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THE IDENTIFICATION AND CLASSIFICATION OF LAMELLIBRANCH LARVAE

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INTRODUCTION.

THE primary aim of this paper is to enable planktologists, with neither the time nor the inclination to specialize in the group, to identify lamellibranch larvae weeks or months after collection. For this, a method based on the shell rather than on the soft parts is necessary. Though the species to be described are those obtained in the North Sea, it is hoped that the method of analysis and the classification presented will greatly ease the task of identification in other areas, particularly in those areas where the lamellibranch bottom fauna is well known and the list of species fairly limited. The classification of the larvae has a direct

bearing on the classification of the Lamellibranchiata, but this major question is not being pursued here.

Descriptions of larval species have been given by several workers, but the planktologist could, from these, identify with confidence only a very few species, far fewer than those described. This is partly because the characteristics described are unsuitable for identification after preservation of the larvae, and also because few groups of larvae of allied species have been described so that it has not been clear how, and by how much, larvae of allied species differ.

Of papers already published, that by Werner (1939) may receive mention since he made a critical review of the larval features suitable for identification. The paper by Jørgensen (1946) is of considerable value, not least because of the comprehensiveness of the references. It would be superfluous to list again the earlier papers, and a reference to Jørgensen in the descriptive part should be taken as embracing the previous literature on the group or species in hand. The small number of described species has prevented any real attempt to establish a natural classification of larvae, though Bernard (1898), with little information, attempted a classification over a small field.

When the investigation was begun it was provisionally postulated that a natural classification of the larvae is possible, and it has become abundantly clear that this is so. The classification of the adults by Thiele (1935), which is now widely accepted, has been used in this report, since it is desirable that the classification of the larvae should conform as far as possible to that of the adults. A few minor adjustments have been made which are suggested by the practical advantage to be gained in the identification of lamellibranch larvae. It is of interest, however, that some of them have support from the classification given by Haas (1926).

The faunal lists of the lamellibranchs of the North Sea are given by Haas (1926). Much of the argument that follows regarding the species of the larvae depends on the accuracy and completeness of these lists. The specific names given by Winckworth (1932) or, when absent in Winckworth, by Haas (1926) are used. Since in some cases the reader might find it difficult to relate a specific name given by Winckworth to the faunal list of Haas the necessary synonyms are given in an appendix on p. 101.

I wish to take this opportunity of expressing my gratitude to Dr. A. C. Stephen for his considerable and unstinted help in many ways, and to Dr. D. Quayle, now of the Department of Fisheries, Victoria, B.C., Canada, who kindly kept me informed of the progress of his investigation of lamellibranch larvae whilst in this country and advised me to use photomicrographs instead of the less satisfactory line drawings.

Professor C. M. Yonge has been kind enough to read the paper in manuscript, and I am very grateful to him for his comments and advice, particularly on the systematics.

METHODS.

Lamellibranch larvae are relatively heavy and can readily be separated from the rest of the plankton by gentle rotation of the containing dish, the larvae collecting together in the centre.

For identification to be based on shell structure it is essential to preserve the larvae in an alkaline medium. Formalin is suitable, at least for a few months, if thoroughly buffered with borax.

In the initial identification it is necessary to see the hinge clearly by separating the two valves from each other and from the soft parts. This can be done in a few minutes by immersing the larvae in sodium hypochlorite solution, 8-10% NaOH through which chlorine has been bubbled. In such a solution the valves gape and eventually fall apart, but the process can be speeded up by inserting the edge of a needle between the valves and wedging them open. The valves should not, in this process, be allowed to slide off each other since in some larvae the teeth break off readily.

The method of illustration by line drawings has proved unsuitable, as may be seen when comparing the drawings by different authors of the same species. Sullivan (1948), who has published photomicrographs of some species, expresses the same opinion. Photographs have usually been taken of single valves with the inside downwards. It is considered essential that this standard view should be adopted since a vaulted valve lying with inside up (or a complete larva) may take up a variety of positions with consequent changes in the apparent outline of the shell, changes as considerable as the difference between allied species.¹ That bivalves, and not the outside of isolated valves, have usually been drawn in previous papers may partly account for the differences in appearance of a species as shown by different authors.

Glycerine jelly is a particularly suitable medium for the observation of the hinge since the valves can be placed in any desired position with the aid of a hot needle. The inside view (see key in Text-fig. 3) is most easily seen and is sufficient where the hinge has an obvious feature or when the teeth are strong rectangular blocks. In cases where the teeth are not pronounced, or when they have sloping sides, the dorsal view assists greatly in an appreciation of the structure of the hinge.

For the dorsal view it is best to tilt the valve slightly from the true vertical so as to reveal more of the hinge structure. The gaps for teeth are roofed over by the shell of the valve and this "roof" is usually sufficiently opaque to hide structures underneath it, particularly the gaps for the reception of teeth.

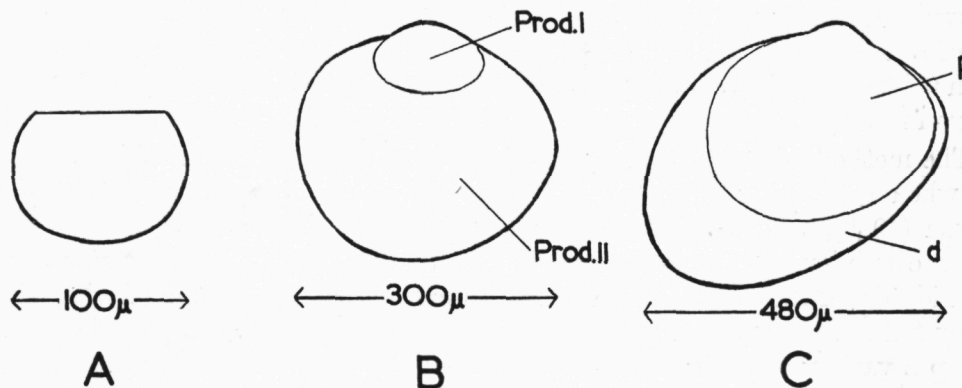
¹ Sullivan's (1948) figs. 3 and 4, Plate X, of *Venus mercenaria* show that this is no exaggeration. The difference in shape between these two views of the same species is greater than the difference in shape within many pairs of allied species.

TERMINOLOGY.

The *length* of a larva is the longest distance in a direction roughly parallel to the hinge. Unless otherwise indicated all measurements given in this paper are of length (in μ). *Breadth* (broad, narrow) is the distance from the tip of the umbo to the ventral margin. *Convexity* (convex, flat) is a measure of the maximum distance through the bivalve from side to side.

Looking at a valve from the side (when only one valve of the bivalve can be seen) the dorsal margins are immediately on either side of the umbo. The remainder of the margin is made up of the two ends and the ventral margin. All these margins, of course, normally merge into each other.

The following terms in *italics*, used later in this paper, have been fully defined by Werner (1939).



TEXT-FIG. 1.—A.—Veliger = “D-shaped larva” = “straight-hinge stage.”

B.—Veliconcha made up of prodissoconch I (Prod. I) and prodissoconch II (Prod. II).

C.—Early bottom-living stage showing prodissoconch (*p*) and dissoconch (*d*).

The trochosphere passes into a bivalve *veliger* (Text-fig. 1A). In the restricted sense of the term as used by Werner (1939), this corresponds to the “D-shaped larva” or the “straight-hinge stage” of previous authors. In particular, the veliger has no hinge differentiation whatsoever. After a pause the final larval shell is laid down and the larva becomes a *veliconcha* (Text-fig. 1B). The D-shaped veliger shell (*prodissoconch* I) is usually distinctly marked off from the veliconcha shell (*prodissoconch* II). After spatfall and metamorphosis the definitive adult shell (*dissoconch*) is laid down, but the prodissoconch is usually clearly marked off (Text-fig. 1C).

MEANS OF IDENTIFICATION.

Identification is based entirely on the shell, primarily on its shape and on the structure of the hinge, with texture being used whenever it is sufficiently distinctive. Shape and hinge structure must have reached a sufficient degree of

development, *i.e.* well into the veliconcha stage. The veligers must as yet be considered unidentifiable though efforts have been made, notably by Werner (1939), to identify a few of them by ratios derived from the hinge length, shell length and breadth. It is hardly likely, however, that trustworthy unique ratios would be found for each of, say, 100 species. In any case, unless one is prepared to go back as far as the egg, one must decide on a suitable stage in development and identify to species only individuals larger than that stage. It is sought here to identify only those larvae whose shape and hinge structure are sufficiently differentiated to allow identification by general appearance. The minimum size allowing identification by general appearance undoubtedly varies with different species and, quite possibly, with different workers.

Shape.

It is a useful rule that the shapes of allied species are variations of a shape characteristic for the group of species. However, two or more groups of allied species may have a similar basic shape so that classification by this character alone cannot usefully be taken very far. Sullivan (1948), for example, classifying by shapes, has grouped together such widely different genera as *Ensis*, *Mytilus*, *Rochefortia* (*Kellia*) and *Venus*. This may be empirically useful in a given locality with a limited number of species, but it fails in universal application.

The three features to be considered are the shape of the shell margin, the prominence of the umbones, and the convexity of the larva. Indication of basic shapes of various groups will be given later, but the best idea of these can be obtained from the grouped photographs (Plates I-V). An appreciation of the basic shapes is essential for easy identification.

The commonest general shape of larvae is that in which one end is broad (or more produced) and the other end narrow. This is, in many cases, rather a loose description but clear enough in practice. In Table I, it is stated of each group, when possible, whether the broad end is anterior or posterior thus allowing orientation of the larvae of the group, though orientation does not greatly matter for identification.

Position of Ligament.

The position of the larval ligament (Text-fig. 2, *lig.*) can be useful both in identification of the basic hinge type and in the orientation of the larvae of the group. It is external in the Solenacea and internal in all other groups. When internal it is situated in relation to the straight hinge part (see below), in most cases away from the centre of it and towards the broad end of the larva. Its position, when possible, is indicated for each group in Table I.

The Hinge Apparatus.

The function of the hinge is to ensure that the valves meet exactly on closure and to ensure that the valves do not slide on each other under uneven pressures

(Dall, 1895). The hinge apparatus, consequently, increases in strength and often in complexity as the larva gets larger, and is roughly proportional to the weight of the shell. In some superfamilies there is no great change in complexity with increasing size (within the identifiable range), only an increase in the strength of the component parts (*e.g.* Saxicavacea, Adesmacea). In other superfamilies new structures are laid down as the larva increases in size (*e.g.* Tellinacea, Mac-tracea). In seeking relationship between hinge structures this fact has to be remembered; only hinges that have reached the same stage in development should be compared. Since the hinge serves a necessary function in the life of pelagic larvae there is always some hinge differentiation in *pelagic* larvae above a certain size (say 150μ or even smaller).

The hinge of every larva investigated has agreed with one of eighteen basic types listed in the left-hand column of Table I. Fourteen correspond to single superfamilies, one corresponds to the Pteriacea and Ostreacea combined (these are combined by Haas (1926) into the suborder Schizodonta), and one to the Pectinacea and Anomiacea combined (combined by Haas into the suborder Isodonta). For the remaining two types the two families of the Myacea are separated and the Myidae joined with the Saxicavacea to give one type, the Aloididae remaining alone to give the other. Haas (1926) does not recognize a superfamily Saxicavacea but joins the Myidae, Corbulidae (= Aloididae), Saxicavidae and Gastrochaenidae into the superfamily Myacea.

All superfamilies with representatives in the North Sea are thus accounted for except the Nuculacea, which have peculiar larva and are recognizable without reference to hinge (see p. 89), the Isocardiacea, which has one species limited to the English coast, and the Gastrochaenacea,¹ with one species limited to the Belgian coast.

The basic types are shown in Text-fig. 3 and the hinge features of each group summarized in Table I: the table should be read in conjunction with the supplementary notes. Before dealing with the hinge of each group, however, it is necessary to explain how the hinge is constructed and the meaning of the various terms used in Table I and the supplementary notes. The various parts to be described are shown in Text-fig. 2.

The two valves of a small bivalve larva meet all round in one plane. A portion of the margin is straight and the straight parts of the two valves remain in contact when the larva gapes; if there were no straight parts there would be only point contact at gape. The straight parts persist throughout larval development though, in a few cases, there may be a curving from the plane of part of the remaining margin as the larva gets larger.

