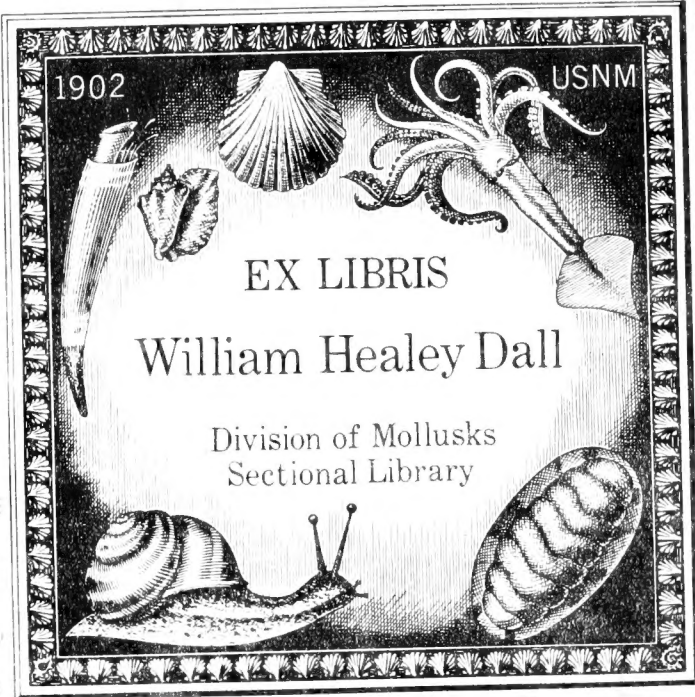
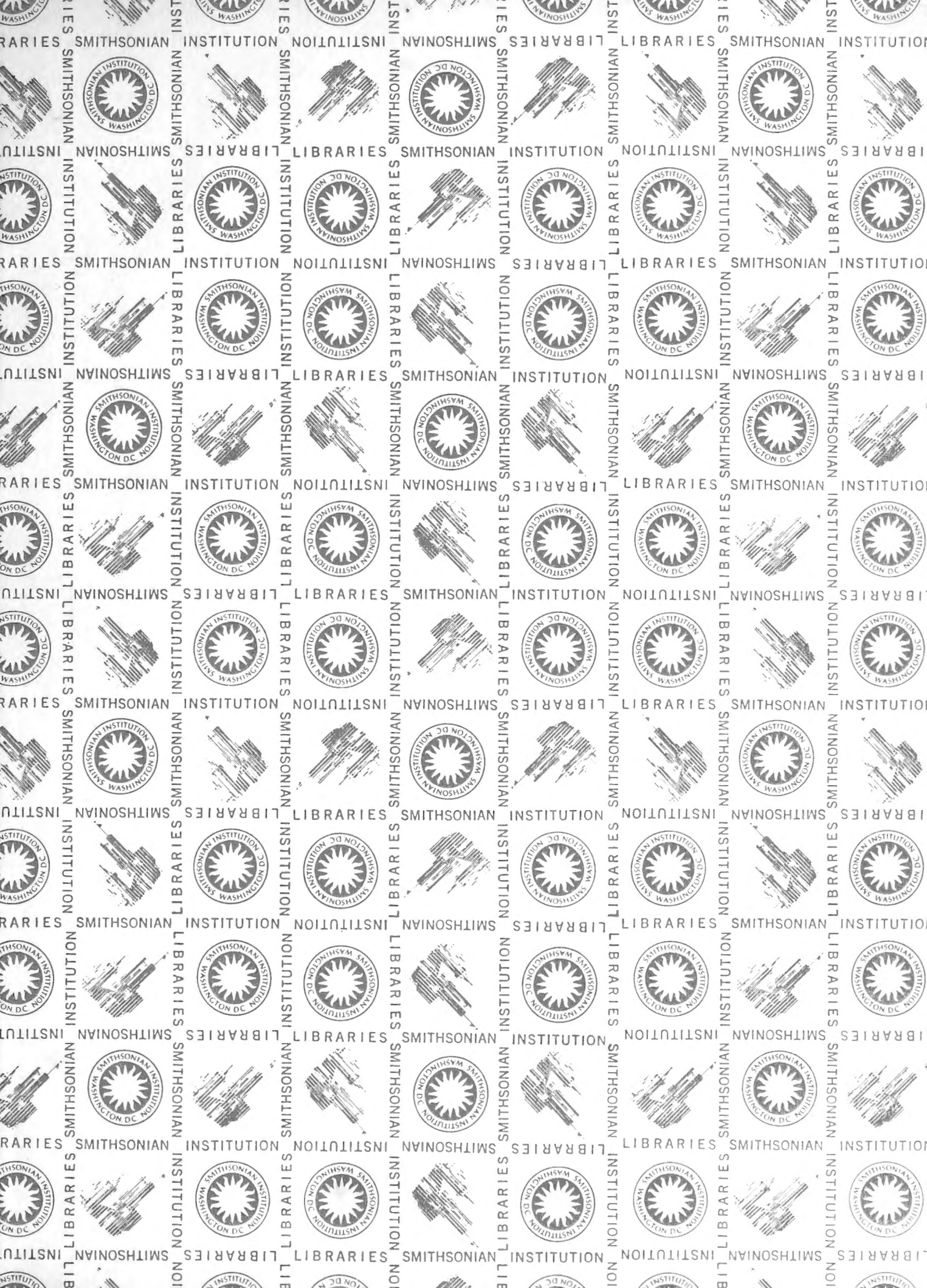


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PHYLOGENY OF THE PELECYPODA,

THE AVICULIDÆ AND THEIR ALLIES.

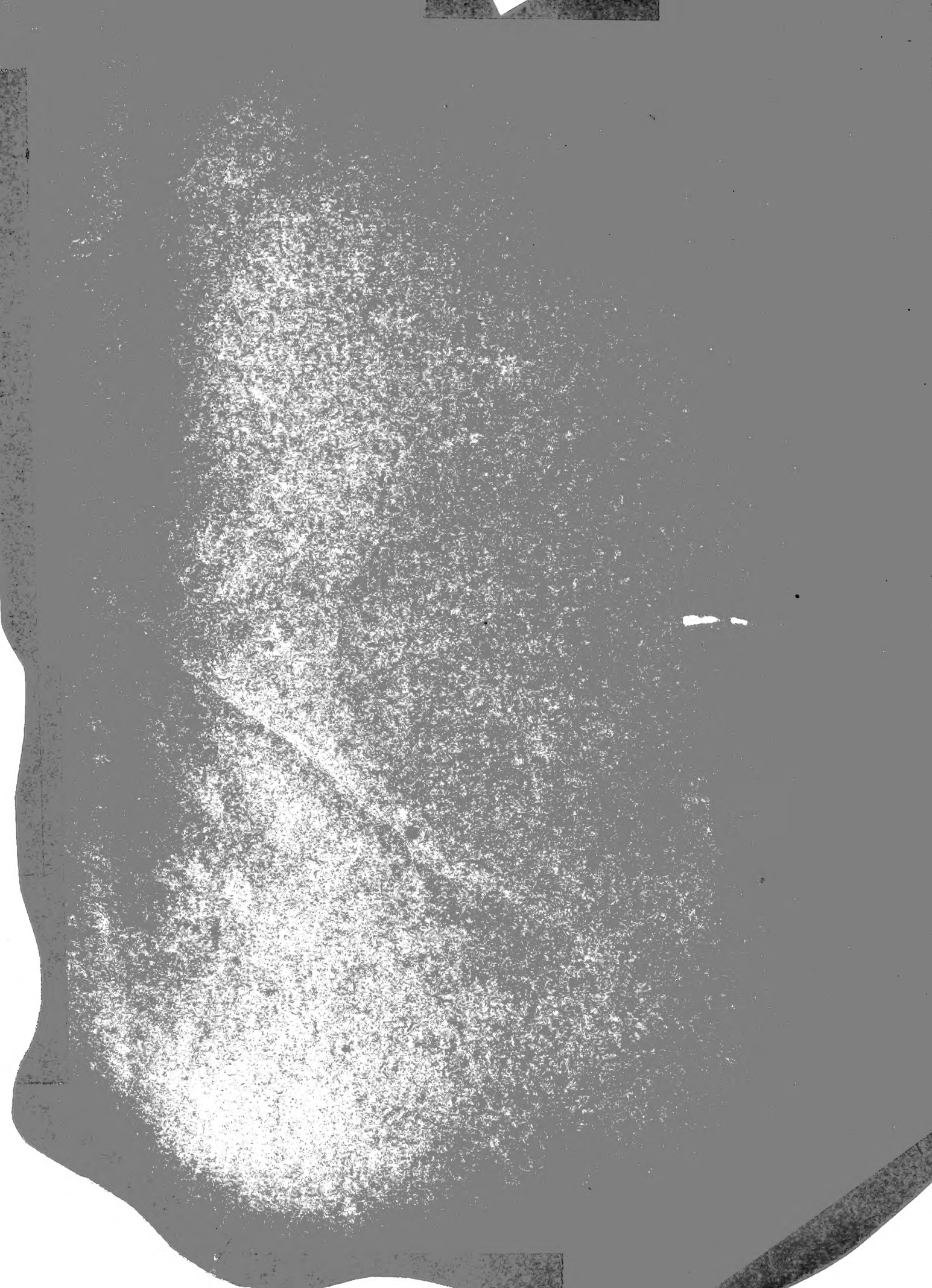
PLATES XXIII—XXX.

By ROBERT TRACY JACKSON, S. D.

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VIII. PHYLOGENY OF THE PELECYPODA.

THE AVICULIDÆ AND THEIR ALLIES.

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BY ROBERT TRACY JACKSON, S.D.

CONTENTS.

I. Introduction	p. 277	IX. Pecten : anatomy and habits	p. 333
II. Sources of material and methods of work	p. 284	X. Pecten : the shell	p. 342
III. Classification of stages of growth and decline	p. 288	XI. Genera allied to Pecten	p. 350
IV. Ostrea : development of the soft parts ; embryology	p. 294	XII. Anomia : anatomy and habits	p. 354
V. Ostrea : development of the soft parts ; the spat	p. 303	XIII. Anomia : the shell	p. 359
VI. Ostrea : development of the shell	p. 311	XIV. Studies of a few other genera	p. 362
VII. Gryphæa, Exogyra and adult Ostrea, with a consideration of the mechanical origin of the ostrean form of shell	p. 317	XV. On the genetic relations of the Prodissoconch	p. 375
VIII. Perna, Avicula and near allies	p. 327	XVI. Genealogical connection of the Aviculidæ and their allies	p. 379
		XVII. List of papers quoted or referred to in the text	p. 394
		XVIII. Description of plates.	p. 395

I. INTRODUCTION.

MY palæontological studies have been carried on at the Museum of Comparative Zoology as a pupil and assistant, first of Professor Nathaniel S. Shaler and later of Professor Alpheus Hyatt. To these gentlemen first are due my acknowledgments in this paper, which was offered as a thesis for the degree of Doctor of Science at Harvard University May 1, 1889.¹ Acknowledgments are next due to Mr. Alexander Agassiz for the opportunity to study the collections in the Museum.

The investigations on which this paper is based were made while associated with Professor Hyatt in the Palæontological Department of the Museum.² I have applied some of the principles which he has deduced as a result of his scientific work, but I wish to state that he has never urged his views upon me, or pointed out their application in the Pelecypods. At Professor Hyatt's special request, I have used entire freedom in rejecting or criticising his views whenever they seemed not in accordance with the facts presented.

