on the gills, palps and mantle and also of the adductor and velum. It is certainly the possession of more efficient mechanisms of this type that has enabled *O. virginica* and *O. angulata* to extend into muddier water than *O. edulis*.

The evolution of these mechanisms opened the way to a variety of alternatives, the most important of which will be briefly considered.

- I. — Before the monomyarian condition had been completely attained efficient cleansing mechanisms were evolved and the animal descended into a muddy environment. Such conditions are typified by *Pinna* which retains the byssus and lives rooted in mud or soft sand and has evolved characteristic means for the removal of waste matter from the mantle cavity.
- II. — After assumption of the monomyarian condition and the evolution of mechanisms for resisting sedimentation, individuals extended their vertical range, i. e. *Pteria*, *Malleus*, *Pinctada*.
- III. — Further specialization led to the condition found in *Monia* where the animal is attached by a calcified byssus with one valve closely applied to the substratum. Further development in cleansing mechanisms enabled these animals to extend their vertical range greatly.
- IV. — From the same stock as III evolved animals which lost the byssus attachment but, owing to their power of resisting the effect of sediment, were able to exist on a soft mud bottom, i. e. *Placuna*.
- V. — From members of II which evolved cleansing mechanisms involving the removal of waste material dorsally on either side of the hinge, there further evolved animals which lost, completely or partially, the byssus attachment and became free-living. By a further elaboration of the adaptations concerned with cleansing they acquired the power of swimming, i. e. *Lima*, *Pecten*, *Amusium*.
- VI. — From V may have evolved, by processes indicated by Jackson (1890), Dakin (1928a), and Watson (1930), other forms which are cemented, namely *Plicatula* and *Spondylus*. The former is probably the older of these, for reasons given by Watson which include the loss of the foot which is still present in *Spondylus*. The presence of hinge teeth in both genera can be accounted for on the assumption made by Jackson (1890) that they are « a modification of the auricular crurae charac-

teristic of most *Pectens* and especially *Amusium* ». For reasons already given there is evidence that these animals have gone back to life in comparatively clear water.

- VII. — Loss of the byssus and attachment by cementation may occur before descent into deeper water and the full evolution of cleansing mechanisms. This would appear to have taken place in the *Ostreidae*. Further evolution after the development of cementation and the subsequent loss of the foot accounts for the varying habitat of different species of this family (Nelson, 1936).

As this rough survey indicates, the evolution of the swimming habit is no more than one line of evolution made possible by the initial change from the dimyarian to the monomyarian condition, with the subsequent acquisition of elaborate cleansing mechanisms which enabled these forms to extend into more sediment-laden waters than those in which they originally evolved.

9. — SUMMARY

1. In the Lamellibranchia alone amongst the Mollusca the ability to swim is not associated with a reduction of the shell.
2. Previous work on the mechanism of swimming in *Pecten* and *Lima* is discussed and the ability to swim shown to depend on modifications in four sets of organs, shell, adductor, velum and receptors.
3. The assumption of the monomyarian condition is probably the result of byssal fixation.
4. The increase in size of the quick muscle and the appearance of transverse striations in this are due to the need for efficient cleansing mechanisms. This is also the reason for the increase in the size and activity of the velum. Dorsal rejection of waste material has made possible swimming, as apart from escape, movements.
5. With the exception of the functional asymmetry of the statocyst in *Pecten* (shown by Buddenbrock), the adaptations present in swimming Lamellibranchia are no more than further developments of those originally acquired for the efficient cleansing of the mantle cavity.

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