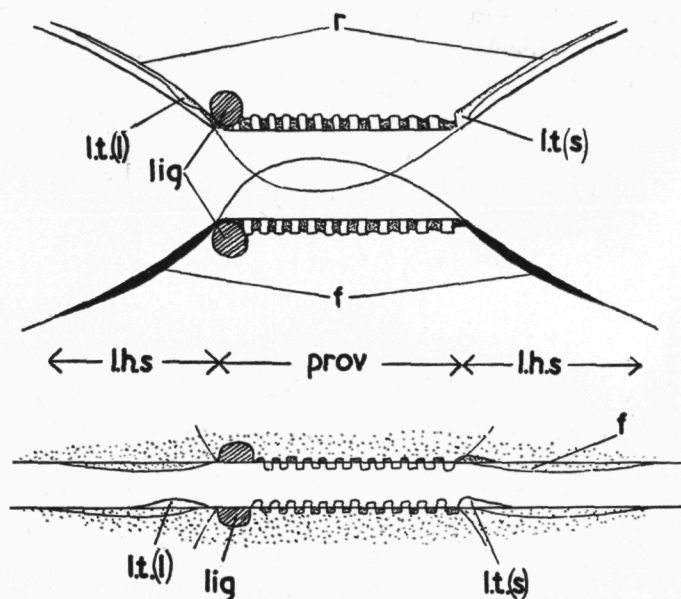
The portion of the shell forming the straight part of the valve may thicken to form a *provinculum* (Bernard, 1898) (Text-fig. 2, *prov.*). The *provinculum*

¹ It is possible that *Gastrochaena* has a hinge similar to that of the Saxicavacea since Haas (1926) includes it under the Myacea.

always bears teeth (*the provincular teeth*) or is moulded into tooth-like projections. Hinge structures, apart from special teeth, present beyond the limits of the provinculum constitute the *lateral hinge system* (Text-fig. 2, *l.h.s.*).

The fully-developed hinge apparatus may, therefore, consist of two parts, the provinculum and the lateral hinge system, together with the *special teeth*.

The provinculum.—(Text-fig. 2, *prov.*). By definition, if there are any teeth or tooth-like projections beneath the straight part of the shell margin a provinculum is present and a provinculum is, in fact, present in all groups except two, the Lucinacea and Erycinacea.



TEXT-FIG. 2.—A diagrammatic drawing of the inside (above) and dorsal (below) views of a larval hinge to show the various components: *f.* = flange; *l.h.s.* = lateral hinge system; *lig.* = ligament; *lt.(l)* = lateral tooth (lamellar); *lt.(s)* = lateral tooth (solid); *prov.* = provinculum; *r.* = ridge.

Provincular structures may be divided into four types :

Type *a.*—There are several or numerous rectangular teeth in each valve, easily seen on inside view of the hinge. This is the type illustrated in Text-fig. 2. These teeth may be regular or irregular in arrangement and equal or unequal in size.

Type *b.*—There are one, two or three strong rectangular teeth in each valve, easily seen on inside views (*e.g.* Saxicavacea, Text-fig. 3).

Type *c.*—There are projections on a thin provinculum. These are not easily seen on inside view, but are quite distinct on dorsal view of the hinge (*e.g.* Pandoracea, Text-fig. 3). This type is probably not essentially different from Type *b*, the latter consisting of projections on a thick provinculum.

Type *d*.—There is a thin strip of very small, spiky or tubercular teeth which, on closure, are inserted into gaps on the other valve, which does not have similar spiky teeth. This type is usually superimposed on provincular structures of Types *b* and *c* (e.g. Cardacea, Text-fig. 3).

The lateral hinge system.—(Text-fig. 2, *l.h.s.*). When present this consists of lateral flanges and calcareous ridges. In some cases projections, referred to as lateral teeth, develop from the calcareous ridges.

When most larvae are opened out and viewed from the inside, it will be seen that one valve (the left) has thicker dorsal edges than the other. The right valve has thin dorsal edges, but an internal calcareous ridge (Text-fig. 2, *r.*) runs more or less parallel to each edge, on either side of the umbonal region. The reason for this is seen when the valves are viewed dorsally. Projecting outside the margin from the dorsal edges of the left valve are flanges (Text-fig. 2, *f.*) which, when the bivalve is closed, underlap the edges of the right valve.

Flanges are present in most groups and usually, but not always, both the flanges, one anterior and one posterior to the umbo, are on the same valve. The calcareous ridges occur on the other valve, *i.e.* they occur in such a way as to appear to act as stops to the flanges.

At the extreme ends of the straight hinge part of the valve with ridges there may be tooth-like projections, to be seen most clearly in dorsal view. These may, at first, be taken as provincular teeth but are, in fact, developments of the calcareous ridges, and therefore part of the lateral hinge system, *i.e.* lateral teeth (Text-fig. 2, *l.t.*).

Two types of lateral teeth can be distinguished both by structure and function. One type is a lamina (Text-fig. 2, *l.t.(l)*), developed from the calcareous ridge, which underlaps the rim of the opposite valve and does not come into contact with any part of the provinculum of the other valve. The other type, also a development of the ridge, is more solid and comes in contact with the outside edge of the provinculum of the other valve on closure (Text-fig. 2, *l.t.(s)*).

Commonly the flanges narrow gradually towards the provinculum (Text-fig. 2) but, in some cases, the flange ends abruptly or even projects at the provincular end, thus giving the impression of a tooth. However, by the present definition, these abrupt terminations or projections are considered to be part of the flanges and not teeth (see p. 86).

Special teeth.—Special teeth are limited to four groups and need no description here. They are projecting teeth which cannot readily be referred either to the provincular or lateral hinge systems.

The Hinge Characters of Each Group.

Now that the generalized hinge structure has been defined we can consider how the various parts are combined to give each basic type. Hinges develop

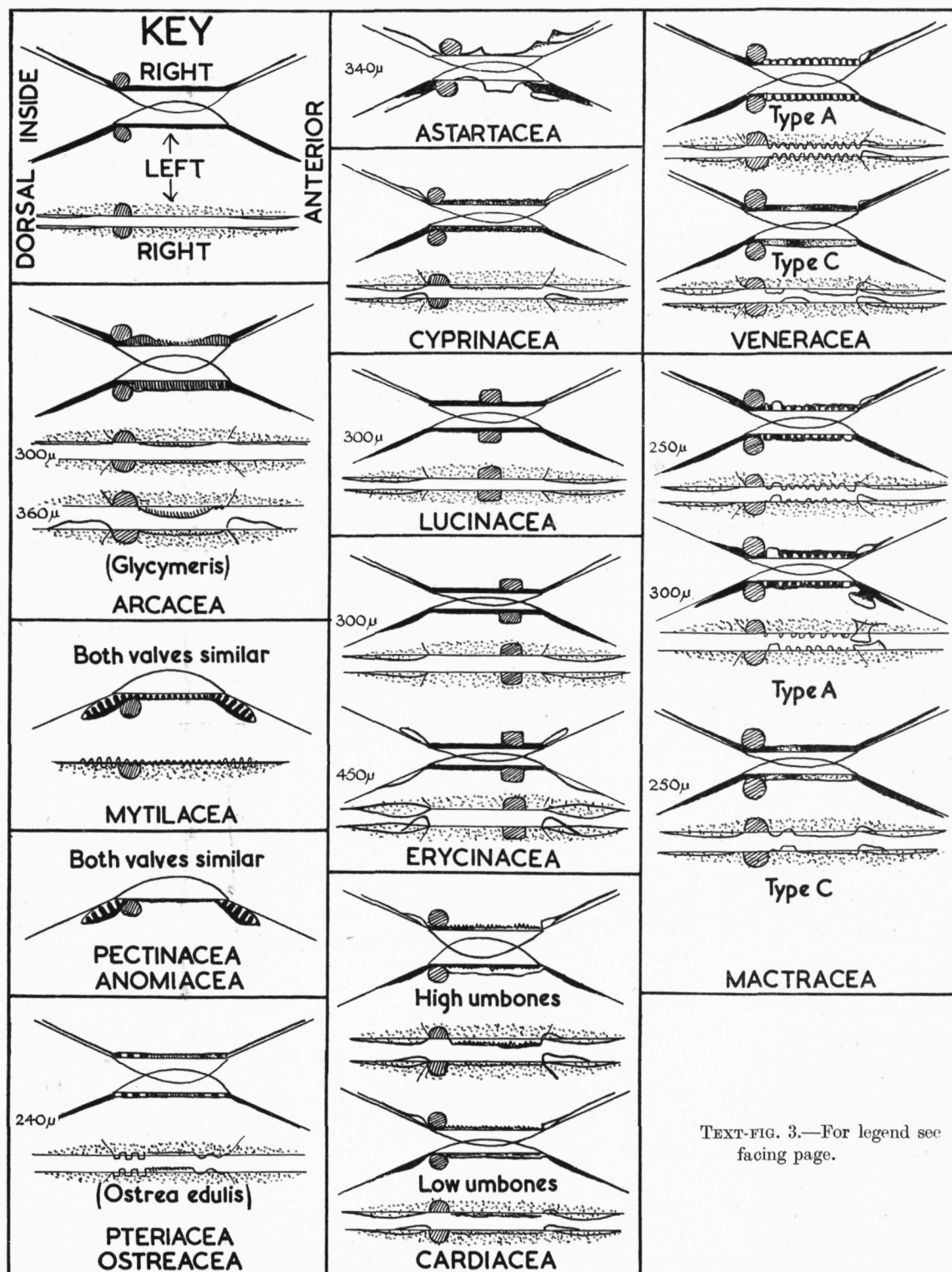
with increasing size, and not every stage in development in each case can, as yet, be described, but the object is to enable identification at some stage; once that is successfully done the identification of smaller and larger larvae of the same species is relatively easy.

The 18 basic types are shown in Text-fig. 3, and the features summarized in Table I. The additional notes below are meant to clarify the figures and table. The orientation of the valves is given by a key figure in Text-fig. 3.

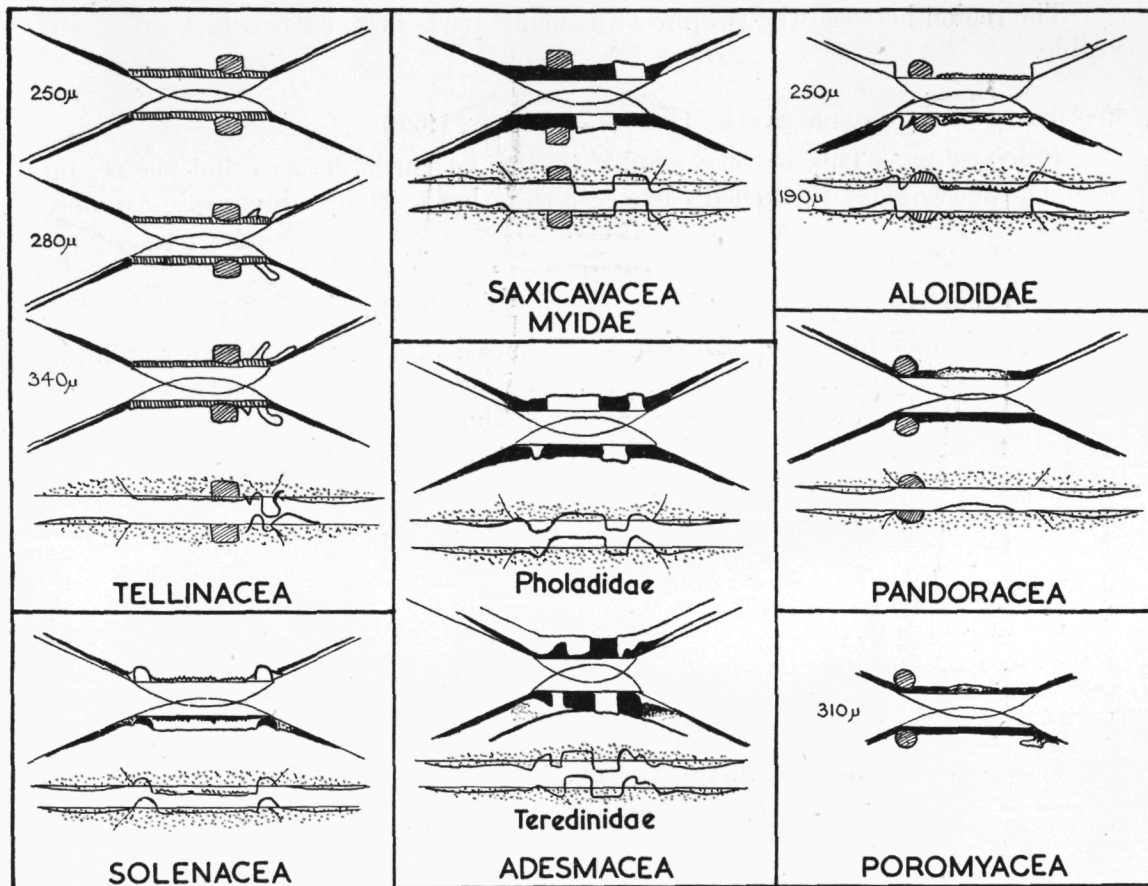
TABLE I.—*Summary of Larval Features in Each Group except Nuculacea, Isocardiacea and Gastrochaenacea.*

X = present; — = absent; ? = no information; A = anterior; P = posterior; Q = equilateral valves; C = centre; L = left valve; R = right valve; E = external; l = lamellar; s = solid; a, b, c, d , = types listed on p. 79.