¹On account of new material obtained, some additions have been made to this paper since it was read before the Society on April 3, and since it was offered as a thesis on May 1, 1889. The additions for the most part

have been made to sections VIII and XIV, and are indicated by the date of the collecting of the material.

²Three years have been spent in that department assisting Professor Hyatt arranging the great collections of Fossil Invertebrates.

For the freest opportunity to study collections under their charge and for frequent assistance while studying those collections my obligations are due to Dr. C. A. White and Dr. William H. Dall of Washington; Professor Angelo Heilprin of Philadelphia; Professor R. P. Whitfield of New York; Dr. J. Walter Fewkes and Mr. Samuel Henshaw. For material borrowed for study, I am indebted to Dr. White, Dr. Dall, the Museum of Comparative Zoölogy, the State Museum of New York and the Boston Society of Natural History. I have to thank Colonel Macdonald, United States Commissioner of Fisheries, for the electrotypes of figures of *Ostrea edulis* and Professor A. E. Verrill for electrotypes of *Vermetus*, *Pecten* and *Anomia*.

In order to unravel with any reasonable hope of success the relationships of the multitude of fossil forms of animal life in which only the hard parts are commonly preserved, and to demonstrate the connection between the living and fossil representatives of allied groups, it is most important to study with minute care the hard parts in living genera. It is necessary to know as far as possible the structure, development and functional expression of the hard parts, both by themselves and in their relation to the soft parts. To attain this end, studies of any given animal should be made on all stages of growth from the embryonic upward, and in so far as the young is considered as a living expression of the adults of ancestral groups, this period of the life-history must be studied with special care.

On the value of anatomy and embryology to the palæontologist studying the affinities of groups I would quote the following passage from Professor Huxley's *Anatomy of Invertebrated Animals*, p. 587. "Already indications are not wanting that the vast multitude of fossil Arthropods, Mollusks, Echinoderms and Zoöphytes, now known, will yield satisfactory evidence of the filiation of successive forms, when the investigations of palæontologists are not merely actuated by the desire to discover time-marks and to multiply species, but are guided by that perception of the importance of morphological facts which can only be conferred by a large and thorough acquaintance with anatomy and embryology. But, under this aspect, the palæontology of the *Invertebrata* has yet to be created."

The results of my investigations give abundant proofs that a study of the soft parts and especially studies of life habits and environing influences will throw light on the meaning of the form of hard parts. They all lead toward the conclusion that external hard parts are built conforming to the needs of the animal and are modified by circumstances of environment. Many facts discussed in this paper are directly opposed to the assumption that hard parts are of prescribed form, to which the animal adapts itself, as I have found most active response in the form of hard parts to changed or changing conditions of the anatomy or habits of the animal. The changes in form thus introduced might well be called cases of "mechanical genesis," adopting Professor Ryder's apt phrase used of the development of toothed forms in Vertebrates.¹ When the meaning of features of shell form in living animals is ascertained, it is recognized that they make important factors in the consideration of fossils and the serial connection of groups.

To unite living and fossil forms of a group of Pelecypoda in a common study is the

¹ Facts bearing on this point are especially considered in the origin of the ostrean form of shell (section VII),

and in the discussion of *Perna* (section VIII), *Pecten* (sections IX and X), and *Anomia* (section XII).

aim of this paper. It is hoped by this means to make connections and differences existing between some genera better understood, and thus to further the knowledge of the relationships of those genera. So much time has been given to the study of living forms that fossils do not figure as largely as they should in a paper of this nature. It is hoped, however, that in future this want may be supplied by investigations in that direction.

The main line of my research is the *study of shell structure and form*. Studies of anatomy and habits are subservient and correlative to those of the shell. Facts observed that have no bearing on shell structure are however frequently given as they may yet be of interest or of serial value. In studying the shell I have sought especially for young shells hoping in them to find characters of interest which would be valuable in attempting to trace the genetic connection of groups. It is to this study of the young, that Professor Hyatt has especially devoted himself in his researches among the Cephalopods, and I owe a debt of gratitude to him for the suggestion to try the same method of research in Pelecypods, as well as for the encouragement and sympathy he has given me in my work.

The young shell of Pelecypods has been very little studied either by itself or in its relation to later stages, and I know of no studies embracing observations on the development of the shell in related genera, or any attempt to trace the connections between the changes of shell form and anatomy during the development of the individual. In Zittel's Palæontology (Barrois' translation) we find in the consideration of the Pelecypoda the following statement: "Quant aux modifications des coquilles à leurs différentes âges, elles n'ont été que bien peu étudiées jusqu'ici, et ces observations n'ont pas encore mises à profit dans la systématique." The researches of this paper may therefore be considered as opening up a new field of investigations, as I consider not only the changes in form and structure observed at different periods of development in several genera, but also trace in many cases the serial connection between those changes in form and the phylogenetic history of the group.

Pelecypods are commonly divided into three groups accordingly as the adults possess a single adductor muscle, Monomyarians; two equally developed adductor muscles, Dimyarians; or two adductor muscles, one large and functionally the most active, the other smaller, Heteromyarians. This classification, I believe, is misleading, as by it are grouped together genera having no close relation and similarly genera closely akin are separated. I show that the size and number of the adductors are closely connected with the relative position of the axes of the body to the hinge axis (section v), and refer to the fact that the single adductor condition is adopted by several genera not related and which it would be entirely disregarding the sense of systematic classification to group together. On this basis of adductor muscle classification even different species of one genus would in one case have to be placed in the Heteromyarians and in another in the Monomyarians (see *Mytilus*, section v, note). The words monomyarian, etc., are occasionally used in the text, but as general descriptive terms, not with the classificatory value ordinarily applied to them.

In the text frequent reference is made to the law of concentration and acceleration of

development. This law was enunciated separately and almost simultaneously by Professors Hyatt (29)¹ and Cope. The law is, *that characteristics acquired in the adult, if inherited at all, are inherited at earlier and earlier periods in successive generations, until they exist only in embryonic stages, or are completely lost through disuse and concentration and acceleration of development.* This law finds strong support in the facts presented in the development of the oyster and other Pelecypods as well, where many peculiarities occur which are well explained by it. A corollary of the law of concentration and acceleration of development is that, *in the young stages are found the equivalents of which are to be sought in the adults of related groups.*

I have met with difficulty in procuring young specimens of Pelecypods to study, for the most part depending on what I collected in the field or found adhering to masses of shells in the museums. Conchologists commonly pay little attention to the young in their collections as they are not considered characteristic. They certainly are not characteristic, in that they have not a full expression of features found in the adult, but they are characteristic of their period in the development of the individual and from this point of view they are well worth collecting and studying carefully.

In section III Professor Hyatt's classification of stages of growth and decline is considered in its application to mollusca. I have there qualified some of his definitions and introduced a new term, *phylembryo*, which is applied to the stage in development where features exist which first render the embryo referable to the class or phylum to which it properly belongs. In considering stages of growth it is a valuable assistance to have an established nomenclature by which any given period may be briefly and definitely expressed, and that given in this paper seems to fill the requirements of such a nomenclature.

The phylembryonic stage of developing Pelecypoda presents some striking features which have not been previously considered as far as known. The shell of this period is characterized by having a straight hinge line as shown in many genera (fig. 25, p. 300, Pl. XXIII, figs. 7-11 and Pl. XXIV, figs. 13-15), although later succeeded by a curved one. An important point is the fact that at this age but one adductor muscle exists, and that one is destined to become the anterior adductor of adults which retain it (dimyarians). The posterior adductor is developed later. The mouth and anus in early embryonic stages of Pelecypods are closely related on the ventral border of the embryo (fig. 23, p. 299) and the anterior adductor muscle develops early on the dorsal side of the alimentary canal (fig. 25, p. 300; Pl. XXIII, figs. 9-11) which position it retains throughout life, in dimyarians. The posterior adductor is not developed until the anus has revolved dorsally from its early ventral position, and then the adductor is formed on the ventral side of the alimentary canal, which position it retains throughout life in all Pelecypods. We see, therefore, in this an explanation of the relation of the adductor muscles to the alimentary canal, one adductor overlying, the other underlying it, Pl. XXV, figs. 9-12 (for full discussion see section V).

¹A list of publications quoted or otherwise referred to is given in section XVII. Where the reference in the text is not perfectly evident, a number in brackets is used which

as in this case corresponds with a number on the reference list.

One of the most important discoveries described in this paper is the existence in young Pelecypods of an *embryonic shell, or prodissoconch comparable to the embryonic shell or protoconch of cephalous molluscs*. The shell of Pelecypods develops from a preconchylian gland, as does the shell of cephalous molluscs; therefore, the two valves of a Pelecypod are together homologous with the single valve of univalves as was shown by Brooks (7). The adult shell of cephalous molluscs has been named the conch, or true shell, and the first formed embryonic shell on account of its differences the protoconch; as the adult double shell of Pelecypods is the homologue of the adult single shell of univalves I have named it the *dissoconch* (double shell); similarly the early embryonic double shell on account of its differences I named the *prodissoconch* (early double shell). A prodissoconch is described in this paper in twenty-four genera of Pelecypods,¹ figures of most of which are given in the plates. It has been found in many species of some genera. These genera are widely separated so that it may be considered as proven that a prodissoconch is a characteristic feature of developing Pelecypod shells (discussion and descriptions, sections VI to XV inclusive).

In the discussion of the prodissoconch it will be seen that stress is laid on the direction of the umbos, as to whether they are inclined anteriorly or posteriorly relatively to the anatomy of the animal at the close of the prodissoconch period. I find that they are inclined posteriorly in *Avicula*, *Perna*, *Ostrea*, *Pecten*, *Spondylus*, *Plicatula* and *Anomia*. On the contrary they are inclined anteriorly in the other genera described except the *Unionidæ*. The value of this feature may be overrated, but I think it is of importance in considering the connection of genera and the derivation of the prodissoconch (section XV).

In considering what value is to be attached to inclination of the umbos, attention should be called to two singular, ancient palæozoic genera, *Antipleura* and *Dualina*, described by M. Barrande. In single species of these genera series of specimens may be picked out in which the umbos are inclined in one direction, and other series may be picked out in which the umbos are inclined in the opposite direction; the two series being apparently identical in every other character. This is a puzzling case, seemingly opposed to all natural laws. M. Barrande figures large numbers of specimens illustrating the two series, and I have studied them in the Schary collection of fossils from Bohemia, now in the Museum of Comparative Zoölogy). Ordinarily, however, the inclination of the umbos is a constant character and therefore I think it is not a mistake to consider it a feature of serial value as I have done in the text.

The prodissoconch of *Ostrea*, *Perna*, *Pecten*, *Anomia* and allies, is composed of homogeneous sub-nacreous lime showing no prismatic cellular layer, fig. 27, section VI, the first stages of the dissoconch growth on the other hand in these genera possesses a prismatic cellular structure making a marked contrast in histological structure with the

¹Previous to the publication of my preliminary paper, an early embryonic shell and its relations to the succeeding shell had been described at some length by Ryder in the oyster, briefly by Morse in *Anomia*, and briefly by Lacaze-Duthiers in *Mytilus*. With these exceptions I believe my descriptions are the first concerning the early embryonic, prodissoconch shell and its relation to the suc-

ceeding dissoconch shell in Pelecypods. In this paper a prodissoconch is described in the following genera: *Ostrea*, several species; *Gryphæa*; *Exogyra*; *Perna*; *Avicula*; *Pecten*, several species; *Spondylus*; *Plicatula*; *Lima*; *Anomia*, two species; *Mytilus*; *Modiola*, *Crenella*; *Argina*; *Unio*; *Margaritana*; *Anodon*; *Sphærium*; *Petricola*; *Scrobicularia*; *Venus*; *Tottenia*; *Mya* and *Saxicava*.

condition in the prodissoconch. In *Mya*, *Modiola*, *Venus* and most other genera studied (section XIV) no prismatic layer was observed in the first stages of dissoconch growth and this difference, with others considered, is deemed sufficient to separate widely these two divisions of genera.