	Broad side.	Ligament.	Provincular teeth.	Flanges		Lateral teeth		Special teeth.
				$A.$	$P.$	$A.$	$P.$	
Arcacea .	A	P	a	—	—	X	X	—
Mytilacea .	P	P	a	—	—	—	—	—
Pectinacea } Anomiacea }	P	P	a	—	—	—	—	—
Pteriacea } Ostreacea }	Q	P	a	—	—	—	—	—
Astartacea .	?	?	b	?	?	?	?	X
Cyprinacea .	P	P	d	L	L	l	l	—
Lucinacea .	A	C	—	L	L	l	l	—
Erycinacea .	A & Q	A	—	L	L	l	l	—
Cardiacea .	P	P	$b, c + d$	L	L	s	l	—
Veneracea .	P	P	a, c	L	L	s	—	—
Mactracea .	P	P	a, c	L	L	X	—	X
Tellinacea .	A	A	a	L	R	X	—	X
Solenacea .	P	E	$b + d$	L	L	—	—	—
Saxicavacea } Myidae }	P	P	b	L	R	—	—	—
Alolididae .	Q	P	$b + d$	L	L	s	s	—
Adesmacea .	Q	P	b	L	L	—	—	—
Pandoracea .	P	P	c	L	L	—	—	—
Poromyacea .	Q	?	c	?	?	?	?	X



TEXT-FIG. 3.—For legend see facing page.



TEXT-FIG. 3 (cont.).—Figures showing the 18 basic types of hinges comprising all groups of North Sea lamellibranchs, with the exception of the Nuculacea, Isocardiacea and Gastrochaenacea, as described in the text. Where hinges increase in complexity with size of larva the approximate larval size is indicated against the hinge. Orientation is shown in a key figure at the top left corner of the facing page.

Arcacea.

The position of the ligament towards the narrow (p. 77) end is exceptional.

Provinculum.—The teeth are numerous, very small and more or less equal in size. In dorsal view they appear to be roofed over and not all separated by clear gaps.

Ridges.—Ridges are present in the smaller larvae.

Mytilacea.

Provinculum.—The term *provinculum* here is extended to include the thickening of the shell beyond the limits of the straight hinge section since this lateral thickening is quite unlike anything to be found in the usual lateral hinge system. It is also historically correct to use the term here to cover the whole hinge system (Bernard, 1898).

The region between the two most thickened parts bears teeth which are easily visible.

Pectinacea and Anomiacea (the Isodonta of Haas, 1926).

Provinculum.—This is very similar to that of the Mytilacea, but the region between the two most thickened parts is so thin that teeth are absent or extremely minute.

Pteriacea and Ostreacea (the Schizodonta of Haas, 1926).

Ligament and Provinculum.—The teeth consist of a strip of roofed-over taxodont teeth and, posterior to this strip, a few bigger rectangular teeth with clear gaps in between. In *Ostrea edulis*, at least, there are some large corrugations anterior to the taxodont teeth, but these are not included in this definition of the hinge type (see p. 92). According to Bernard (1898) and Borisjak (1909) the ligament lies between the taxodont strip and the posterior rectangular teeth.

Astartacea.

No further information is available apart from the drawing of a large larva (340 μ) in Text-fig. 3. The large special tooth of the left valve is spatulate.

Cyprinacea.

Provinculum.—It is doubtful whether this should be regarded as a Type *d* only or a combination of Types *c* and *d* as in the low-umboned species of the Cardiacea.

Lucinacea and Erycinacea.

These are the only two groups without a provinculum.¹ The straight edge of very large larvae of some species may appear on inside view rough or corrugated, giving the impression of feebly-developed teeth. In such deceptive cases the dorsal view is decisive; no structures project beyond the shell margin in the region of the straight part (*cf.* the dorsal views for these two superfamilies with those for all other types shown in Text-fig. 3).

As far as is known the only difference in the hinges of the two groups is that the ligament is central, or possibly posterior to centre, in the Lucinacea and anterior to centre in the Erycinacea.

Cardiacea.

Provinculum.—In the right valve the provinculum is very thin and consists of a strip of spiky teeth. The provinculum of the other valve is thicker and

¹ This statement may not be true for large larvae ($> 300\mu$) of the Lucinacea but it is, in practice, adequate since in all other groups normally pelagic larvae have a provinculum at a size of 200μ upwards. Too few larvae of the Lucinacea have been obtained for full definition.

projects as a long tooth with gaps along its dorsal inside edge for the reception of the spiky teeth. The detail of this structure is best made out in the high-umboned larvae; in the low-umboned larvae the provinculum is built on a smaller scale making the detail difficult to appreciate.

Veneracea.

Provinculum.—In the Type *c* hinge the projections may be rough and give an impression of numerous incipient teeth on inside view. In dorsal view the constant feature of this type is a long projection on the anterior of the left valve which is apposed to the solid lateral tooth of the right valve on closure. There are other projections.

Mactracea.

Provinculum.—The two types are very similar to the two of the Veneracea. In most species of Mactracea of Type *a*, however, one of the rectangular teeth towards the posterior of the right valve is prominent and distinctive (see p. 95).

Special tooth.—A special tooth arises from about the size of 270μ . This becomes a well-developed spatulate tooth which is pressed ventrally against the lateral tooth, which has formed earlier, when the larva is closed.

Tellinacea.

Provinculum.—There is a series of tiny, rectangular teeth which resemble the taxodont type when viewed towards the inside.

Ridges and flanges.—Like the Saxicavacea, and unlike all other groups, these alternate, one flange on the right valve and the other on the left.

Special teeth.—These arise in succession with increasing size of larvae (see Text-fig. 3).

Solenacea.

Ligament.—The ligament is external but does not appear till late ($> 270\mu$).

Provinculum.—On the left valve there is a rectangular tooth reaching nearly the full length of the provinculum, and on the right valve a small tooth at each end of the provinculum. Above a certain size (*ca.* 340μ) one of the two small teeth increases in length (Text-fig. 4). The system of spiky teeth is very like that of the Cardiacea.

Saxicavacea and Myidae.

Provinculum.—There is one strong provincular tooth in each valve. In the low-umboned species (*Mya*), which have a thin provinculum, these teeth may almost be described as merely projections.

Ridges and flanges.—These alternate as in the Tellinacea.

Aloididae.

Provinculum.—The system of spiky teeth is very like that of the Cardicea. In the left valve there is a distinct tooth posterior to the ligament, constituting one side of the gap that receives the posterior solid tooth of the right valve.

Adesmacea.

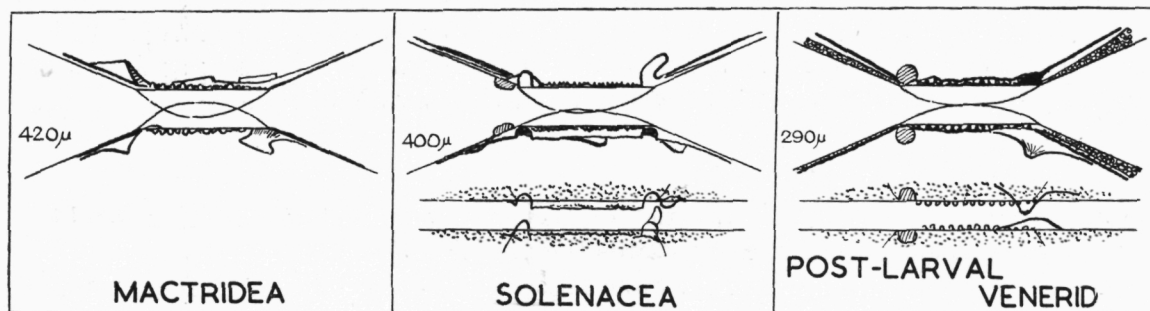
Provinculum.—The Pholadidae can be distinguished from the Teredinidae by the fact that the central tooth is much longer in the former.

Pandoracea.

Provinculum.—There is a long projection on the right valve and none on the left.

Poromyacea.

No further information is available apart from the drawing shown on Text-fig. 3. At 300μ the hinge has a distinctive special tooth.



TEXT-FIG. 4.—The hinges of unusually large Mactracean and Solenacean larvae and of a post-larval Venerid.

Following the policy of keeping the description of the hinge as simple as possible, lateral teeth have been defined as developments on valves without flanges, *i.e.* as developments of the calcareous ridges only. Any thickening forming a tooth at the provincial end of the flanges has been neglected. However, such "flange teeth" occur in the Saxicavacea (and Myidae) and possibly the hinges of the Adesmacea could be more exactly defined if this extra component was recognized.

Dall (1895) combined the Veneracea, Tellinacea, Solenacea and Mactracea into the Teleodonta. Special teeth have been shown (Text-fig. 3) in the Tellinacea and Mactracea and it would be of interest to see if there was a similar development of special teeth in the two remaining superfamilies. In Text-fig. 4 hinges of unusually large Mactracean and Solenacean larvae are shown, together with the hinge of a Venerid specimen in which the dissoconch had begun to form (prodissoconch 250μ in an overall length of 290μ).

Texture.

The nature of the concentric lines and similar sculptural features, the strength or fragility of the shell, and the colour of the shell (not of the soft parts) are useful

features for the identification of larvae. Unfortunately these features are inadequately illustrated in the plates, but outstanding textures are mentioned in the descriptive part.

Texture changes with increasing size. Thus it is common for shells to be relatively strong at small sizes and fragile at large sizes. Colour, if present, increases in intensity with size. Unless otherwise stated the texture described in the text is that of the larger larvae illustrated.

Allied larvae tend to have similar texture.

When a larva has been identified by the shell shape and the hinge, the texture should be observed as it will be found that this is of assistance in subsequent routine examinations of plankton samples. Once the species of larvae have been learnt they are recognized by their general appearance, by their shape and texture.

THE SPECIFIC IDENTIFICATION OF LARVAE IN THE NORTH SEA.

The surest method of determining the species of a larva is by culturing. In the present investigation no culturing has been done and the identification is consequently indirect. It is therefore necessary to indicate the indirect sources that have led to specific identification, apart, of course, from the available literature on the subject.

That a natural classification of larvae is possible is of very considerable help. This has been the most fruitful of the indirect sources and brings the larva down to a short list, sometimes a very short list, of species. For example, a larva can be placed in the Solenacea without doubt. There are, it appears, only four species of this superfamily in the North Sea (Haas, 1926) so that the larva can be only one of these four, thus eliminating well over 100 other species.

Of some, but limited, use is the postulate that in a group of allied species the differences between the larvae are reminiscent of the differences between the adults. This has been applied, for example, to the species of *Abra*.

Specific identification is often possible through the agreement between the distribution and frequency of a larva and the known distribution of the adults.

One further aid to identification is the fact that the larval shell (prodissoconch) is usually marked off at the umbo from the definitive shell (dissoconch) in young bottom-living bivalves (Text-fig. 2). On the whole it has not seemed possible to identify larvae to species by the shape of the prodissoconch, but it is possible to obtain an indication of the type of shape to be expected of the larvae of the genus.

Two limitations to this process of indirect identification may be mentioned. Firstly, the lamellibranch fauna in the area being worked must be thoroughly known and it can hardly be claimed that this is the case over the whole North Sea. Secondly, there is not universal agreement on the specific status of some forms, particularly in the Mactracea. Eventually the larvae should help to clarify the

position. In the meantime, however, this doubt about the specific status of some forms makes indirect identification more difficult.

Altogether 77 pelagic larvae have been described in the following part. Haas (1926) lists over 120 species occurring in the North Sea proper (*i.e.* excluding forms limited to the coast). Some of these are known to have non-pelagic larvae, accounting for at least another 16 species (including the Nuculacea) and, with our present knowledge of the hinge, six additional species can be identified from previous literature. The fitting of larvae to species has in many cases been speculative and a convention has been adopted giving three degrees of certainty. When there is confidence the name is given directly, *e.g.* "*Mytilus edulis*." When there is doubt the larva is lettered and the specific name given in brackets with a question mark *e.g.* "PHOLAD A (? *Pholas dactylus*)"; when the specific name cannot be suggested the larva is lettered only, *e.g.* "PECTINID D."