A discovery of much importance is the existence of *two adductor muscles in the prodissoconch stage of Ostrea*, Pl. XXIV, figs. 1-2. From the form of the shell and from analogy, a similar condition is predicated in *Pecten*, *Avicula*, *Perna*, *Anomia*, etc. All these genera possess but one adductor muscle in the adult and it has not been demonstrated before (excepting in *Ostrea* in my preliminary paper) that two exist in the young. Professor Huxley in 1883 showed that the first formed muscle of the oyster (fig. 25, p. 300, this paper) could not be that of the adult and that a new, second muscle to be retained throughout life must develop. On this basis and knowledge of early types of Pelecypods, he argued that *Ostrea* must have developed from a dimyarian ancestry and my discovery of the early two-muscled stage, therefore proves the truth of his assumption (discussion, sections IV and XV, also briefly in other sections on *Perna*, *Pecten*, etc.).

There is commonly little consideration given to the true relations of the axes of the body to the shell in describing Pelecypods. In dimyarians the hinge is dorsal and in monomyarians the hinge area is also considered as dorsal almost universally. Professors Hyatt (28), Brooks (9), Ryder (60) and Lacaze-Duthiers (39), have pointed out the true condition of affairs in *Ostrea* and *Anomia*, where on account of the changed position of the axes of the body the hinge line is anterior, not dorsal. I have endeavored to maintain this more careful consideration of the true relation of parts in my paper and this must be borne in mind in reading the text. For instance, in *Pecten* the hinge line being anterior, the free ends of the valves are posterior and the ears are truly ventral and dorsal, not anterior and posterior as usually described. This changed position of the axes is intimately connected with the relative size of the adductor muscles of the valves; a change in position coinciding serially with the decrease and final loss of the anterior adductor, together with the increase and final exclusive retention of the posterior adductor, as described in section V.

The *Ostreadæ* is a group having a peculiarly modified highly irregular shell which has been a perplexing problem to naturalists in seeking the affinities of the group. As the result of my studies I have come to the conclusion that the *ostrean form of the shell is due to the mechanical conditions of direct cemented fixation*. The proof of the conclusion is that all Pelecypods which are directly attached by the cementation of one valve assume a similar form of growth. The form claimed as the result of cementation of one valve is a concave, highly modified, attached valve and a less modified, commonly much flatter free valve, often differing so widely from the attached valve, as not to be recognizable as belonging to the same species unless found in place. Cementation also apparently induces a camerated structure of the shell. (See Pl. XXV, fig. 8 and Pl. XXVI, figs. 1-15, as proof of the effects of cemented fixation.) *This statement contains important conclusions*, which are discussed in the text (sections VII and XI) but they may be briefly stated here. The normal Pelecypod is bilaterally equivalvular, but when attached this feature is lost, asymmetry replacing the typical condition. The cemented valve is highly modified, the free valve less markedly so; therefore it is the free valve

which retains more of the ancestral features, and to it and the free young, before modifying cementation takes place, we must turn in studying the relationships of attached Pelecypods. It is an animal with one side modified, losing ancestral features; the other side, less modified, therefore retaining ancestral features. The actual change from an unmodified free form to a modified cemented form may be studied in *Ostrea* (Pls. xxiv, xxv), *Hinnites* and *Mulleria* (Pl. xxvi, figs. 3-7) and *Spondylus* (Pl. xxvii, fig. 4). The irregularity of attached shells being due to the condition of fixation we may study their relationships with an entirely new light on the subject, as the irregularity is a character superimposed on any regular form of Pelecypod by special given conditions. The aberrant forms of the *Chamidæ* and their greatly specialized allies the *Rudistæ* (Pl. xxvi, figs. 8-12 and 20) are considered as extremes of modification in the ostrean line of variation. What the mechanical causes of this line of variations probably are, and what they lead to as their highest expression is considered in section VII.

Finding that irregularity commences with the introduction of the fixed period we have a powerful argument in explaining the absence of features in the young dissoconch stages of *Ostrea* which might, if free, have retained the form of related ancestral groups, as is the case in the young of *Perna*, *Pecten*, *Spondylus*, etc. *Ostrea* is cemented at the close of prodissoconch period so that stages of shell growth later than that are all modified. The free valve should retain more ancestral features than the attached valve and this is the case with the oyster. The prodissoconch, the free valve and anatomy of the adult, all unite in characters which refer the *Ostreadæ* to a type, which is *Perna*, or some close ally of that genus (sections v-vii).

I have described the development of the gills of the oyster with some care, as it is but slightly treated of by other investigators of this mollusc. In order to understand the serial development of the several lamellæ and to show the relations of the direct and reflected borders of the filaments, diagrams are given (Pl. xxiv, figs. 6-12) of the development of the gills of *Ostrea*, together with diagrams of adult gills in some related genera.

In *Perna* (Pl. xxvii, figs. 1-3) I find a prodissoconch very closely like that of *Ostrea*; but the initial stages of dissoconch growth show indications of a byssal notch not seen at all in the prodissoconch. This character of a byssal notch originating in the initial stages of dissoconch growth, but not seen in the prodissoconch, is described also in *Avicula*, *Pecten* and *Spondylus* (Pls. xxvii-xxviii, sections viii-xi).

In *Pecten*, interesting facts are presented in regard to the life habits of crawling, byssal attachment and mode of swimming, new points are discussed and the shell is described at length in the young of five species. In all these young I found a prodissoconch with important characters. The first stages of dissoconch growth in four species were found to possess well defined prismatic structure in the right valve whereas this is not known in the adults of these species, and in the extensive researches of Professor Carpenter on shell structure, prismatic tissue was found in only one species of *Pecten*. The *Pecten*s are allied to a group of Pelecypoda which has prismatic structure, in the shell, and it is a highly interesting fact in accord with other conclusions, that in the extreme young this feature exists, though early lost and not seen at all in adults. In the young dissoconch stages of *Pecten* (Pl. xxviii) in many species I find characters in the form of the

shell which are referable in the closest manner to ancestral groups in early geologic times, from which the Pectens were doubtless evolved. The life-history of Pecten shows most strikingly how the phylogenetic history of a group may be traced by the series of stages presented in the early development of the individual (sections IX-X).

Studies were made of young *Anomias* (Pl. XXIX) growing on glass slides and yielded facts of high interest, especially in connection with Professor Lacaze-Duthier's observations on the adult. In the young the three muscles, adductor, posterior pedal and byssal, are widely separated, though in the adult they almost come in contact, rendering their nature ambiguous. The byssus of *Anomia* was seen to originate from a cleft in the foot and in the young consists of separate threads. The calcareous plug is formed by the aggregation into parallel lines of separate disc-like centres of calcification, each centre being comparable to a separate byssal-thread attachment found in ordinary Pelecypoda which have a byssus. These and other points of habits, anatomy and shell structure are discussed in sections XII and XIII.

The section XIV, entitled Studies of a few other Genera, considers the young of *Mytilus*, *Argina*, *Venus*, *Mya*, etc., and is intended principally to show the extension of the prodissoconch to other genera besides those with which this paper is more especially concerned. Brief accounts are given of the young of several genera and a comparatively extended description of the development of the siphon and byssal attachment in *Mya*. The considerations of this section are for the most part of a preliminary nature and it is hoped to give a full description of these and other genera in a future publication.

After studying the prodissoconch in *Ostrea* and its allies, *Pecten*, *Perna*, etc., I have summed up in section XV the evidence of anatomy, shell structure and palæontological occurrence, all of which points towards *Nucula* or a nuculoid form as the probable ancestral type of which the prodissoconch is the representative in the development of these several genera. Passing to the next section (XVI), I have attempted to give in tabulated form the serial relations existing between the genera studied. These two sections may be considered as the culmination, to which the studies of shell growth at different ages of the individual and in related genera have gradually led.

As a matter of technique I would call attention to the benefit received from the use of drain-pipe traps containing glass, as described in section II. By its means attached forms were studied on a transparent medium and free forms of small size were entrapped and easily found.

For the guidance of readers attention is called to the italicized paragraphs on pages 295 and 300. Every care has been used to give full references to all observations borrowed from authors and equal pains have been taken to give full credit to investigators where their observations seemed similar to mine, or to have bearings on the various facts and conclusions discussed. The facts described and inferences from them not specially credited in this paper are my own.

II. SOURCES OF MATERIAL AND METHODS OF WORK.

In the summers of 1887 and 1888, several weeks were spent at a fine collecting locality on Buzzards Bay, which is situated on the southern shore of Cape Cod, from which I walked, or rowed, to my laboratory not far off.

The water of the bay is remarkably clear and pure. It is warmed by the Gulf Stream, and also by rising tides which flow over great areas of sun-heated flats. The water is freshened by Monument River, and by brooks and percolating water entering the bay from the low, gravelly shores.

The site chosen for operations is a low-lying neck of land in the township of East Wareham. At this locality a sand bar is formed by the tide as it rises and flows on the one side to Onset and on the other to Buttermilk Bay. The force of the current is very great and it is a noted spot amongst the fishermen for a "set" or "fall" of oyster spat. On the north side of the neck of land a small sinuosity in the shore line forms an almost enclosed pond which is bare at low tide. The greater part of the young Pelecypoda studied, were obtained on the bar and in this pond. For the use of a temporary laboratory, the bar and the pond, I am indebted to Dr. E. B. Larchar. I am also indebted to him for occasional assistance in prosecuting my work.

In studying forms of animal life that become fixed to foreign bodies during their early stages of development, it is an advantage if they can be induced to attach themselves to transparent media, such as glass or mica, so that they may be studied by transmitted light without disturbance under the microscope.

Several attempts have been made by Ryder (62), Horst and Winslow, but with only very partial success, to secure oysters on glass. As I was anxious, if possible, to get oysters growing on glass, in 1887 I tried several methods to accomplish the desired end, which were described in my paper on "Catching Fixed Forms of Animal Life on Transparent Media for Study." The following method was tried and found successful. On the 15th of July, 1887, at the suggestion of Dr. Larchar, earthenware drain-pipes were partially sunk on the sand bar in an upright position, and loosely filled with broken glass. Six-inch and four-inch pipes were used, and at different elevations above the sand. I did not secure any spat in the four-inch pipes. A six-inch pipe sunk nearly to the level of the bar was successful, but in an unlucky day was filled with sand, and the young oysters buried. Six-inch pipes, reaching about ten inches above the bar, were perfectly successful, and on the glass in them I got large numbers of young oysters. During the summer of 1888 the attempt to get oysters on glass was repeated. On the 18th of July, four six-inch drain pipes were sunk perpendicularly on the bar at the lowest point available at low tide. They stood about fifteen inches above the sand. The last of July, four eight-inch pipes were sunk in a similar position, all were filled loosely with broken glass, and met with entire success. The eight-inch pipes were preferred to other sizes as large pieces of glass could be put in them and the spaces between contiguous plates could be more easily maintained. Long strips of glass, two to four inches wide, the trimmings of glaziers, were used. They were arranged perpendicularly in the pipes, and were readily taken out, examined and cleaned. They were cut as required by one of the rotary, hard steel wheels sold by hardware dealers for that purpose. This size of pipe and glass gave such satisfaction that I should use it in future if occasion demanded to the exclusion of other methods that were tried. Suitable conditions for the success of the undertaking were therefore as follows: (1) a strong tide-way, which would bring plenty of free-swimming fry, and afterwards abundant food for their maintenance; (2)

an area of quiet water within the pipe, in which the fry could settle and attach themselves to the smooth glass; (3) the absolute shutting-out of violent currents which would detach them from their precarious abiding places.