There has been no hesitation in publishing descriptions of larvae which, as yet, cannot be assigned to species. The most serious lack in our present knowledge is how, and by how much, allied species differ and this question must be settled before confident specific identification can be made. For example, the larva of *Mytilus edulis* has been described about 10 times. Yet Jørgensen (1946) undoubtedly described a mixture of *Mytilus edulis* and *Modiolus modiolus* under the former species, and Lebour (1947) identified larvae as "*Mytilus* or relative." The apparent uncertainty in the identification of *Mytilus* larvae is due to ignorance of the extent of inter-specific differences; are the larvae of *Modiolus barbatus*, for example, so like those of *Mytilus edulis*, that there is uncertainty in the identification of *Mytilus edulis*? In consequence, every additional Mytilid larva which is described and shown to be recognizably different from *Mytilus* larva increases the certainty in identification of *Mytilus*, even though the species of the newly-described Mytilid may not be known. The identification of lamellibranch larvae is a process of comparison and contrast.

It is not certain that all the larvae described below are truly pelagic. Spat forms, which can easily be distinguished from larvae, are occasionally found in the recorder material. Presumably these have been brought up from the bottom in turbulent water, and it is possible that non-pelagic larvae, which have not been distinguished from pelagic larvae, have also been brought up in the same way and collected by the recorder. Such a possibility is mentioned below in the consideration of two larvae (*Astarte* sp. and *Gari fervensis*). Even allowing the possibility of one or two others, however, the total effect must be of little importance.

Since most of the species of larvae have been identified by indirect means there may well be errors in the identification. Readers who recognize such errors, or who can give information on the doubtful and unidentified larvae, are asked to inform the author so that these revisions can be included in a later report.

A detailed description of each form is unnecessary. When an unrecognized larva is found the first step is to determine its type of hinge. The hinge of a larva

may differ in detail from one of the basic types shown in Text-fig. 3, but there should be no difficulty in deciding that a particular hinge belongs to one basic type, and no other. Once the type has been decided the next step is to try and fit the shape of the larva to one of the photographs, grouped according to hinge types, in the plates. If a fit is obtained, the description in the text should be checked.

On the whole the descriptions need only include texture since the photographs usually give all the necessary information on shape. In most larvae the concentric lines of the shell are fine and close-set. If, therefore, no comment is made on the concentric lines it can be assumed that they are of this character.

Some of the larvae have been obtained very rarely and indication of the number of specimens is given in brackets immediately before the descriptions, thus (1), (2), (+) a few, (++) many, (+++) very many.

ORDER TAXODONTA.

Superfamily Nuculacea.

[For references see Jørgensen, 1946.]

The Nuculacea are probably all either non-pelagic or pelagic only for a very short time (say three or four days), the pelagic larvae being surrounded by large velar cells giving a barrel-shaped structure (Drew, 1899 and 1901). No members of this superfamily have been identified in our material.

Superfamily Arcacea.

Three species are shown in Plate 1.

Glycymeris glycymeris (Linné) (++)—This is an easy larva to recognize at a size of 360–420 μ . The shell is strong and heavy, and the pallial line which runs parallel and close to the margin of the shell is very distinct.

The hinge has been described in general terms on p. 83. In the left valve of this species the ventral edge of the strip of teeth, as seen inside, is straight and smooth, whilst in the right valve the ventral edge is jagged (Text-fig. 3).

Distinct from the hinge apparatus there is, in the left valve, a shallow rim which encircles the whole valve except at the hinge, and for a small arc of about 5°. This rim underlaps the margin of the right valve which has an internal calcareous ridge corresponding to the rim. Thus there is a pill-box arrangement. The internal ridge starts on either side of the umbo and extends about half-way round at a size of about 340 μ .

Lateral ridges, comparable to those of other species, are present in smaller specimens.

The species is probably incubatory in the earlier larval stages, and pelagic stages smaller than 260 μ have not been recognized.

ARCACEAN A (1).—The hinge is basically like that of *Glycymeris* but without the distinctive jagged edge to the taxodont strip. The shell is strong, with a pill-box system.

ARCACEAN B (? *Limopsis* sp.) (+).—This has a thinner shell than the above two species and the hinge is simpler. Large specimens have the pill-box system.

The appearance, structure and distribution of the first described larva can leave little doubt that it is of *Glycymeris*. However, the prodissoconchs at the umbones of five small bottom-living specimens of *Glycymeris* (4–8 mm.) provided by Dr. Stephen were quite different, these forming very distinct caps 170–210 μ across. Outside the cap the shells had growth lines with no distinct area marked off, but the run of the lines near the umbo clearly resembled

the described larvae. Similarly, there was a distinct cap about 160μ across on three bottom-living specimens of *Limopsis aurita* (Broochi). On two specimens there was no other clear area marked off, but on the third there was an area 320μ across shaped not unlike the larva tentatively referred to *Limopsis* (ARCALEAN B). Whilst Haas (1926) lists only *L. aurita* in the North Sea Schrader (1911) recorded *L. minuta* (Phil.) also.

ORDER ANISOMYARIA.

Superfamily Mytilacea.

[For references see Jørgensen (1946) : in addition Sullivan (1948) has described *Mytilis edulis* and *Modiolus demissus* (Dillwyn)]. Members of this family are easily recognized by the hinge. The only other type of hinge which has any resemblance to it is that of Pectinacea. Nine species are shown in Plate I.

Mytilus edulis Linné (+++).—Nelson (1928) gives good photographs of bivalve larvae. Jørgensen (1946) refers to a wide variation in shape and colour and later suggests that the resemblance between this species and *Modiolus modiolus* is so close that a confusion of the two species may have taken place. It is believed that this has, in fact, occurred, but that the variation he mentions is a function of size. Larvae of the two species, all of the same size (not too small), are quite distinct. *Mytilus* is described in comparison with *Modiolus*.

Modiolus modiolus (Linné) (+++).—In the smaller specimens of *Mytilus* and *Modiolus* the shape is similar, though the narrow end is more pointed in the latter. In later stages the two shapes become more differentiated, the more pointed end of *Modiolus* remaining a distinctive feature and, in addition, the broad end of the same form droops ventrally and backwards, to a degree considerably more than in *Mytilus*, size for size.

The smaller specimens of the two species are more easily separated by their texture than by shape. The shell of *Modiolus* is a much stronger one than *Mytilus*, and, correspondingly, the hinge is relatively more massive, the umbo more pronounced, the concentric lines more distinct. The empty shell, too, is more strongly coloured, flaxen, particularly on the ventral side. In the intact bivalve, *Modiolus* is more opaque than *Mytilus*. Probably Jørgensen's drawing (his Fig. 167B) is of *Modiolus modiolus*.

An interesting feature is that in both species the dorsal shoulder of the broad end is separated from the main body by a very shallow furrow. This furrow is fairly distinct in single valves above 300μ but indications of it may be seen in small forms, even at 200μ .

Musculus marmoratus (Forbes) (+).—Described by Jørgensen (1946). Figs. 11 and 12 of Odhner (1914) are certainly of this species. The shell may be imagined as a *Modiolus* shell shortened dorso-ventrally. It is recognizable at 150μ , possibly earlier.

Adula simpsoni Marshall (+).—This has a strong shell with a rich brown colour. The concentric lines are very distinct and moderately set. A comparison of this larva with adults of *A. simpsoni*, collected by Dr. Stephen, has left no doubt about the correctness of the identification.

MYTILID A (++).—The shell is firm, like *M. modiolus*, but the concentric lines are fine and close set. The main part of the shell is colourless but in large forms ($>300\mu$) the rim is yellowish and usually the dorsal margins are rose coloured. The umbo is low. A specimen measuring 380μ has been found.

MYTILID B (1).—The umbo is very low. The shell is rather thin and strongly coloured a yellow brown with rose along the dorsal margins, more strongly coloured than *M. modiolus* and much more so than *M. edulis*.

MYTILID C (2).—The shell is fragile and nearly colourless, with very indistinct concentric lines.

MYTILID D (1).—The shape is very distinctive with a break on either side of the umbonal region. The shell is strong but the concentric lines are very indistinct.

MYTILID E (? *Crenella* sp.) (1).—The shape is almost equilateral and the umbo low. The shell is colourless.

Jørgensen (1946) records that the size of the prodissoconch of a bottom stage of *Crenella decussata* (Montagu) was 750 μ . On two specimens, provided by Dr. Stephen, there is a non-decussated area about 600 μ across within which a line delimits an area 290 μ across. It is possible that it is the smaller area which corresponds to the prodissoconch. Outside this the non-decussated area may be an interdissoconch as described by Jørgensen (1946) in *Musculus marmoratus* where the shell characteristic of the species does not form until the spat is 1 mm. in length. The shape of MYTILID E certainly suggests that it is a larva of *Crenella*.

Of the other unidentified larvae, MYTILID A may prove to be *Modiolus phaseolinus* (Philippi).

Musculus discors (Linné) and *Musculus niger* (Gray) have non-pelagic larvae (Thorson, 1935).

Superfamily Pectinacea.

[For references see Jørgensen (1946)]. Only Jørgensen has described larvae, within the identifiable range, of any North Sea species of *Pecten* (*Chlamys*). Five species of the Pectinidae and one of *Lima* are shown on Plate I.

Chlamys striata (Müller) (1).—This has been described by Jørgensen (1946).

PECTINID B (+).—This is slightly inequivalve. The more convex valve curves deeper towards the other valve at one place, with a corresponding retraction of the margin of the other valve. This curvature of the margin gives a characteristic slight concavity in the outline of the ventral edge. The shell is tough with a strong flaxen colour towards the ventral edge. Towards the margin the concentric lines are well marked and set moderately apart. No specimens over 220 μ in length have been seen.

PECTINID C (+).—The shell is thin and coloured. A specimen measuring 280 μ has been found.

PECTINID D (+).—Equivalve. One specimen has a fringe of dissoconch shell on one valve and had therefore just undergone metamorphosis at a size of 220 μ .

PECTINID E (+).—The two specimens shown on Plate I are believed to be of the same species but this is not certain. The larvae are equivalve and have thin shells.

For the present we cannot go far with the specific identification of the above larvae, especially as 13 species are listed as occurring in the North Sea. Of these we can possibly eliminate *Chlamys similis* (Laskey) since the prodissoconch of bottom-living specimens measures only 125–150 μ (Jørgensen, 1946). On a single bottom specimen of *C. distorta* (da Costa) the prodissoconch measured less than 200 μ .

Lima sp. (++).—The photograph is sufficiently similar to the drawing of *Lima loscombi* Sowerby (Jørgensen, 1946) to make such a specific identification probable. The shell is firm and colourless.

Superfamily Anomiacea.

[For references see Jørgensen (1946)]. Sullivan (1948) gives photographs of small larvae, before the pedal sinus is formed, and it will be seen from these that the genus, at least, can be recognized in quite small specimens. Three species are shown on Plate I.

Anomia ephippium Linné (++).—Described by Odhner (1914) whose drawing is excellent. This is distinguished from the following species by the slight shoulder on the dorsal side of the broad end. This is more obvious in the complete larva than in the single shell.

Heteranomia squamula (Linné) (++).—Described by Stafford (1912), Lebour (1938b) and Jørgensen (1946). The broad end in this falls away directly from the umbo.

Monia squama (Gmelin) (1).—This has a stronger shell than either of the above and the concentric lines are well marked. At 230μ there is a distinct lump towards the ventral side of the broad end leading to a distortion of the concentric lines. There is, also, a smaller lump opposite it on the flat valve.

The only other species listed in the North Sea is *Monia patelliformis* (Linné) and, according to Bernard (1896), this larva has a pedal sinus in both valves.

Superfamily Pteriacea and Ostreacea.

The definition of the hinge type is based not only on personal observations of the hinge of *Ostrea edulis* (Linné) (Text-fig. 3), but also on the description by Bernard (1898) and Borisjak (1909) of *Ostrea* and *Pinna* hinges. The definition given is limited to the series of Arcacean-like teeth and posterior Mytilacean-like teeth, since the anterior teeth or corrugations of *Ostrea edulis* are not described as present in *Ostrea* spp. or *Pinna* spp. by Bernard.

In *Ostrea edulis* (Linné) the two valves fit in a pill-box fashion as described for *Glycymeris*, the underlapping rim being very narrow. No specimens have been obtained by the recorder; material for the observation of the hinge being kindly provided by Dr. R. H. Millar. The larva has been described by Erdmann (1935).