I first found spat on the glass on the 25th of July, 1887, and on the 28th took out a pane 6 by $4\frac{1}{2}$ inches square on which I have counted eighty-two young oysters, as it is still in my possession intact. This was only exceptional in the size of the glass, as other pieces bore nearly or quite as many spat proportionally to their area. Spat were secured in the pipes until the 29th of October, 1887, when few were left, large numbers having dropped off by the natural dissolving action of the sea-water upon the organic cement by which they are attached. In 1888 the first oysters were found on glass on August 1st, and they continued to set into the month of September. The lateness was probably due to the comparative coldness of the summer.

Besides oysters, the young of many invertebrates and algæ attached themselves to the glass, affording admirable opportunities for studying them alive and undisturbed. The following attached invertebrates were noted: *Molgula manhattensis*, Verrill; *Balanus balanoides*, Stimpson; Serpulas, and other tubicolous worms; *Crepidula fornicata*, Lam.; *C. plana*, Say; *Ostrea virginiana*, Lister., in profusion; *Anomia glabra*, Verrill, nearly as abundant as the oysters; *Pecten irradians*, Lam., attached by a byssus, both very young and quite large individuals, varying from 4 to 13 mm. in height; *Modiola plicatula*, Lam., attached by a byssus; *Argina pexata*, Gray, attached by a byssus; *Membranipora pilosa*, Farre, often in large sheets; *Escharella variabilis*, Verrill.¹

The drain-pipes formed a sort of trap, into which many free-moving, crawling, or swimming molluscs found their way. When in the pipe they would have some difficulty in getting out, and much valuable material was thus obtained. The following Gasteropods were found entrapped: *Scalaria lineata*, Say; *Urosalpinx cinerea*, Stimpson. This gasteropod destroys many oysters both young and adults by boring into the shell and killing the animal. I have not seen holes bored by *Urosalpinx* in *Anomias*, though they are quite as exposed as are oysters to its attacks. *Littorina litorea*, Menke, was found entrapped, both adults and young, in great abundance. In moving about on the more or less dirt-covered glass, this animal makes a trail by the lingual ribbon with which it assiduously scrapes the glass for its food. The tracks consist of zigzag series of short, parallel lines of cleaned glass, arranged with the longer axes in the direction of the trail. The short lines are almost confluent with the lines of the next succeeding row; being at first nearly confluent on one side and then on the other, producing a zigzag pattern as the animal moves along. *Ilyanassa obsoleta*, Stimpson, was found in great abundance in the pipes. This species makes a track similar to that of *Littorina*, but much smaller, as might be supposed from the size of the animal. The differences are that the individual, parallel, short lines are less distinctly separable one from another and there is a much larger angle between the successive zigzag series of lines in the track of *Ilyanassa*, than is the case with the track of *Littorina*. The last two gasteropods did good

¹ Our sea-anemone, *Metridium marginatum*, attaches itself freely to glass slides when in confinement. The plan of placing glass in enclosed traps would be a desirable and

probably successful method to adopt in studying the development of corals where very fine results might be obtained by its employment.

service in eating vegetable growth on the glass, that would have been injurious to the young oysters and other fixed forms, which I was studying.

The following free Pelecypods were also caught in the pipes as entrapped forms; many specimens of young *Mya arenaria*, L., varying from 0.5 mm. to 6 mm. in length, and very young *Venus mercenaria*, L., 0.5 mm. to 2 mm. in length. *Argina pexata* appears again under this list of entrapped forms, as I found a very young specimen 0.75 mm. long which was free. *Pecten irradians* also belongs to both the lists of free and attached forms, a number of unattached individuals varying from 0.75 mm. to 1.5 mm. in height being secured. It is a stage of development preceding the attached byssated stage as described in the text. Occasionally adult Pectens and *Lævicardium mortoni*, Perkins, were entrapped.

A bottle, bearing many oyster spats and Anomias, was washed up on the shore during a storm, showing that they may be caught on glass under other conditions than those afforded by the drain-pipes. Probably the oysters set in the bottle when it was in comparatively deep water, where moderate quiet prevailed.

The nature of my researches was such that young oysters with shells as clean and perfectly preserved as possible were desired. Year-old oysters perfectly cleaned were found very beautifully preserved in the inside whorls of a dead *Sycotopus* shell, where they were completely protected from all eroding action. To imitate these conditions, in the salt-pond above referred to, a large number of inverted flower-pots, two-and-a-half and three inches in diameter, were suspended from galvanized wire stretched between stakes driven firmly into the sand. The pots were raised about six inches from the sand. This met with entire success, the pots in many instances being almost literally covered with spat. On the outside of the pots very little, and on the inside no sediment was deposited, as the pots hung like suspended bell-jars, so that the oysters were clean and well preserved. Further, on account of the porosity of the earthenware, the oysters had less hold than on natural cultch of stones and shells, and were easily removed for study. The owner of the pond in the winter of 1887 built a dam across the entrance so as to hold about two feet of water in the pond. Under these changed conditions, inverted pots were again suspended on the 17th of July, 1888. Oysters set on pots quite as successfully as in 1887, when the pots were exposed at low tide, and they grew much more rapidly.

In four large inverted pots microscope slide boxes filled with slides were suspended. The boxes were strengthened by brass nails, as they were simply glued and would have fallen apart in the water. One hundred slides were thus exposed in an horizontal position, but they were not as successful as glass exposed in the drain-pipes. They became coated with sediment on their upper faces and covered with minute vegetable and animal growths on their lower faces. The last is ascribed to the fact that the slides were so close to one another that the scavenger gasteropods, *Littorina* and *Ilyanassa*, could not get at them and destroy the objectionable growths as they did in the loosely-filled drain pipes.

In 1887, a number of wooden plates, such as are used at picnics, were exposed in the salt-pond. Holes were punched in the plates which were then strung on galvanized iron

wire and suspended between stakes. The plates were placed in pairs with the edges apposed so that the centres were widely separated and chambered pockets were thus formed. They were fairly successful. In 1888 when the pond was continually full the plates worked more successfully, the oysters growing with extreme rapidity. The rapid growth was probably due to the fact that the oysters were suspended and therefore kept very clean and also to the increased warmth of the water in the shallow pond as compared with water in the open bay. In the chambers formed by the apposed plates, similar forms to those found in the drain pipes were attached or entrapped. The value of obtaining fixed forms like oysters on thin wood is that they are easily removed for study or may be decalcified and sectioned without removal. Should wooden plates be desired, it is best to secure those which are cut from the block in a dish-form, not those which are cut flat and then pressed into a dish-form; because the latter flatten out when exposed in water, whereas the former retain their curved shape.

Cocaine was found a most valuable reagent in paralyzing Pelecypods which it was wished to kill distended or to dissect alive. A four per cent solution was used and was added gradually to a small volume of sea-water containing the animal. By this means only was I successful in killing young Pectens with the byssal attachment intact. Additional material was collected at various localities near Boston and some was loaned me by museums as noted in the text.

III. CLASSIFICATION OF STAGES OF GROWTH AND DECLINE.

In successive stages of growth of the individual, peculiarities are often found which are characteristic of definite periods. These periodical characters have been studied, especially in their later phases, by Professor Hyatt in fossil Cephalopods, and as a convenience in considering the several periods, he has (33-4) devised a nomenclature of the stages of growth and decline,¹ which he believes is applicable throughout the animal kingdom.²

We will now consider this classification in its application to the mollusca. The nomenclature devised for early embryonic stages consists of names very broadly recalling the grand divisions of the animal kingdom. They are protembryo, mesembryo and metembryo. The following names, neoembryo and typembryo, are applied to later stages of embryonic development.

Professor Hyatt considers that the neoembryo mollusc is the trochosphere stage, and that it has not yet acquired characters peculiar to a mollusc. The trochosphere stage (Pl. XXIII, figs. 3-4), before the formation of the shell-gland, certainly has not yet acquired characters which would define it as a mollusc, and we would limit the neoembryo stage to that period of development.³ A comparison of this stage in molluscs with Pro-

¹ Besides the references cited, this paper was published in the *American Naturalist* October, 1888. An abstract was published in *Science*, Vol. XI, No. 260.

² Professor Hyatt says that his nomenclature is similar to that adopted by Professor Haeckel; but is also supplementary, and based on morphological, rather than on physiological grounds. In his paper he discusses the relations of the two systems of nomenclature.

³ The ideal trochosphere of Professor Lankester (44) as that author says: ". . . exactly agrees with the larval form of many Chaetopod worms and other Cœlomata; most remarkable is its agreement with the adult form of the wheel animalcules or Rotifera . . ." Again he says: "So far the young mollusc has not reached a definitely molluscan stage of development, being only in a condition common to it and 'other Cœlomata.'" Some of

fessor Hatschek's figures (36-53) of developing Eupomatus (Serpula) shows a close similarity in structure, proving the identity of the two types at this early stage.

The name *typembryo* Professor Hyatt applies to the period in developing animals when the characteristics of the greater divisions begin to appear; when the embryo has characteristic features of the sub-kingdom to which it belongs. He considers the *typembryo* of molluscs to be the veliger stage, at which period the embryo is sufficiently far advanced to be recognizable as a mollusc. He speaks of the protoconch (completed embryonic shell) as a *typembryo*.

I think Professor Hyatt has not given the necessary limitations to his *typembryo* period in the mollusca. The shell-gland which produces the first rudiments of the primitive shell is considered characteristic of all molluscs (*vide* p. 297). It is the first definitely molluscan feature to appear, and as it is singularly alike in all molluscs where known, the embryo at the period when the shell-gland exists is referable to the mollusca; but has no characters yet which refer it to the class or phylum to which it properly belongs. The veliger stage, however, is referable, not only to the sub-kingdom mollusca as claimed by Professor Hyatt, but also to that class of mollusca to which the embryo really belongs. The veliger Pelecypod, fig. 25, p. 300, Pl. XXIII, figs. 9-11, has two valves and an anterior adductor muscle; the veliger Gasteropod, Pl. XXIII, fig. 19, has a spirally twisted shell and characteristic foot, tentacles and eyes; the veliger Scaphopod, Pl. XXIII, figs. 13-14, has a saddle-shaped shell known nowhere else in developing molluscs; the veliger Pteropod has an anatomy peculiar to itself. I would therefore suggest an alteration in Professor Hyatt's definition of the *typembryo*. In the mollusca the *typembryo* is the period characterized by the existence of a shell-gland and the plate-like beginnings of a shell; in it normally the ciliated trochosphere disc is becoming transformed into the velum and the foot is developing. Examples of *typembryo* molluscs are given in the summary of stages later.

I have shown that the veliger stage of molluscs is referable to the class or phylum to which the embryo really belongs. As it is a period most distinct and important, I suggest for it the name *phylembryo*.¹ *The phylembryonic mollusc is an early period in development, yet having characters in the shell and anatomy which make it referable to the class to which it belongs.* Commonly a velum exists at this stage; but the stage is not meant to include the whole veliger period.² Examples of *phylembryos* are given in the summary of stages.

The completed protoconch and prodissoconch of molluscs is a period later than that at which the *phylembryonic* features are fixed and yet is very distinct from the period

Lankester's and Balfour's figures of the trochosphere stage have already acquired a shell gland and in regard to this character cannot be considered as purely trochospheres according to Lankester's definition, for, with the shell gland they acquire a feature which makes them referable to the mollusca. They are trochospheres in which characters typically occurring later are very early inherited so as to cause an overlapping of stages.