According to Bernard (1898) three species of *Pinna* have triangular larvae. It can therefore be assumed that the larva of *Pinna fragilis* Pennant has a triangular shape and this, together with its hinge, should make it easily recognizable.

ORDER EULAMELLIBRANCHIATA.

Suborder HETERODONTA.

Superfamily Astartacea.

The larva shown on Plate II cannot be fitted into any other group. Its shape, texture and strength of the hinge are certainly reminiscent of *Astarte*. The inside view of the hinge, which must be regarded as incompletely observed, is shown in Text-fig. 3. It should be noted that the only hinge structure given is of a large, heavy larva (340μ).

The shell of the single specimen was tough and pinkish in colour with well-marked concentric lines.

According to Thorson (1936), larvae of *Astarte borealis* (Chemn.), *A. montagui* (Dillwyn) and *A. elliptica* (Brown) are non-pelagic. It is possible that our specimen is not a truly pelagic form but has been washed up from the bottom. Spat forms of other groups have occasionally been found in our collections.

Superfamily Cyprinacea.

A larva believed to be that of *Cyprina islandica* (Linné) is shown on Plate II. This is not the same larva as that indirectly identified as such by Jørgensen (1946), and it is suspected, from the incomplete description, that his larva is, in fact, a *Cardium* species.

Cyprina islandica (Linné) (+).—This larva may easily be mistaken for one of the Cardiaceae. It is, however, rather a flat larva and the hinge is different, but careful observation is required to distinguish the two types. The hinge resembles that of the Lucinacea and Erycinacea in having both the lateral teeth lamellar, and it is due to this resemblance that the larva has been identified as *Cyprina*.

Superfamily Cardiacea.

[For references see Jørgensen (1946): in addition Sullivan (1948) has described *Cardium pinnatulum* Conrad.]

The larvae of this superfamily may have high umbones, as in *Cardium ovale* Sowerby (Jørgensen, 1946) and *C. pinnatulum* (Sullivan, 1948), or low umbones as in *C. edulis* Linné (Jørgensen, 1946 and Lebour, 1938), *Cardium* spp. (Odhner, 1914) and *Forma* μ (Borisjak, 1909). Some are very convex as in *C. echinatum* L. (Lebour, 1938) or not convex as in *C. crassum* Gmelin, *C. scabrum* Philippi and *C. edulis* (all three in Lebour, 1938). In spite of these apparently large differences the larvae of the Cardiacea conform to a basic type. Five species are shown in Plate II and the resemblance between them is clear, though *Cardium* A (*C. ovale*) is high-umboned and the other four low-umboned, and *Cardium* D and E very convex and *Cardium* A, B and C not convex. The resemblance is enhanced by the rather distinct pallial line which is set well away from the shell margin. The hinges of the high-umboned and low-umboned types are shown in Text-fig. 3.

Cardium A (? *C. ovale* Sowerby) (++).—This larva has relatively high umbones and is fairly convex, but by no means as convex as some other *Cardium* species. Larvae as large as 340 μ have been obtained.

Cardium B (++).—This is the least convex of the five larvae. The concentric lines are quite distinct but closely set. The largest larvae seen were 260 μ .

Cardium C (1).—This resembles *Cardium* B in convexity and texture.

Cardium D (++).—This is a very convex larva. Texture resembles *Cardium* B.

Cardium E (1).—This resembles *Cardium* D in convexity and texture.

Of the eight North Sea species of *Cardium*, five have already been described by Jørgensen (1946) and Lebour (1938) so that at least two of the above have been previously described. There has been, however, little success in assigning the above larvae to species from these descriptions. *Cardium* A agrees quite closely with Jørgensen's description of *C. ovale* (as *fasciatum*). It is certain that *C. edule* and *C. scabrum* are not included in them and probably not *C. crassum*. The convexity of the larvae and their frequency suggests that *Cardium* C is *C. minimum* Reeve, *Cardium* D is *C. echinatum* and *Cardium* E either *C. aculeatum* Linné or *C. exiguum* Gmelin.

Superfamily Veneracea.

[For references see Jørgensen (1946); in addition Sullivan (1948) has described *Venus mercenaria* L., *Petricola pholadiformis* Lam., *Pitar morrhuana* Gould and *Gemma gemma* Totten.]

This is a difficult group since the larvae do not, as a rule, reach a large size and specific differences need to be recognized at a size of 200 μ to 250 μ .

Eight species are shown on Plate III and the difficulty of separating these eight is apparent from the photographs. The hinges do not greatly help since seven of them have Type *c* hinges (Text-fig. 3) and only VENERID G has Type *a*. In practice texture is a valuable aid but, unfortunately, is not adequately illustrated. Nevertheless, the seven species with Type *c* hinges are divided into four groups according to texture.

- (a) Concentric lines well marked and well separated (VENERIDS A and B).
- (b) Concentric lines moderately marked and moderately set (VENERID C).
- (c) Concentric lines moderately marked but close set (VENERIDS D and F).
- (d) Concentric lines fine and close set (VENERID E and *Petricola*).

The shells of Venerid larva have a light flaxen colour. The lateral ridges are very distinct, the posterior one extending about half-way round to the ventral side and the anterior about one-third of the way round.

VENERID A (? *Venus ovata* (Pennant)) and VENERID B (? *Venus striatula* (da Costa)) (+++).—

The hinges and texture of these two larvae are identical. In some specimens the concentric lines are well marked and well separated right up to prodissoconch I; in others the lines become less marked and closer set towards the prodissoconch. These two types, however, appear in both species and such a difference cannot be used to delimit species.

In order to distinguish the two larvae the only suitable feature is the shape of the dorso-lateral edge of the narrow end. In VENERID A this is nearly straight whilst in VENERID B it is convex. In the former too, the narrow end is rather more ventral than in VENERID B.

Jørgensen (1946) has described larvae which may be either *V. striatula* or *V. ovata* or a mixture of both.

VENERID (? *Venus*) C (+).—The curvature of the dorsal part of the narrow end is greater than in VENERID B and the larva is almost equilateral. Texture immediately distinguishes this larva from VENERIDS A and B.

VENERID (? *Venus*) D (+).—The dorso-lateral part is not so curved as in VENERID C. The 290 μ specimen, though exceptionally large for North Sea Venerids, had a hinge no different from the Type c hinge of much smaller specimens (<200 μ). An interesting feature was a break in the dorso-lateral edge of the narrow end, marking off a lunule towards the umbo, from the main body.

VENERIDS (? *Dosinia*) E and F (+).—It is noticeable that, in the four species just described, the broad end falls away immediately from the umbo, and it can hardly be said that there is a dorsal edge. In these two larvae a dorsal edge is recognizable (left-hand side of photographs). In VENERID E this dorsal edge is more obtuse to the hinge line, in comparison with VENERID F, and the pointed part of the narrow end is situated more towards the dorsal side. Texture, too, distinguishes the two forms, but not very definitely.

VENERID (? *Paphia*) G (+ +).—This is readily distinguished from the other species described by the Type a hinge. The concentric lines are moderately marked, and moderately set towards the rim and fine and close set towards the umbo. A specimen in which the dissoconch had begun to form had a prodissoconch of 240 μ .

Petricola pholadiformis Lamarck (1).—This has been identified by Sullivan's (1948) description. It has a firmer shell than is usual in the larvae of the Veneracea and is more strongly coloured. As to be expected with a heavy shell, the main provincial projection is relatively strong.

From the distribution of the larvae and the shape of the prodissoconchs of bottom-living stages there is little doubt that VENERIDS A and B are *V. ovata* and *V. striatula* (or vice versa). The basic shape and hinge of the genus *Venus* are thus indicated so that VENERIDS C and D also seem to be *Venus* species though *Mysia undata* (Pennant) must also be considered as a possibility. The basic shape for VENERIDS E and F is different though not markedly so, and they are therefore considered to be the two species of *Dosinia*. VENERID G is thought to be a *Paphia* species since its hinge is unlike those of the suggested *Venus* and *Dosinia*. Furthermore, Miyazaki (1936) described the larva of *Paphia philliparum* as having a "taxodont" hinge and Dr. Quayle has told me that *Paphia* sp. investigated by him at Millport had a Type a provinculum. From the appearance of the prodissoconch of the bottom stages it is unlikely that the larva of *Garfarium minimum* (Montagu) is represented in the above.

Superfamily Mactracea.

[For references see Jørgensen (1946); in addition Sullivan (1948) has described *Spisula solidissima* (Dillwyn) and *Mulinia lateralis* Say].

There is more disagreement about specific boundaries in this group than in any other, and it is perhaps hardly surprising that the larvae of more species have been proposed here than are listed by Haas (1926).

The two types of hinges are described on p. 85 and shown in Text-fig. 3. Six species are shown in Plate III and of these all except *Mactra corallina* (?) have the Type a hinge. It

is desirable here to add to the general description of the Type *a* hinge given above. Of the rectangular teeth that constitute the provinculum one, in particular, is prominent. This is on the posterior of the right valve. There is a tendency for the other teeth to be suppressed, making this tooth even more prominent, the amount of suppression being greater in some species than others. In *S. elliptica* (?) there is little and consequently this posterior right tooth is by no means so prominent. In *S. subtruncata* (?), *S. solida* (?) and *Lutraria lutraria* (?) there is a variable but good degree of suppression and the tooth is very prominent. In MACTRID E the suppression is midway between *S. elliptica* (?) and the others.

The prominent tooth makes it possible to place a larva in the Mactracea at a size (150 μ) which otherwise would be too small for certainty. The species of these larvae have been determined chiefly on the basis of their distribution and there is not much doubt as to the species of MACTRIDS A-D.

MACTRID A (? *Macra corallina* (Montagu)) (++).—The Type *c* hinge immediately separates this species from the other five. In shape it is easily recognized due to the very low umbones and the truncated broad end. The shell is yellowish along the ventral side and the concentric lines are very fine and close set with two or three stronger lines at wide intervals.

MACTRID B (? *Spisula solida* (Linné)) (+).—This is easily recognized by the very well-marked, well-separated concentric lines. The shell has a characteristic rich brown colour due to a chitinous covering of the same type as found in some adult shells of the species. A specimen measuring 360 μ has been obtained. The texture allows identification of this species at 170 μ , possibly earlier.

MACTRID C (? *Spisula subtruncata* (da Costa)) (++).—This has been described by Kändler (1926) and Jørgensen (1946) but in neither case is the description adequate.

There is a distinct dorsal shoulder to the broad end. The smaller larvae are narrower than the other Mactrid larvae of the same length.

The shell has two textures, a surface texture of fine, close-set concentric lines and a deeper texture of concentric markings widely separated. This deeper texture gives the impression of being a much reduced form of texture found in *S. solida* (?). The shell is yellowish and in most, but not all, specimens there is a tinge of rose colour at the narrow end.

MACTRID D (? *Spisula elliptica* (Brown)) (+++).—The truncated broad end and the high umbones are characteristic, the truncation being very clear in the bivalve condition. The concentric lines are fine, tending to group in bands. The shell is yellowish and the larger larvae have rather fragile shells. The largest measured was 355 μ .

MACTRID E (++).—The intact larva was at first mistaken for *M. corallina* (?) which it resembles in shape and texture. The umbo is, however, rather higher and the narrow end is round, rounder than in the other Mactrids and consequently it is more equi-valve than the others. The texture is rather firmer than in *M. corallina* (?) and the concentric lines, though close set, are very distinct. The mactrid tooth appears later; there is no sign of it at 290 μ .

MACTRID F (? *Lutraria lutraria* (Linné)) (++).—The hinge of this larva is very similar to *S. subtruncata* (?) and *S. solida* (?) but it is, nevertheless, difficult to assign it to any species other than *L. lutraria*.

Specimens, believed to be of this species, over 400 μ in size have been found in the recorder material. In these a part (an arc of ca. 20°) of the ventral edges of the two valves curled outwards, leaving a gap when the valves were closed.

There is one more Mactrid larvae than the distribution list of adults will allow. It is much more likely that this extra larva (which we believe to be MACTRID E) is of a species which has been taken to be merely a variety than that it is of a species still to be discovered in the North Sea. The possibility arises that it is the larva of *S. truncata* Montagu and that *S. truncata* is a true species and not simply a variety of *S. solida*. It may be pointed out that many workers have also taken *S. elliptica* to be a variety of *S. solida* (e.g. Jeffreys, 1863) though recent lists give them as distinct species.

Superfamily Tellinacea.