¹ *φύλον*, a race, tribe stock, phylum, and "Εμβρυον, an embryo.

² The existence of a velum cannot be used very closely as a diagnostic character in considering stages of growth. It is frequently nearly or quite absent, as in *Unio*, *Anodon*, Pl. XXIII, figs. 7-8, *Cyclas*, and *Sphærium*, Pl. XXX, fig. 4, or it may exist long after the period of its normal disappearance. In studies of developing *Sycotopus canaliculatus*, Pl. XXIII, fig. 20, I have found that a large, highly developed velum exists for a considerable time after the formation of the true shell, although it is lost before the young leave the egg cases.

of growth which immediately succeeds it (see figures referred to in the summary). In view of the fact that it is the close of the embryonic shell period and is expressible as a completed protoconch or prodissoconch, I do not think it is necessary to name the period of growth. The period in Pelecypods and Gasteropods, where both anatomy and shell are known in many genera, is referable in origin to the adults of known allied forms.

In the early period of growth of the true shell, which succeeds the first formed embryonic shell, stages have been found which are referable to adult ancestral forms. Professor Hyatt studied these stages in Cephalopods and named them the silphologic (grub) stages. In a footnote to this paper¹ he has given up the use of the term silphologic and supplied in place of it the word nepionic.²

My investigations of young Pelecypods and Gasteropods, and also studies of published figures of Scaphopods, lead to the conclusion that nepionic stages in molluscs have characters referable to ancestry in most cases quite close to those naturally grouped as near allies of the adult. In the nepionic period (see figures referred in the Summary), it is quite common to find a shell with characters almost inseparable from those of the adult, or at least so near that the genus can be correctly determined. In other cases, on the contrary, wide differences from the adult condition may be observed at this early stage.

Periods later than nepionic are named by Professor Hyatt successively as neologic (youthful), epheboic (adult), and geratologic (old age) stages.

We will now give a brief summary of the stages of growth and decline as applied to the mollusca, with figures or references to known forms which may be used as types illustrative of the various stages. The illustration of the stages is a new feature, not given in Professor Hyatt's paper. Definitions in this summary are taken from that author's paper with the exception of such alterations as are suggested in the foregoing pages.

A classification of stages of growth and decline, in its application to the various groups of the animal kingdom, must be separately worked out for each group. It is believed, however, that the following classification contains the essential features necessary for such applications. New terms may be needed in some groups, but those here used will probably be applicable to the principal periods of growth in all animals.

Protombryo. The ovum and stages of segmentation of the egg preceding the formation of the blastula cavity. Examples: figs. 10-15, p. 295, of developing *Ostrea*, also Professor Brooks' figures 1-25 of a developing oyster and Dr. Patten's figures 2-14 of developing *Patella*.

¹The use of the word "silphologic" derived from *σιλφη*, a grub, when applied to the younger stages of all animals is likely to lead to confusion of ideas. I have ascertained, by recent studies of insects, the truth of Brauer's opinion, that the grubs, maggots and caterpillars common among insects are not normal progressive stages of development, such as are most common in other types of animals; but are, strictly speaking, cases of retrogressive or more or less degraded specializations. I desire, therefore, to give up the use as a general term of the word *Silphologic* and propose in its place *Nepionic*, or young an-

imal, from *Νηπιος*, an infant. This word also is more in accord with other terms of the nomenclature proposed in my paper on "Values in Classification of the Stages of Growth and Decline," Proc. Bost. Soc. Nat. Hist. Vol. XXIII, 1888. Signed, ALPHEUS HYATT.

²The word nepionic is particularly suitable for early yet post embryonic stages. Besides its meaning of infant, applied to the young of man, I am told by Mr. Ernest Jackson that it is used twice in the Iliad, of young animals, and by Theophrastus of young plants.

Mesembryo. The hollow blastula stage comparable to the condition found in the adults of *Volvox* and *Eudorina* types of the Mesozoa.¹ Examples: Pl. XXIII, figs. 1, 1*a*, of developing *Patella*.

Metembryo. The gastrula, comparable to the lower Porifera in which three cell-layers exist, as in the lowest Hydrozoa. Examples: Pl. XXIII, fig. 2, of developing *Paludina*, also Hatschek's figure 5, of developing *Teredo*.

Neoembryo. The trochosphere. Stages not yet possessing the essential diagnostic characters of the mollusca; comparable to the embryos of Chætopod worms and other Cœlomata. Examples: Pl. XXIII, figs. 3-4, of developing *Patella*, also Professor Butschli's figure 6, of developing *Paludina*.

Typembryo. The period at which an essential molluscan feature, the shell-gland, and plate-like beginning of the shell are discoverable, and yet the embryo is not referable to the class to which it properly belongs. Examples: fig. 22, p. 297, of developing *Ostrea*; Pl. XXIII, fig. 5, of developing *Pisidium*; Pl. XXIII, fig. 6, of developing *Pleurobranchidium*, also Lankester's (44), fig. 72, of developing *Limnæus*. A comparison of the molluscan typembryo and neoembryo stages with Hatschek's figs. 36-53, of a developing *Eupomatius* (*Serpula*) shows graphically the value of these stages in classification.

Phylembryo. Early veliger stages in which the characters of the class subdivisions are indicated, and the structure of the shell and other features render the embryo referable to the group of mollusca to which it belongs. Examples: p. 299, figs. 23-24, of developing *Ostrea*; Pl. XXIII, fig. 19, of developing *Sycotopus* and Pl. XXIII, fig. 13, of developing *Dentalium*, also Lankester's (43), Pl. 8, fig. 22, of developing *Apysia*, and our figs. 7-11, Pl. XXIII, of developing *Anodon*, *Modiola*, *Cardium* and *Montacuta*.

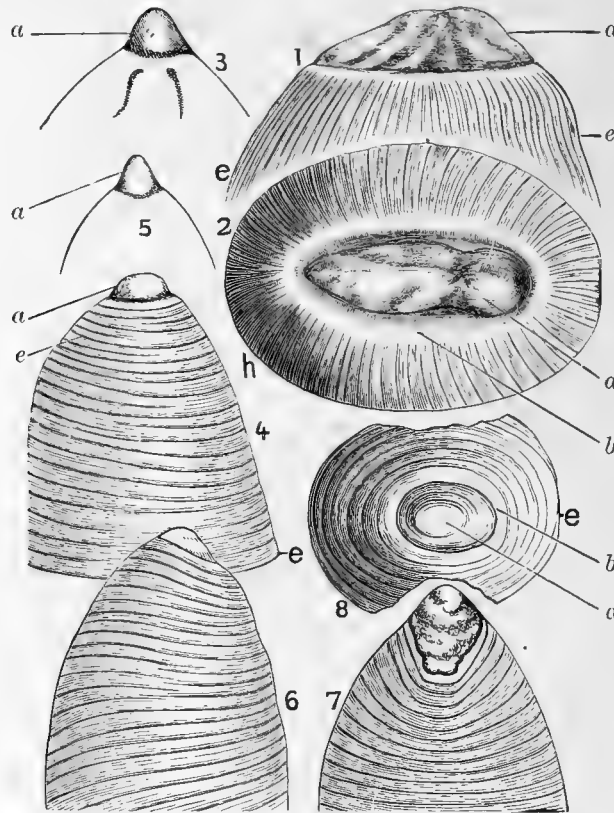
Completed protoconch and prodissoconch. The completed first-formed shell of molluscs, the ovisac, fry shell, embryonic shell and larval shell of authors. It finds its representative in the globular, cup-shaped, or spirally coiled protoconch of Cephalopods. Examples: Pl. XXIII, figs. 15, 16, of developing *Goniatites*. Also see Professor Hyatt's (27) figures of developing *Ammonites* and Zittel's figures of young *Ammonites*, *Belemnites* and *Spirula*. The existence of a cicatrix at the base of the conch in Nautiloids is claimed by Professor Hyatt (27) as proof that a protoconch existed in the young and a parallel fact in favor of this conclusion is the finding of a cicatrix at the tip of the conch in *Acmæa* as described below.

A withered, irregular bulb, found at the apex of the conch in some *Orthoceratites*, figs. 1-8, Professor Hyatt considers as the remains of a protoconch, probably originally of conchyolin structure. M. Barrande (3) figures cicatrices and withered bulb-like protoconchs in many Nautiloids. See his figures of Cephalopoda, Pls. 487-490, inclusive. Several of his figures are taken from unpublished drawings of Professor Hyatt's.

In some Pteropods a bulb-like expansion of the tip of the shell seems to be the equivalent of the protoconch in other mollusks. Examples: Pl. XXIII, fig. 17, also several figures in Bronn's *Thier-reichs*. In well-preserved *Tentaculites* a globular or elongate protoconch is sometimes found. Examples: *Tentaculites acuaris*, Pl. XXIII, fig. 18; also see figures in Hall's *Palæontology of New York* and other authors.

¹ For the consideration of *Volvox* and *Eudorina* as mesozoa see Hyatt, Reference No. 30.

The protoconch in Gasteropods is represented by a spirally twisted embryonic shell.¹ Examples: *Sycotopus canaliculatus*, Gill, Pl. XXIII, fig. 19. Older specimens than this from egg cases show a well-marked protoconch at the tip of the conch and I have also observed a well-defined protoconch in young specimens of *Fulgur carica*, Con., *Purpura lapillus*, Lam., *Vermetus radricula*, St., *Buccinum undatum*, L., and *Crepidula for-*



FIGS. 1-3. *Orthoceras elegans*, Müntz. Apex of conch and protoconch, viewed from the side, below and in front.

FIGS. 4-5. Apex and protoconch of another specimen.

FIGS. 6-8. *Orthoceras politum*, Klipst. Apex of conch and protoconch viewed from the sides and below.

a, protoconch; e, apex of conch; b, shoulder of apex.

All from the Triassic of St. Cassian (after Hyatt).

nicata,² Pl. XXIII, figs. 21 and 23. *Eolis* has been figured with an embryonic shell and it is important that this genus which possesses no shell in the adult has a typical, spiral protoconch when young. A very interesting condition is that which I recently found in the young of *Acmaea testudinalis* var. *alveus*, Verrill, Pl. XXIII, fig. 24, which I collected at Vineyard Haven, Martha's Vineyard. No protoconch exists at the apex of the conch;

¹The embryonic shell or protoconch of Gasteropods is commonly spoken of by embryologists as a "Nautiloid" shell; but this is not strictly correct. A Nautiloid shell is spirally coiled in one plane as in the *Nautilus* from which the name is borrowed; but the protoconch of Gasteropods, in all the numerous cases which I have seen, either as specimens or figures, is coiled in a spiral plane and should not be confounded with the Nautiloid form from which it is totally distinct.