[For references see Jørgensen (1946); in addition Sullivan (1948) has described *Tellina tenera* Say, *Macoma balthica* (L.) and *Cumingia tellinoides* Conrad.]

The basic shape of the larvae of this superfamily is similar to that of the adults. The species of *Tellina* can be distinguished from those of *Abra* by the fact that in the latter the umbones are higher and there is a distinct junction at the meeting of the umbonal sides and the body sides.

This distinction breaks down with the larva of *Tellina tenera* (Sullivan, 1948) which is of the *Abra* type. *Macoma balthica* (Sullivan, 1948), which is also a member of the Tellinidae has, however, the *Tellina* form.

The hinge and its development is described on p. 85 and shown in Text-fig. 3. The sizes placed against the stages in the figure are only a very approximate guide since there is considerable variation. It is possible that the hinges differ in the position of the ligament, the ligament being central, or nearly so, in *Tellina*, between the centre and the anterior end of the provinculum in *Abra* and at the anterior end in *Donax vittatus* (?). It cannot yet be said, however, that this is a definite rule.

Nine species are shown on Plate IV.

Tellina fabula Gmelin (++).—This may be recognized by the slight concavity of part of the dorsal edge of the broad, anterior end. The shell is almost colourless with moderately marked, moderately spaced concentric lines and a distinct pallial line. The larva has been identified by its distribution as in the case of the next larva.

Tellina A (? *T. pygmaea* Loven) (+).—This may be recognized by the angular character of the narrow posterior end. The shell is fairly firm and lightly coloured. The pallial line is distinct.

Tellina B (? *Tellina crassa* Pennant) (+).—In the larger specimen shown in Plate IV the dissoconch has begun to form. The larva is readily distinguished by the well-marked concentric lines on the prodissoconch; on the dissoconch the concentric lines are even more widely separated. Of the North Sea species of *Tellina* only *T. crassa* has strong concentric lines, the other species having fine lines.

Tellina C (1).—This is, presumably, either *T. squalida* (Pult.) or *T. donacina* L.

Abra prismatica (Montagu) (+++).—The *Abra* species are more easily identifiable in the bivalve state than in the single valve. This larva has very faint concentric lines between somewhat stronger lines placed at frequent intervals.

Abra nitida (Müller) (++).—The outline of this larva is more curved than that of *A. prismatica*. The narrow end is relatively longer. The concentric lines are very faint and the sculpturing is less than in the previous larva.

Abra alba (Wood) (+).—The broad end is much broader than in the two previous larvae. The concentric lines are very faint and somewhat irregular.

SPECIES A (? *Gari fervensis* (Gmelin)) (1).—This curious larva has an interesting resemblance in outline to the larva of *Cumingia tellinoides* (Sullivan, 1948).

It is distinctly inequivalve, the right valve being more convex than the left. The side views of both valves are shown in Plate IV, and it will be seen that there is a difference, too, in the concavities on both sides of the umbo, those on the right valve being more pronounced. The shell is fragile and colourless.

An inequivalve larva does not necessarily result in an inequivalve adult (see Solenacea) but such is to be expected unless there is other evidence. Amongst the Tellinacea only *Abra longicallus* (Scacchi) and *Gari fervensis* are distinctly inequivalve and in the former it is the left valve which is the more convex, in the latter the right valve. It is therefore likely that this larva is of *Gari fervensis*.

Jørgensen (1946) suggests, on the basis of egg size, that *Gari* (= *Psammobia*) *fervensis*

has non-pelagic larvae. This may be true and the single specimen found in the recorder material may have been washed up from the bottom. In fact, if *G. fervensis* has pelagic larvae, many more specimens should have been found in the material.

SPECIES B (? *Donax vittatus* (da Costa)) (+).—The texture of this shell is firmer than that of the three species of *Abra* described above. The shell is yellow-brown and usually with rose-red at the narrow end.

Of the remaining species of Tellinacea there should be no difficulty in identifying *Macoma balthica* from the information given by Werner (1939) and Sullivan (1948). *Macoma calcarea* (Chemn.) is non-pelagic (Thorson, 1936).

Suborder ADAPEDONTA.

Superfamily Solenacea.

[For references see Jørgensen (1946); in addition Sullivan (1948) has described *Ensis directus* (Conrad).]

It is considered that the description by Werner (1939) of *Cultellus pellucidus* really is of *Ensis ensis*. There is an easily recognizable difference between the hinge of *Cultellus* on the one hand and that of *Ensis ensis* and *Ensis siliqua* on the other, the hinge of the former being relatively shorter and stronger than in *Ensis*. The *Cultellus* hinge is shown in Text-fig. 3 and may be compared with that given by Werner which is now regarded as the *Ensis* hinge.

A distinctive feature for the group is the external ligament. In *Ensis* this begins to appear about 280 μ and becomes prominent with increasing size. It is shown in Sullivan's photograph of *E. directus*. (This feature in *Ensis* was pointed out to me by Dr. Quayle.) It is not a good diagnostic for *Cultellus* since it appears only in some very large specimens (>350 μ) and even then is not prominent.

It is a curious fact that the three species to be described are inequivalve, the umbo of the right valve being higher than that of the left. This has not been noticed by previous authors, but it is not unimportant since a failure to recognize this feature leads to some confusion in separating small *Cultellus* and *Ensis siliqua*.

Three species are shown on Plate IV.

Cultellus pellucidus (Pennant) (+++).—Described by Jørgensen (1946) and others. The narrow end is pointed and is, or is nearly, upturned. The umbones are pronounced, though that of the left valve is distinctly lower. A larva of 400 μ has been seen but this is an exception. The hinge teeth are present in larvae of 140 μ , or possibly less, in length.

Ensis siliqua (L.) (+).—Described by Lebour (1938). This is not so narrow as *Cultellus* and the posterior end is not so pointed and upturned. The height of the umbones is intermediate between *Cultellus* and *E. ensis*, the right umbo being comparable in height to the left umbo of *Cultellus*.

Ensis ensis (L.) (++).—This is readily distinguished by shape from the other two species. The posterior broad end is shorter and truncated and the larva is broader. The umbones are both low, with the left the lowest. This species is recognizable at 160 μ , possibly earlier.

Solen marginatus Montagu has not been recognized but the only North Sea records of the species are from the Continental west coast.

Superfamily Saxicavacea and Family Myidae.

[For references see Jørgensen (1946); in addition Sullivan (1948) has re-described *Mya arenaria* L.] The hinge structure is shown in Text-fig. 3 and the valves in Plate V.

Mya truncata Linné (+).—This has been described by Jørgensen (1946) as having no hinge differentiation apart from the ligament. The accuracy of this, however, is to be doubted.

The shape agrees with the details given by Jørgensen, particularly in that the umbones are low. In components the hinge is identical with that of *Hiatella*, but the provinculum is thinner and the teeth much less pronounced. This identity extends even to the alternating lateral flanges.

The shell is slightly yellowish round the rim, and thin in comparison with *Hiatella*. The pallial line is comparatively indistinct.

There should be no difficulty in identifying *M. arenaria* from Sullivan's photographs and the hinge structure.

Hiatella arctica (Linné) (+++).—Described by Jørgensen (1946). Sullivan's (1948) description of *H. arctica* actually applies to *H. gallicana* but *gallicana* and *arctica* are sometimes taken to be merely varieties of one species, e.g. by Johnson (1934) whose nomenclature Sullivan has adopted.

This has a tough shell with a firm pallial line which is very noticeable even in intact bivalves. The shells have a yellowish colour round the rim, the concentric lines becoming better marked and more widely spaced away from the apex. The largest measured was 380 μ .

Hiatella gallicana (Lamarck) (++).—Described by Jørgensen (1946) and by Sullivan (1948) as *S. arctica*.

This is a rounder larva than *H. arctica* and the shell is thinner.

SPECIES A (? *Panomya arctica* Lamarck) (I).—In texture the strong shell is very similar to that of *H. arctica* but with a deeper colour. The pallial line is prominent.

SPECIES B (+).—The shell is fairly strong with moderately marked, moderately set concentric lines towards the margins. The shell is slightly yellow outside the fairly well-marked pallial line.

SPECIES C (I).—The shell is fairly strong with concentric lines fine and close set towards the umbo and more widely spaced towards the rim (230 μ). The shell is yellowish outside the well-marked pallial line.

From Sullivan's (1948) photographs it can be said that *Mya arenaria* is not included in SPECIES A-C; neither can we fit any one of them to *Saxicavella jeffreysi* Winckworth as described by Jørgensen (1946, p. 303), but this identification is not certain. According to Haas' list there remain the following species in the North Sea: *Sphenia binghami* Turton (English coast only) and *Panomya arctica*. One must allow, however, for a further possibility in *Hiatella pholadis* (Linné) which is not accepted as a species by Haas (1926), is given as a doubtful one by Winckworth (1932) and accepted by Dautzenberg and Fischer (1912).

It is suggested that SPECIES A is *Panomya* on the basis of its texture. SPECIES B has been found chiefly off the Aberdeenshire coast which, following the distribution given by Haas, eliminates *Sphenia*. There is an impressive resemblance between the shapes of *H. arctica*, *H. rugosa* and SPECIES B, with *H. rugosa* forming the central type. While one cannot, of course, press the point, the interesting possibility that SPECIES B is *Hiatella pholadis* cannot be overlooked.

The identification of SPECIES C must remain unsuggested. Were it not for Jørgensen's (1946) drawing it would have been suggested that it is the larva of *Saxicavella jeffreysi*.

Family Aloididae.

Aloidis gibba (Olivi) (+).—This has been indirectly identified by Jørgensen (1946), but his drawing bears little resemblance to the photograph on Plate V and much resemblance to some of the *Cardium* spp. (Plate II). The shape of our larva so clearly recalls that of the adult that it is very unlikely that the present identification is incorrect.

It is inequivalve, the umbonal region being more pronounced in the right valve (from about 150 μ) and is very convex, almost as convex as it is broad.

The inside view of the hinge at 250 μ is shown in Text-fig. 3. The dorsal view has, unfortunately, been obtained only for larvae no larger than 190 μ .

The concentric lines and the pallial line are well marked.

The resemblance between this larva and the adult *Aloidis* is so marked that it may seem surprising that Jørgensen selected another larva as being this species. However, Boysen Jensen (1919) found that *Aloidis gibba* breeds (or a new brood appears in the bottom fauna) very seldom, and it is therefore possible that, though the adult is fairly common in the Sound, no larvae appeared in Jørgensen's collections during the period of his investigations.

Superfamily Adesmacea.

Family Pholadidae.

[For references see Jørgensen (1946); in addition Sullivan (1948) has described *Zirfaea crispata*]. Four species are illustrated in Plate V. The typical pholad hinge, which is recognizable at 150 μ , possibly earlier, is shown in Text-fig. 3.

Zirfaea crispata (Linné) (+ +).—The larva is characterized above 300 μ by a ventral notch, with teeth, discussed by Werner (1939). The larva becomes more convex with increasing size. The shell is yellowish, particularly round the rim. Concentric lines are moderately marked, close set, with somewhat stronger lines set at frequent intervals.

PHOLAD A (? *Pholas dactylus* (Linné)) (+ +).—This is not easy to separate from *Zirfaea* at sizes less than 300 μ . It is, however, more truly round than *Zirfaea*. In *Zirfaea* the breadth is very slightly greater than the length whilst in this larva the length is slightly the greater. The texture is like *Zirfaea*.

PHOLAD B (? *Barnea candida* (L.)) (+).—This is a deep larva with distinctive shape. The shell is almost colourless. There are frequent well-marked concentric rings with finer rings in between. One larva measuring 260 μ had a ventral notch as in *Zirfaea* but this may have been the result of unusually early development.

PHOLAD C (? *Xylophaga dorsalis* (Turton)) (+).—This is of the same type as PHOLAD B, but the corner on one side is more towards the centre of the breadth.

PHOLAD A resembles Kändler's (1926) *Pholad* spp. which he believed to be *Pholas dactylus* or *Zirfaea crispata*. Since the latter is now known it is likely that this species is *Pholas dactylus*. Jørgensen (1946) has described *Barnea candida* which is very similar to PHOLAD B. The prodissoconch on a young *X. dorsalis* has the type of shape to which PHOLAD B and PHOLAD C conform, and it is therefore believed that PHOLAD C is this species.

Family Teredinidae.

[See Jørgensen (1946); in addition Sullivan (1948) has described *T. navalis* L.]. A single species is shown in Plate V and the hinge in Text-fig. 3.