²The spirally twisted protoconch of *Crepidula* proves that the almost conical form of the adult is not due to

a primitive, simple condition in which the spiral has not yet become developed; but rather to a modified condition in which the ancient spiral form, shadowed in the protoconch, is almost entirely lost in the adult. Similar observations have been made on *Fissurella* in an exhaustive paper by M. Boutan. The protoconch is very sharply defined and is beautifully clear in the young of *Crepidula fornicata*, Lam., and *C. plana*, Say, both of which species are common on our shores and may be collected in abundance in July and August. A short paper on this shell is now in preparation for publication.

but, instead, a well-defined cicatrix marks the position where the protoconch has become separated off. The cicatrix consists of granular lime and fills as a plug the space which otherwise would be a foraminal opening in the shell. In form the cicatrix simulates the outline of the base of the separated protoconch as will be evident by comparing the scar of fig. 24 with the protoconch of *Crepidula* in Pl. xxiii, fig. 23. The cicatrix of *Acmæa* is made up of two areas, one circular and surrounded by a ring of similar nature, the other roughly triangular ovate. I find that a similar outline is formed by laying a small, slightly muddy Gasteropod on a clean glass slide. The closely related genus *Patella* from Patten's studies is known to have a typical spiral protoconch. Therefore, there can be no question as to the meaning of the cicatrix in *Acmæa*. Professor Hyatt assumed, as noted above, that the existence of a cicatrix in *Nautilus* predicated the presence of a protoconch in the young and it gives me great pleasure to offer this corroborative evidence of the truth of his assumption from another class of molluscs.

In Scaphopods the embryonic shell has been named a periconch by Professor Hyatt (33) on account of its peculiar saddle-shape form. See *Dentalium*, Pl. xxiii, figs. 13-14. In Pelecypods the bivalvular embryonic shell or prodissoconch is figured in many genera in this paper. Examples: see almost every plate.

Nepionic period. The period of the first formation of the true shell which succeeds the embryonic shell and is normally retained throughout the rest of life. The period is commonly characterized by marked stages. Examples: figures of developing *Ostrea*, Pls. xxiv and xxv, figures of developing *Perna*, *Pecten*, *Anomia*, *Argina* and other young Pelecypods figured on Pls. xxvii to xxx, inclusive. Also Professor Hyatt's (27) Pl. iv, figs. 7-9, of a young *Nautilus koninckii*. These last figures have a smooth, nepionic period, succeeded by a fluted, neologic stage. The nepionic stage is shown in *Crepidula fornicata* and in *Acmæa testudinalis* var. *alveus*, Pl. xxiii, figs. 21, 23, 24. It may be observed in *Sycotopus*, *Fulgur* and *Buccinum* when removed from their egg cases, in which condition the shell is very finely preserved.

Neologic period. The period succeeding the nepionic and preceding that period which may properly be considered as the adult. It is frequently characterized by marked stages, being a period in which the growing animal often differs widely from the adult, and as it is of considerable size, the differences and stage are easily recognized. Examples: *Hinnites cortesi*, Pl. xxvi, figs. 3-4, has a pecteniform neologic stage sharply marked off from the ostreaform adult condition. *Stava fibrosa* from the paleozoic Pl. xxiii, fig. 12, is one of the most striking cases of definition of the neologic period that I have ever seen. The neologic stage as shown in the figure is concentrically plicated and is highly arcuate, whereas the succeeding epebolic period is radially plicated, spread out in a fan-like fashion and is much less arcuate. Many species and individuals of this remarkable genus are figured by M. Barrande. The period is strongly marked in the well-known *Clavagella* and *Aspergillum* and the last mentioned genus has a definitely marked nepionic stage as well. The young shell of these two genera has up to the close of the neologic stage two equal valves. In the adult the bivalvular condition is lost; the two valves having united so as to form a single tubular shell, which by itself would not be recognizable as a Pelecypod. In the Gasteropoda, *Vermetus*, fig. 9, and *Magillus*, the neologic period is close coiled, whereas the adult is loosely coiled and vermiform having

lost nearly all the characteristics in the shell of the Gasteropod form. Marked nepionic and nealogic stages of growth are a striking feature of many Gasteropods as seen in *Yetus*, *Cypræa*, *Strombus* and *Pteroceras*. These and other stages are also strongly marked in many Cephalopods, where they are described by Professor Hyatt (34 and other papers).



FIG. 9. *Vermetus radicularis*. St. (After Verill.)

Ephebolic period. That period best characterized by saying that in it the adult characters find fullest expression; it is often separable by marked stages from the earlier nealogic period, and also from the later or senile period. As examples we would refer to the adult (middle age) condition of the figures referred to as illustrating the nealogic period and also the next or geratologic period. In *Slava fibrosa*, Pl. XXIII, fig. 12, the radially plicated area is referable to the ephebolic period. In *Hinnites cortesi*, Pl. XXVI, figs. 3-4, the ostreaform stage is ephebolic and in *Vermetus radicularis*, fig. 9, the vermiform stage is the ephebolic period.

Geratologic period. The period of decline of the individual, often marked by distinct stages. The geratologic period is subdivided by Professor Hyatt into the clinologic and nostologic periods, signifying the early and later periods of decline of the individual. As examples of geratologic stages, I would refer to *Venus Tridacnoides* from the Miocene Tertiary of this country and to *Cardita planicosta*, Say, from the Eocene Tertiary of Claiborne, Ala. In both forms old age is strongly indicated by a loss of costations and other characters found in the ephebolic period, the new period assuming a strikingly different appearance. In the old age of a Brachiopod, *Atrypa rugosa*, may be observed a most marked change; the regular even plications of the adult become irregular and spread out in a fan-shaped fashion. This is shown in many of M. Barrande's figures and is more or less completely developed in some specimens of any large collection of American or European specimens.

IV. OSTREA: DEVELOPMENT OF THE SOFT PARTS.

EMBRYOLOGY.

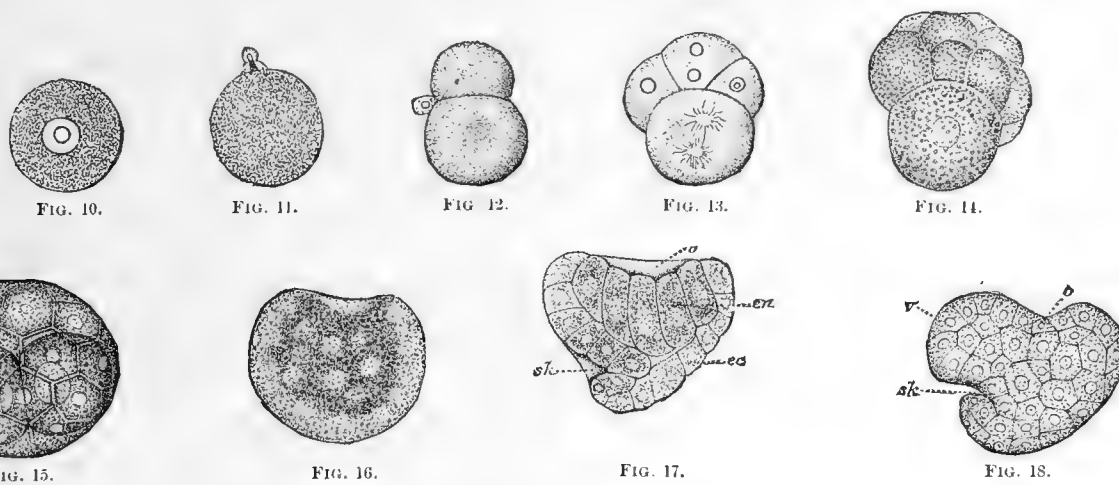
The early embryonic development of the oyster may be followed in the writings of Dr. R. Horst on the European oyster, *O. edulis*, L., and Professor W. K. Brooks on the development of our oyster, *O. virginiana*, Lister. The later stages of development have been described by Professor Huxley and Dr. R. Horst in the European oyster, and Professor J. A. Ryder and the author in our species.

The European species, *Ostrea edulis*, L., is hermaphroditic according to European investigators and Professor Ryder, and the embryos undergo considerable development in the gill chambers of the parent. Our species, *O. virginiana*, Lister, on the contrary, is not hermaphroditic, according to Brooks (9), and Ryder (61), and differs from *O. edulis* in that the eggs are discharged from the parent and undergo their whole development in the sea. It produces many more eggs than the European species, and the embryos are much smaller than those of *O. edulis*.

I have not followed the early embryonic development of the oyster, and therefore, for the stages considered make reference to the publications of Professor Brooks (9), Dr. Horst (23, 24) and Professor Huxley (26).¹

As will be seen in studying the oyster both the soft parts and the hard, we have to deal with a member of a highly peculiar and aberrant group, varying much from the characters commonly met with in molluscs. Many of the characters, and especially their period of occurrence in the life of the individual, are well explained by the law of concentration and acceleration of development, which is considered in the introduction. By this law a highly modified or "concentrated" type is one which acquires characteristics very early in its development, earlier than the normal, so to speak, and such is found to be the case in a marked degree in the oyster.

The egg after fertilization undergoes a period of segmentation until it becomes a solid mass of cells, see Brooks' figs. 1-29 and our figs. 10-15. These stages, following our classification, are considered as protembryo stages. (Nomenclature of stages, section III.)



DEVELOPMENT OF OSTREA EDULIS (AFTER HORST).

FIG. 10. Egg of oyster, with germinal vesicle and spot visible within the vitellus.

FIG. 11. Beginning of development; the germinal vesicle has become invisible and polar globules appear.

FIG. 12. First stage of segmentation; the egg is divided into two spheres of unequal size (animal and vegetative).

FIG. 13. More advanced, the egg being divided into four spherules.

FIG. 14. Stage when the egg shows one large vegetative sphere and several animal spheres.

FIG. 15. More advanced stage seen from above, where the vegetative sphere is divided into two spherules.

FIG. 16. Embryo side view at the beginning of invagination (gastrular).

FIG. 17. Embryo more developed; optical section, with invagination of the entoderm and beginning of the pre-conchylian gland: *ec*, ectoderm; *en*, entoderm; *o*, blastopore; *sk*, pre-conchylian gland.

FIG. 18. Embryo a little older, side view: *v*, pediform appendix; other letters as in fig. 17.

The next stage in the development of the embryo, taking as a normal that which has been commonly observed by embryologists, should be the formation of a morula stage, the cells arranging themselves in a peripheral layer around a hollow sphere. According to the investigations of Professor Brooks and Dr. Horst, there is no true morula stage

¹ In the consideration of these early stages such points are selected from the writings referred to as serve to illustrate this paper. I do not pretend in any sense to give

an abstract or even a discussion excepting in a limited sense of the early development.

in the oyster, the gastrula invagination commencing before the formation of a hollow sphere. We have, therefore, no stage comparable to our mesembryo stage, Pl. XXIII, figs. 1, 1a, its absence being explicable as a case of extreme concentration of development in the oyster.

In the later segmentation stages, Brooks' figs. 22-28, also our fig. 14, we find that those cells which are of ectodermic and entodermic nature are clearly defined. The entoderm consists of a single macromeric cell surrounded in an increasing degree by micromeric cells up to the period shown by Brooks' fig. 26. The single macromere then divides into two, Brooks' fig. 28, then into several cells, his fig. 30. Coincident with the splitting up of the entodermic cells there is, according to both Brooks' figures and our fig. 16, a flattening of the embryo from above downwards, and a pushing in of the entodermic cells, which commencing as a slight depression, Brooks' fig. 31, our fig. 16, soon forms a deep invagination, the gastrula cavity; see Brooks' figs. 32-35 and our fig. 17.

From this point on there are some important differences in the observations of Professor Brooks and Dr. Horst. As Horst's observations were made on embryos of *O. edulis*, which are much larger than those of *O. virginiana*, and as they are more in accordance with observations made on the development of other Pelecypoda and mollusca I have for the most part followed them where differences exist.

In our classification of the stages of growth, the metembryo mollusc represents the gastrula stage, Pl. XXIII, fig. 2, being a period in which two well-formed and an incipient third layer exist. Professor Brooks' figures 32-35 represent different aspects of the gastrula oyster according to his observations. His fig. 33, an optical section, shows an embryo with a primitive gastrula cavity and body cavity. It also has a velum slightly developed. These figures answer well the requirements of the metembryo stage and may be said to represent that period in the development of *Ostrea virginiana*.