Teredo sp. (2).—This is a convex larva with opaque, brownish shell. The concentric lines are very distinct and well spaced. The larva is characterized by radial rays which are very distinct. Sullivan's photographs clearly show that this is not *Teredo navalis*. Jørgensen has described *T. megotara* (Hanley) and Lebour (1938) *T. norvegica* (Spengler). Neither, however, mention the radial rays. The only other North Sea species is *T. bipinnata* (Turton) from the English coast.

ORDER ANOMALODESMATA.

Superfamily Pandoracea.

Three larvae with shapes sufficiently distinct to show that they belong to different genera have the same type of hinge structure. It seems probable, therefore, that they are representa-

tives of the Anatinacea; the hinges of every other superfamily in the North Sea with three or more genera have been described above. The three larvae are shown in Plate V and the hinge in Text-fig. 3 and described on p. 86.

(? *Thracia* sp.) (+).—The shell is colourless, the concentric lines and pallial line poorly marked. The larva is slightly inequivalve, the right umbo being the more pronounced.

(? *Cochlodesma praetenue* (Montagu)) (1).—This was identified to the genus by its resemblance to the prodissoconch of a young *C. praetenue*, which is the only North Sea species.

The concentric lines are fairly well marked and closely set. The provincular projection is rough and appears toothed on inside view.

(? *Lyonsia norvegica* (Gmelin)) (++).—This larva has a very fragile shell, a feature in keeping with the adult character of the suggested species. Larvae of 300 μ are slightly inequivalve, the right umbo being very slightly the more pronounced.

Corresponding to the fragility of the larva the hinge is weakly developed and the provincular projection of the right valve is very small, even at a size of 260 μ .

Sullivan (1948) gives a photograph of the spat of *Pandora gouldiana* (Dall) in which the prodissoconch shape is shown very clearly. This establishes the generic shape of *Pandora* larvae.

Superfamily Poromyacea.

A larva which apparently belongs to this superfamily is shown on Plate V and the inside view of the hinge of a 300 μ larva in Text-fig. 3. The 300 μ larva has two or three well-marked concentric lines, the rest of the lines being faint. There is no further information.

APPENDIX.

A short list is given below of the synonyms used by Winckworth (1932) and by Haas (1926).

Winckworth.	Haas.
<i>Musculus niger</i> (Gray)	= <i>M. discrepans</i> (Leach).
<i>Chlamys distorta</i> (da Costa)	= <i>Hinnites pusio</i> (L.).
<i>Astarte montagui</i> (Dillwyn)	= <i>Astarte compressa</i> (Mont.).
<i>Astarte elliptica</i> (Brown)	= <i>Nicania banksii</i> (Leach).
<i>Cyprina islandica</i> (Linné)	= <i>Arctica islandica</i> (L.).
<i>Myrtea spinifera</i> (Montagu)	= <i>Lucina spinifera</i> (Mont.).
<i>Phacoides borealis</i> (Linné)	= <i>Lucina borealis</i> (L.).
<i>Mysella bidentata</i> (Montagu)	= <i>Montacuta bidentata</i> (Mont.).
<i>Montacuta ferruginosa</i> (Montagu)	= <i>Tellinmya ferruginosa</i> (Mont.).
<i>Cardium ovale</i> Sowerby	= <i>Cardium fasciatum</i> Mont.
<i>Cardium crassum</i> Gmelin	= <i>Cardium norvegicum</i> Spengl.
<i>Cardium scabrum</i> Philippi	= <i>Cardium nodosum</i> Turt.
<i>Venus striatula</i> (da Costa)	= <i>Venus gallina</i> (L.).
<i>Mysia undata</i> (Pennant)	= <i>Lucinopsis undata</i> (Penn.).
<i>Gafrarium minimum</i> (Montagu)	= <i>Gouldia minima</i> (Mont.).
<i>Paphia Röding</i>	= <i>Tapes</i> Meg.
<i>Mactra corallina</i> Montagu	= <i>Mactra stultorum</i> L.
<i>Tellina pygmaea</i> Lovén	= <i>Tellina pusilla</i> Phil.

Winckworth.	Haas.
<i>Abra</i> Lamarck	= <i>Syndosmya</i> Recluz.
<i>Gari fervensis</i> (Gmelin)	= <i>Gari ferroensis</i> (Chemn.)
<i>Solen marginatus</i> Montagu	= <i>Solen vagina</i> L.
<i>Hiatella</i> Bosc	= <i>Saxicava</i> Bellevue.
<i>Hiatella gallicana</i> (Lamarck)	= <i>Saxicava rugosa</i> (L.).
<i>Panomya arctica</i> (Lamarck)	= <i>Panomya norvegica</i> (Spengl.).
<i>Saxicavella jeffreysi</i> Winckworth	= <i>Saxicavella plicata</i> (Mont.).
<i>Aloidis gibba</i> (Oliv.)	= <i>Corbula gibba</i> (Oliv.).

SUMMARY.

1. A method of identification of lamellibranch larvae, based entirely on the shells of larvae which have developed beyond the veliger or "D-shaped stage," is described.

2. The characters of use are shape, hinge and texture.

3. The shapes of allied species are variations of a shape characteristic for the group. Since two or more groups of allied species may have a similar basic shape a classification of larvae by shape only is not satisfactory.

4. All pelagic larvae above a certain size (150μ or less) have a hinge. By reference to some simple components all hinges can be reduced to a limited number of basic types. Classification of larvae by hinges results in a classification closely parallel to a classification of adults.

5. Generalizing, a larva can be assigned to a superfamily by its hinge, to genus and species by its shape, and its texture can sometimes be used to aid identification to species.

6. Seventy-seven types of North Sea lamellibranch larvae are described.

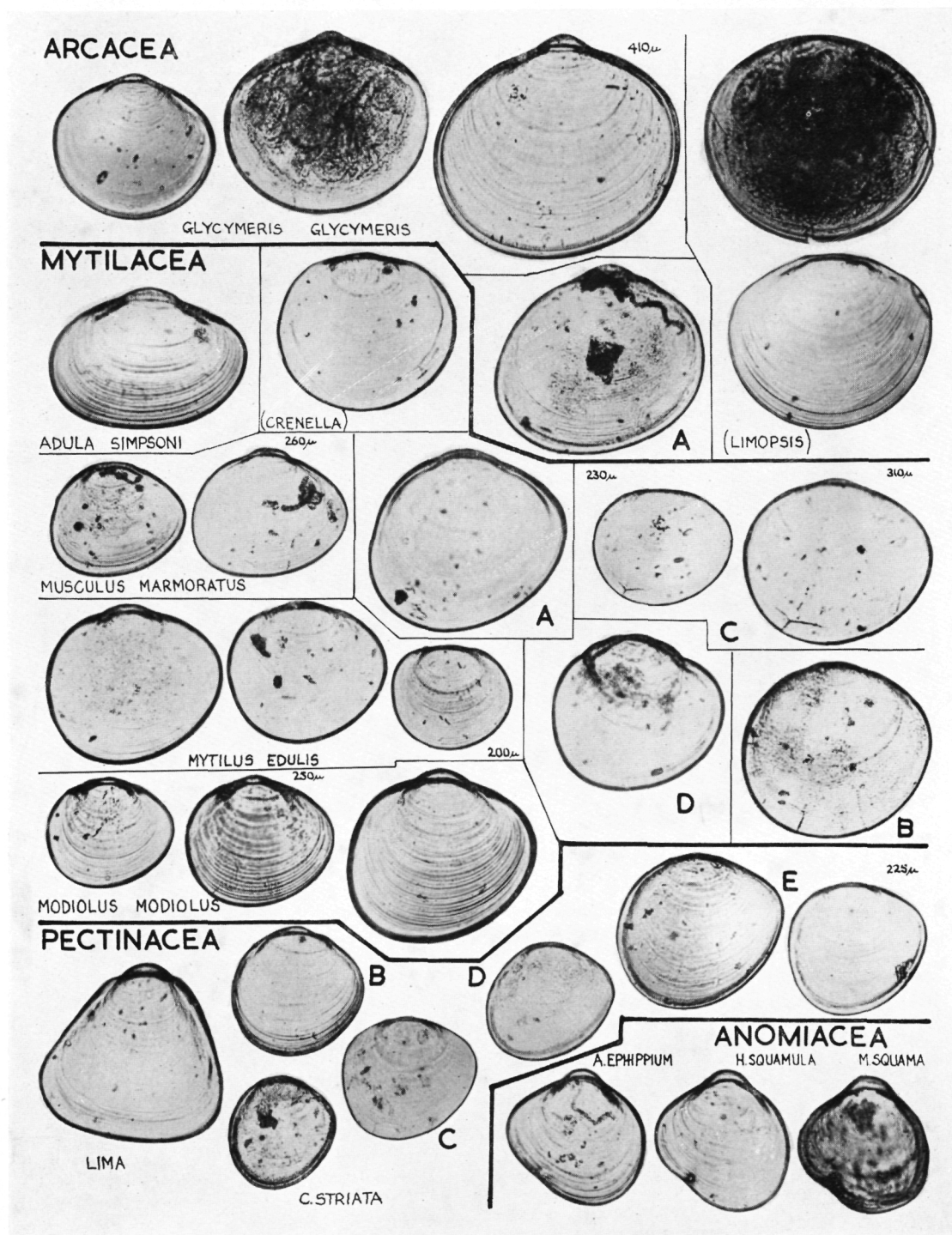
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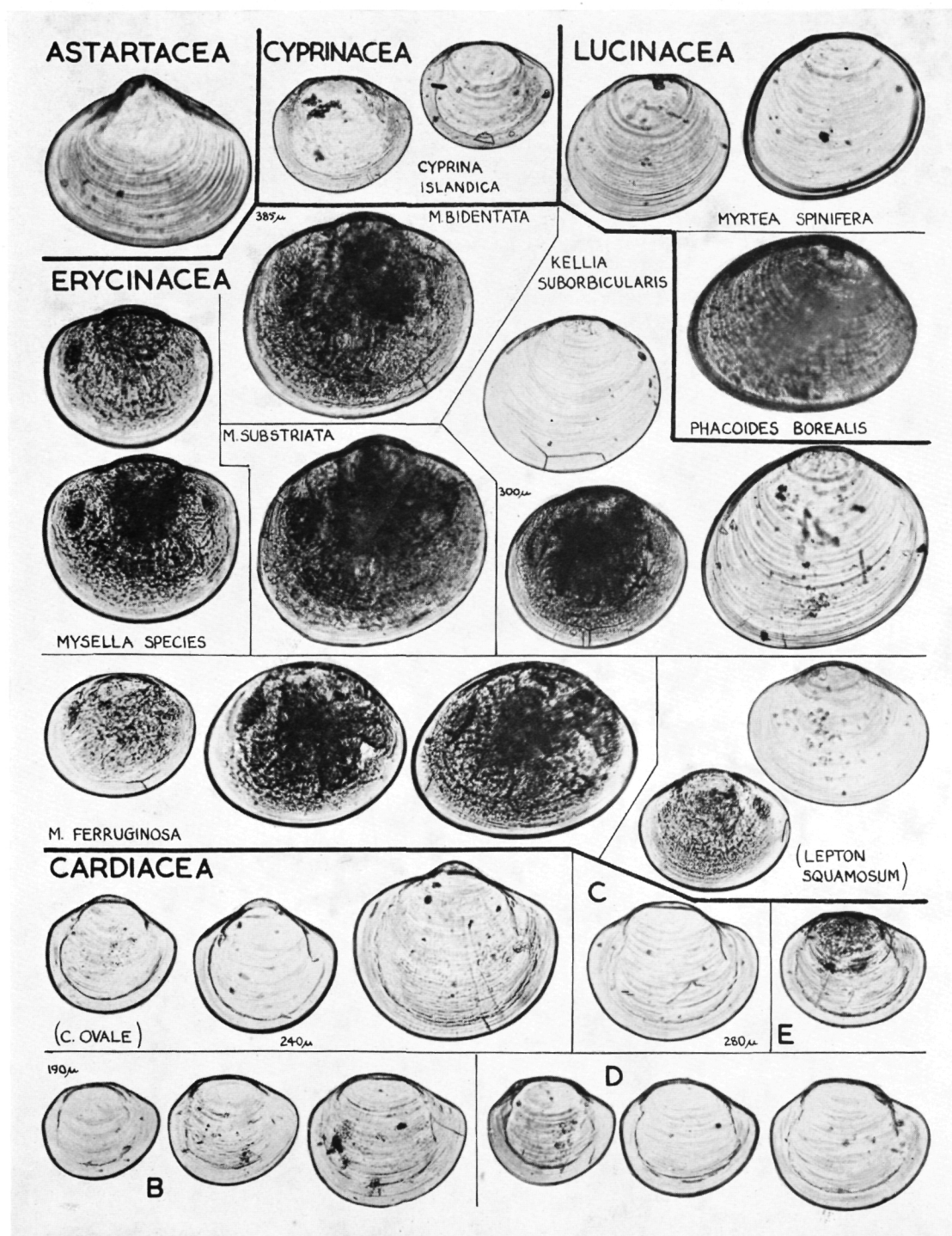
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EXPLANATION OF PLATES I-V.

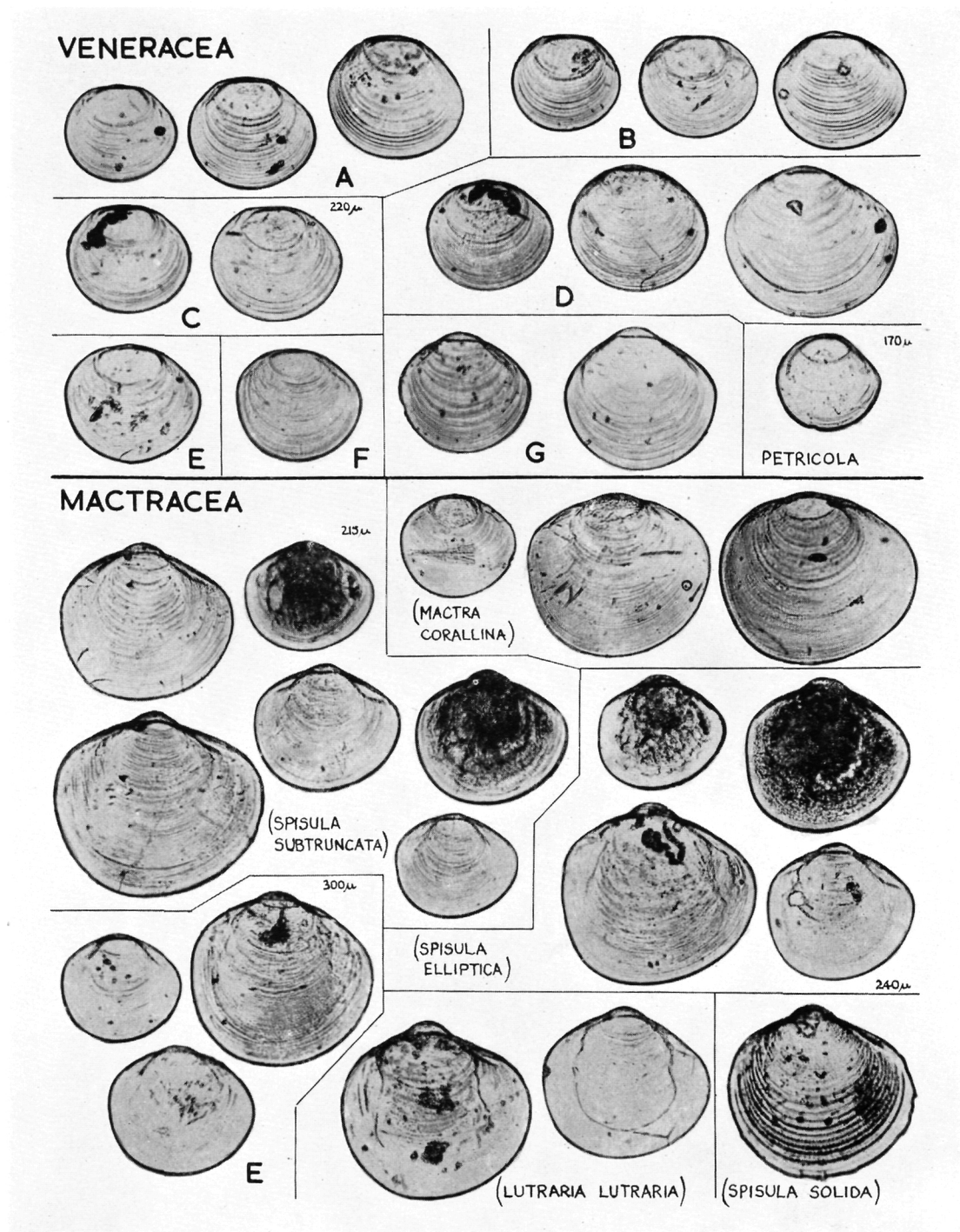
Photomicrographs of lamellibranch larvae grouped into superfamilies or families. The photographs are all equally enlarged ($\times 90$) and the lengths of a few of the larvae are given on each plate. It should be noted that identifications in brackets are less certain than the others, as explained on p. 88.



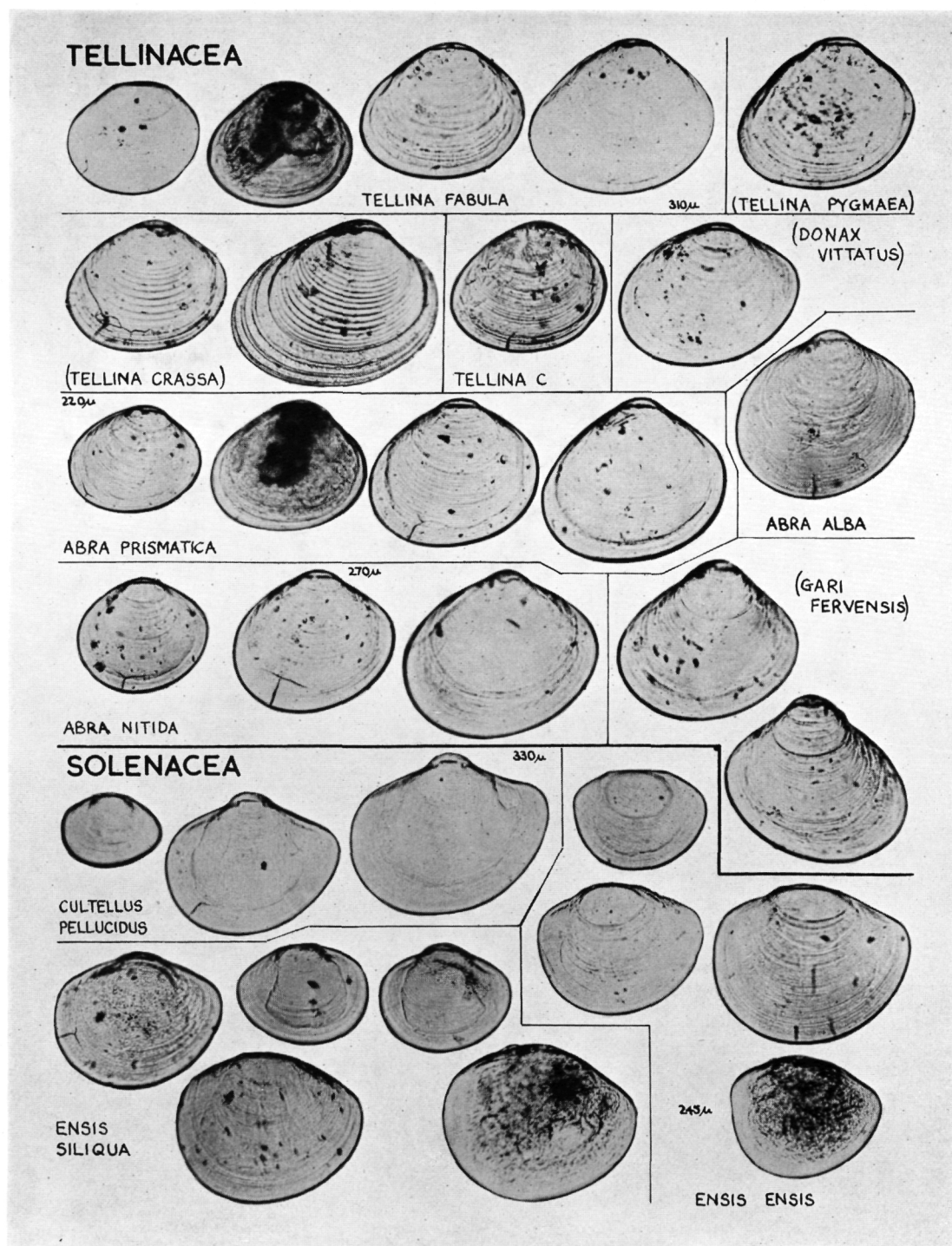
Larvae of the Arcacea, Mytilacea, Pectinacea and Anomiacea.



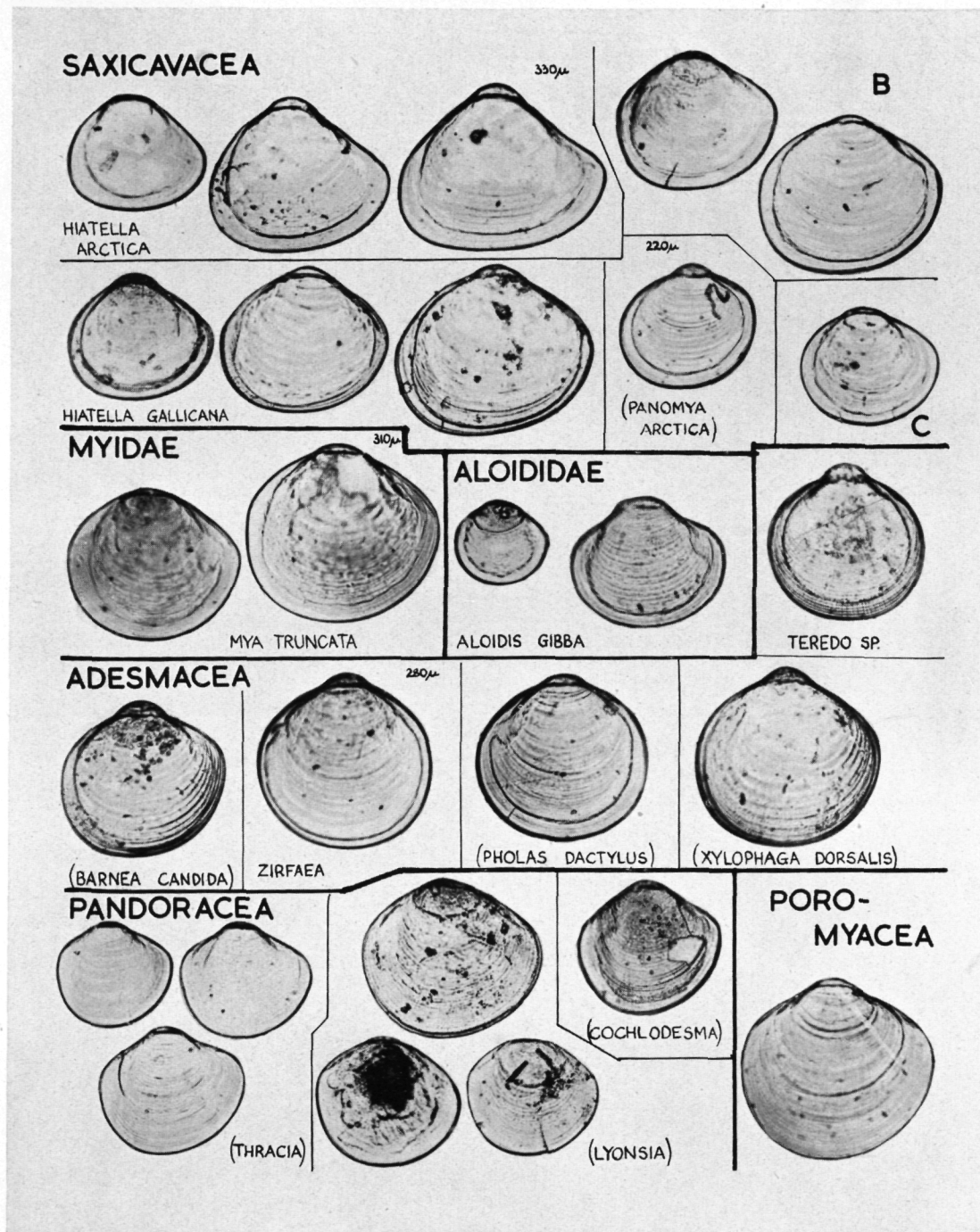
Larvae of the Astartacea, Cyprinacea, Lucinacea, Erycinacea and Cardicea.



Larvae of the Veneracea and Mactracea.



Larvae of the Tellinacea and Solenacea.



Larvae of the Saxicavaceae, Myidae, Aloididae, Adesmaceae, Pandoraceae and Poromyacea.

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