Dr. Horst, considering the stages (our figs. 16-17) which are referable to the gastrula period, says, "there can however be no question of a genuine invagination because there is no cavity of segmentation; we have here, so to speak, an intermediate form between an embolic gastrula and an epibolic gastrula."¹ He notes the remarkable fact that coincident with the gastrula invagination at the vegetative pole, there is also a very distinct depression at the other pole, a little below the dorsal side, our fig. 17sk. This second invagination by further development (our figs. 18-19) he shows is the beginning of the preconchylian invagination.

The gastrula invagination, according to his figures, begins before the preconchylian invagination; but the latter exists before the completion of the gastrula invagination. Horst's figures do not show any trace of a velum at this period, which is somewhat peculiar, as he represents the oyster as so much more advanced in its molluscan characters than does Brooks, who figures the velum at the gastrula period. The early absence of the velum in *O. edulis* may be connected with the brooding habit of that species, for in Pelecypoda,

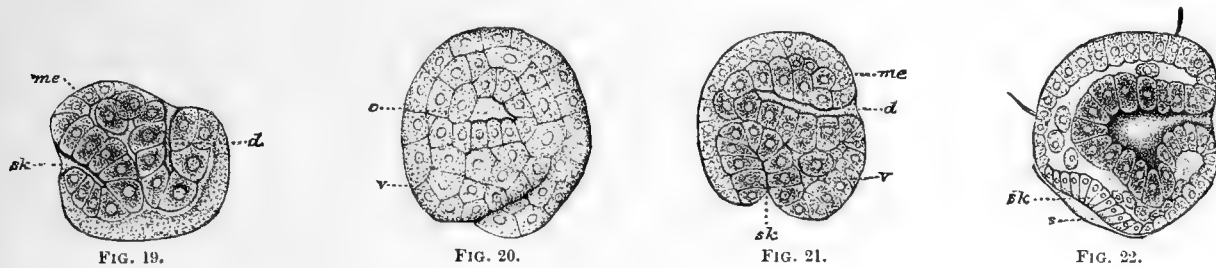
¹ According to Hyatt (Larval Theory of the Origin of Tissue, p. 156), in the formation of epibolic gastrulae the growth of the ectoblast cells is so rapid that the endoblast cells become enclosed, and the gastrula is formed by

a process much shorter than is usual in embryos of the embolic type. He accounts for the epibolic gastrula by heredity and extreme concentration of development.

which brood the young, as *Unio* and *Pisidium*, the velum is highly reduced or wanting. From Horst, we may gather the conclusion that the metembryo (gastrula) stage in the European oyster, fig. 17, is not a pure gastrula, but has already acquired by concentration of development, some of the characters which would normally appear later.

Professor Brooks says that the primitive blastopore closes over, becomes the dorsal aspect of the embryo and gives rise to the shell; the permanent mouth and anus forming on the opposite side of the embryo and independent of the blastopore. This differs so essentially from the observations of Dr. Horst in the European oyster and from those of other investigators except Rabl, in the development of various groups of mollusca, that we prefer to follow Dr. Horst's observations. Professor Brooks himself says (9), p. 76, that the whole evidence furnished by comparative anatomy and embryology tends to show that the mouth, anus and shell-gland can be homologized perfectly in all the classes of true molluscs and that they are not only homologous with each other, but must be perfectly homologous also with similar structures in the ancestral form of which the molluscs are modifications. It is evident that these several organs would not be "perfectly homologous" if in one case the shell-gland arose from the closed blastopore and in another from the opposite pole of the body, and the same would be true of the derivation of the mouth and anus.

Dr. Horst in considering the development of the preconchylian gland¹ says that when the embryo is viewed from the side the glandular depression is seen as in our fig. 18, *sk*, and in fig. 17 in optical section. During the further development, our figs. 19 and 21, a small



DEVELOPMENT OF *OSTREA EDULIS* (AFTER HORST).

FIG. 19. Embryo same stage as fig. 18, optical section; *me*, mesoderm; *d*, primary gastrula invagination; *sk*, shell-gland.

FIG. 20. Embryo a day older, front view, with the primitive mouth opening.

FIG. 21. The same embryo, optical section.

FIG. 22. Embryo a day older, with a wreath of vibratile cilia, a stomachic cavity and the beginning of a shell, *s*.

invagination is formed bordered by walls of high cylindrical cells with a narrow opening.

Considering fig. 19, Horst says that the gastrula cavity has deepened, and behind the mouth are cells, probably mesodermic. The blastopore continues to be very distinct, and as far as he could ascertain, it did not disappear but remained and was transformed into the mouth.

¹ The preconchylian gland was discovered by Lankester (44) in 1871, and has been figured by him (44) in *Loligo*, *Aplysia*, *Pleurobranchidium*, *Limnaeus* and *Pisidium*. It has also been observed and figured by Fol in a Heteropod (see Balfour); by Rabl in *Planorbis* (see Claus); by Butschli, in *Paludina* (see Claus); by Bobretsky, in

Nassa (see Balfour); by Patten, in *Patella*; by Brooks in a pulmonate Gasteropod; by Hatschek, in *Teredo*; by Horst in *Ostrea* and in other genera by various investigators. This array of genera confirms the opinion of Lankester that it is typical of all developing molluscs.

Dr. Horst says that great changes take place during further growth of the embryo. The preconchylian gland gradually loses its primitive character of a glandular invagination and forms a thickening of the ectoderm composed of long, conical cells, fig. 22, *sk*. A thin, cuticular membrane secreted by these cells is the first indication of the shell, and at this position in the adult the hinge is found.¹ Horst maintains, therefore, that the shell of the oyster originates as a single plate in accordance with the observations of Brooks in *Anodon* and Hatschek in *Teredo*.² Meanwhile in fig. 22 a body cavity has formed by the separation of the ectoderm and entoderm, a velum has developed and the gastrula invagination has formed a spacious cavity in the base of which is a diverticulum, now closed, but which later communicates with the ectoderm and forms the posterior part of the alimentary canal. The neoembryonic mollusc in our classification is represented by the trochosphere stage before the development of the shell-gland, Pl. XXIII, figs. 3-4. In the developing European oyster the shell-gland, according to Horst, originates early, closely following the gastrula invagination and before the formation of a normal trochosphere stage. I think, therefore, that we must consider the neoembryo stage as skipped in the oyster by the overlapping of stages due to extreme concentration and acceleration of development.³ Fig. 22, on the other hand, is the nearest approach to the ideal typembryo stage that we have in the developing oyster (definition of typembryo, see p. 291). The primitive gastrula cavity has not yet become connected with the ectoderm by the secondary opening, the anus, as is ordinarily the case, but the existence of the shell-gland, with the beginnings of the velum, entitles it to be considered as a typembryo. The existence of these comparatively high characters in the young oyster, at a period when the primitive oral invagination still retains almost its early simplicity and no second alimentary opening has been formed, must be considered as strong proof of the highly concentrated development of this type.

Taking up Horst's account of the developing oyster again, he says that on the following day (our fig. 23) the shell, which has grown very much, covers a large portion of the body. It already contains carbonate of lime, as shown by treatment with acids. Of fig. 24, Horst says, the velum now forms a very distinct part of the body, which is almost entirely covered by the shell. The surface of the velum surrounded by a wreath of vibratile cilia already shows in its centre a thickening which is the beginning of the cephalic shield. An oesophagus in the shape of a funnel leads to a large, pear-shaped

¹A horny plug, the product of the cells of the shell-gland, has been described in Gasteropoda and Pteropoda (Lankester (44), Balfour). The typical universality of the shell-gland cannot be doubted (note, p. 297) and the ligamentous union of the valves of Pelecypoda occupies the precise position of the shell-gland. It seems reasonable to follow Lankester's suggestion, based on *Pisidium* (43) and homologize the horny ligament of Pelecypods with the horny plug of embryonic Gasteropods and Pteropods. To quote Lankester, "In *Pisidium* as will be seen from Pl. IV, figs. 38a and 39, the two calcareous valves do not make their earliest appearance in close contact one with the other. The central portion of the shell-gland is not concerned with them; and since it is precisely that point which in the Gasteropods cited gives rise to a chitinous plug, may we not see in the ligament of the bivalve,

"which occupies so precisely the required position, the homologue of that production."

²The primitive shell in *Cyclas* and *Unio* has also been observed by investigators to begin as a simple, unpaired cup.

³Lankester, in his article *Mollusca* (44), refers to Horst's fig. 14 (our fig. 23) as the trochosphere stage. But as the shell has not only considerably developed, but consists of two valves, we think this figure is referable to the class of Pelecypoda, a period later than the trochosphere stage. Lankester's own definition of the trochosphere is that at this period the embryo has not yet acquired molluscan features and is comparable to the larval forms of many Chaetopod worms and other Cœlomata, which is not the case in the figure cited.

stomach which communicates with the outside through the intermediation of an intestinal canal.

Our fig. 23 is distinctly the essential equivalent of Brooks' figs. 38-42. Our fig. 24 again is reasonably close to Brooks' fig. 44. At this last stage there are two well-developed valves, a stomach, mouth and anus, a ciliated foot and a large velum. In fig. 24 a

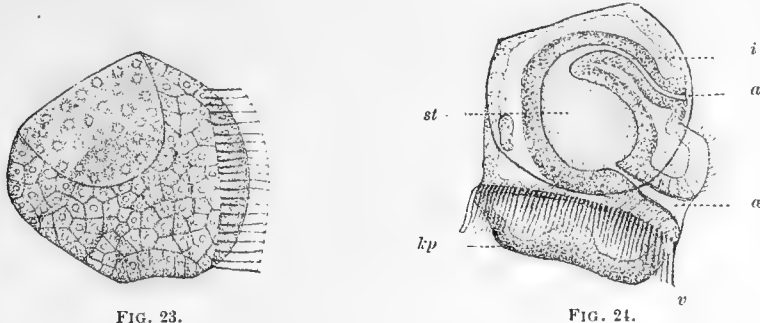


FIG. 23.

FIG. 24.

DEVELOPMENT OF OSTREA EDULIS (AFTER HORST).

FIG. 23.—Embryo at more advanced stage than fig. 22, side view, with shell more developed.

FIG. 24.—Embryo still more developed; *v*, velum; *a*, œsophagus; *st*, stomach; *a*, anus; and *kp*, cephalic plate.

body is represented which, although Horst does not mention it, appears to be the beginning of the adductor muscle of the valves. It is in the same position as that occupied by the adductor in Horst's fig. 16, Brooks' fig. 44 and our fig. 25, p. 300.

I have described as the phylembryo an early period of development (see section III) where, however, the class characters are recognizable, and I consider figs. 24-25 as phylembryonic stages of the oyster. They have two equal valves and an anterior adductor muscle, characters which render the embryo referable to the phylum or class Pelecypoda, to which it properly belongs, although not referable to any known adult form.

The mouth and anus when developed arose in close proximity on the ventral border of the embryo, Brooks' fig. 38, our fig. 23, which is a generalized characteristic of a molluscan embryo. It is seen in fig. 24 that the first adductor muscle develops anteriorly and close to the dorsal margin of the velum. The retractor muscles of the velum and liver then develop. The anus, from its early ventral position, revolves dorsally in the plane of the valves (see Brooks' figs. 38-44). The intestine by interstitial growth makes a single loop-like curve on the left side; this with some other slight changes brings us to the stage, fig. 25, described by Huxley (26). Ryder (63), remarking on this stage, notes that the intestine is already flexed on itself in much the same manner as in the adult, though it does not extend as far anteriorly, and its position is modified later by flexions of the stomach and œsophagus.

The shell of the stage, fig. 25, is symmetrical, equivalvular, and of about the period of development of Pl. xxiv, figs. 13-16, of the developing shell of this same species. The mouth has yet no palps, a sac-like process of the stomach on either side represents the liver, two pairs of muscles serve to retract the velum, and the single adductor muscle closes the valves. Huxley observes that this early anterior adductor cannot be the equivalent of the single adductor of the adult as it is on the ventral side of the alimentary canal whereas that of the adult is on the dorsal side. He says that a second posterior

adductor must be developed and this early anterior adductor lost in later development. This was all that was known concerning the development of the adductor muscles of the oyster when I published my preliminary paper in which it was shown that two adductors exist at the completed prodissoconch stage.

A stage of *O. virginiana* of similar age to our fig. 25 of *O. edulis* has been figured

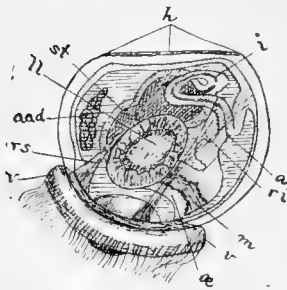


FIG. 25.
EMBRYO OF OSTREA EDULIS
L. (AFTER HUXLEY).

The phylembryo stage, viewed from the left side. *a*, *ad*, anterior adductor muscle, which alone exists at this stage; *m*, mouth; *æ*, oesophagus; *a*, anus; *i*, intestine; *st*, stomach; *ll*, left lobe of the liver; *v*, velum; *rs*, *ri*, superior and inferior muscles, which retract the velum into the shell, *sh*; the hinge, *h*, is straight. Compare with Pl. XXIII, figs. 7-11 of phylembryonic stages of developing Pelecypods, where as here the hinge line is straight and the anterior adductor alone exists.

by Ryder (62). The valves were nearly disc-shaped, but flattened at the hinge area. A ciliated velum existed, and as Ryder noted, "the embryos appeared to be attached to the glass by a marginal extension of the mantle over the edge of the lower valve, forming a sort of lip," but they were not firmly fixed as "the embryos swung to and fro." He did not succeed with later attempts in getting similar attachments, and from my own observations I have every reason to believe that the fixation was of a transitory nature, not to be confounded with the fixation which young oysters later acquire when they become fixed for life.

I have thus far considered the early development of the oyster, using facts observed by other investigators. This is done in order to make clear the later portion of the embryological development and also to bring out some facts elucidating the development of the group of Pelecypoda. All later observations are my own, excepting where specially credited.

Between the stage fig. 25, and our next stage, Pl. XXIV, figs. 1-2, there is a blank in the knowledge of the development of the oyster. It has not been described in the European species, and all attempts to obtain it in our species have failed. In artificial confinement the oyster dies at this stage.

The next step in the anatomy which I have to consider is that of the oyster when it has completed the prodissoconch growth and just preceding the beginning of the dissoconch, or "spat growth." This period is the last of the embryonic stages, using as bases of consideration the structure of the soft parts and the hard as well as a comparison with a similar period in other developing Pelecypoda. In my preliminary paper (36) I showed the important fact that the oyster at this stage has two adductor muscles, situated relatively to the alimentary canal as they are in adult dimyarian Pelecypods. The specimen then figured was from alcoholic material collected at Buzzards Bay, and the parts had contracted so that some features were not successfully made out; the muscles however were rendered clear by treating the specimen with dilute acetic acid, and thus dissolving the calcareous shell. Living material of this age was obtained later growing on glass slides, so that it could be studied more satisfactorily.

On the third of August, 1888, clean glass was put into a drain-pipe trap on the sandbar. The following day it was examined and a young oyster, Pl. XXIV, figs. 1-2, was found attached. No spat growth had taken place, but the embryo was firmly attached by the ventral margin of the left valve. On driving a current of water forcibly over the glass from a pipette it did not rock or move from its position, thus demonstrating

the firmness of the fixation. As the oyster had been attached less than twenty-four hours, the anatomy and shell here represented must have been developed while it was a free, unattached embryo. The fact that the embryonic shell is always fixed by the extreme ventral margins only, is further proof that fixation takes place at the close of this period.

The embryo was yellowish-green and lively, constantly extending and retracting the mantle and gills and moving the palps. The important feature of the two adductor muscles was clearly made out as shown in Pl. XXIV, fig. 1, viewed from the right side, and in fig. 2, viewed from the left side through the transparent glass to which the embryo was attached. The intestine wraps around the dorsal aspect of the posterior adductor, as in all later stages. A large, lobed, ciliated velum still exists and is situated on the ventral aspect of the anterior adductor muscle, lying close up to that body. The ciliated and lobed palps are situated close up behind the velum. Club-shaped, tubular, ciliated gills, Pl. XXIV, fig. 1, also fig. 6, with the tips not recurved upon themselves, exist. The mantle border is broad and thick, bears no tentacles and is capable of considerable extension beyond the margins of the valves. Within the umbo of the lower left valve was a rhythmically, rapidly pulsating body, as of a large blood-vessel. The liver forms a large, light green mass in the upper part of the body and extending into the umbos.

About three and a half hours after the specimen was first seen a slight spat growth had taken place along the ventral margins of the valves. It was kept alive several days, during which growth proceeded rapidly and was studied at intervals; Pl. XXIV, fig. 3, being three days older than figs. 1 and 2. We will now discuss this stage, which is of great importance, both in the development of the oyster and related Pelecypoda as well.

The anterior adductor muscle of the early development, fig. 25, p. 300, is still existent in this stage, Pl. XXIV, figs. 1-2, *a, ad*, but there is another muscle, the posterior adductor, as well. We have then the interesting feature of a monomyarian Pelecypod in its early stages possessing two muscles, situated relatively to the alimentary canal as they are in typical adult dimyarians. The anal part of the intestine revolves dorsally during the early development of the oyster and the posterior muscle when formed must have originated on the ventral aspect of that organ. If the posterior muscle had developed on the dorsal side of the intestine it would always have retained that relative position as the permanent anterior adductor of dimyarians does in relation to the mouth and œsophagus. One of the striking characteristics of the ostrean prodissoconch is, that the umbos point posteriorly as shown in Pl. XXIV, figs. 1-2. This is contrary to the condition observed in developing dimyarians, as in them the umbos point anteriorly, but an exception is found in *Nucula*, the embryo of which, according to Lovén, has umbos directed posteriorly. This character of the umbos is discussed in its serial connections in section xv.

In *Ostrea*, fig. 25, indisputably the anterior adductor is first developed; also in *Cardium*, *Modiolaria* and *Montacuta*, Pl. XXIII, figs. 9-11, in *Pisidium* according to Lankester (43) and in *Anodon*,¹ Pl. XXIII, figs. 7-8, according to Schierholz², the anterior adductor is first developed. I have found only two possible exceptions to the rule of the

¹ In the embryo of *Anodon*, Pl. XXIII, figs. 7-8, the first formed adductor muscle is in the larger side of the shell. According to Schmidt's figure of a later stage, the larger side is the anterior end of the embryo. Therefore the

first formed adductor is probably in part, at least, the beginning of the permanent anterior adductor as in the other Pelecypoda above considered.

² Schierholz' paper, see Schmidt's reference list.

anterior adductor being developed first. These are *Mytilus* and *Unio*. As the nearly related *Modiola* and *Anodon* follow the rule these two genera may be considered as exceptions, or perhaps illustrate errors of observation as discussed in my preliminary paper, (35), p. 535.

In *Ostrea* the mouth and anus develop ventrally, the anal extremity of the intestine revolves dorsally and the anterior adductor is developed. Later, the posterior adductor develops on the ventral side of the intestine. When one compares this with the figures and descriptions of the development of the above-mentioned genera (excepting *Mytilus* and *Unio*), together with the anatomy of the adults, it seems that there is a close uniformity of plan. The genera mentioned are not numerous, but they are taken from widely separate groups of Pelecypoda. There is then strong evidence in favor of the development of the anterior adductor first in Pelecypods as the typical mode, and the development of the posterior adductor later, after the intestine has revolved into place, from its early ventral position. This theory easily explains the constant relative positions of the mouth and anus to the two adductors in the adults of dimyarians, or to the single adductor, where only one exists, as in monomyarians.

It is seen that there are two distinct stages of development of the muscles of the embryonic oyster. First, a single-muscled stage, the early monomyarian, fig. 25, p. 300, pointing towards a problematical ancestor, which in the adult condition had only one adductor muscle, and that one in the anterior portion of the body.¹ The second stage is the two-muscled stage, dimyarian, Pl. xxiv, figs. 1-2, pointing to an ancestral adult form which had two muscles like the typical dimyarians. The figure of this stage shows the early formed velum to be still existent, but it is not supposed that the early dimyarian, adult ancestor possessed a velum. It exists here presumably because of the lapping over of stages, due to concentrated development, which is most marked in the early embryonic development of the oyster. The shell which covers these stages is continuous in outline.

As stated, a velum still existed at this dimyarian stage, Pl. xxiv, figs. 1-2. The long vibrating cilia were in active motion and some motion of the velum as a whole was noted; but it was not seen to extend beyond the margins of the shell. Attempts have been made by Horst and Ryder (62) to discover the method by which the young oyster attached itself to the object of permanent fixation and both investigators surmised that it might have a brief byssal attachment. Ryder, in considering the fixation of the embryos described by him,² thought that it was effected by means of the border of the mantle reflected over the edge of the undermost valve as shown in his figure. The nearest approach to a foot known in the developing oyster is that shown in fig. 24, p. 299, and I discovered no traces of a foot in my youngest specimens. As the byssus is an organ developed in the ventral portion of the foot, the high reduction or almost complete absence of that organ is in itself strongest evidence against the suggestion that the attachment

¹ It is possible that the first formed muscle does not point to an ancestral single-muscled Pelecypod, in which only the anterior adductor was developed. It may point to some muscle in the primitive ancestral mollusc from which the Pelecypoda were derived, and which muscle became the anterior adductor of the Pelecypoda.

² The fry described is comparable in age to my Pl. xxiv, figs. 13-16, and is not to be confounded in its attachment with the permanent attachment made at the close of the prodissoconch stage, Pl. xxiv, fig. 17.

of the young oyster is effected by means of a byssus of however short a duration. In my studies of the young of *Avicula*, *Perna*, *Pecten* and *Anomia*, Pls. XXVII-XXIX, it is shown that a notch for the projection of the byssus, or foot, is marked in the dissoconch shell immediately after the close of the prodissoconch stage. On most careful study no such indications of a byssal attachment were seen on the lower valve of attached oysters, and as they were growing on transparent media, fullest opportunity was enjoyed to make such observations. In view of the evidence it is therefore safe to conclude that the oyster does not have a byssus at any period of its development. The preliminary fixation is probably effected by means of the reflected mantle border, as described by Ryder, and is then immediately succeeded by a cementing conchyolin attachment of the extreme edge of the lower left prodissoconch valve.

The fact that a velum, or swimming organ, exists up to the period of permanent fixation, accounts for the great reduction of the foot, because that organ is unnecessary while the animal is provided with another locomotive organ, and is useless for progression after the animal is permanently attached. The reduction of the foot is clearly attributable to disuse and a high degree of concentration of development. This is another of the cases of extreme concentration of development seen so markedly in the development of the oyster.

The gills of the young oyster, Pl. XXIV, figs. 1-2, and fig. 6, consist of two rows of filamentous appendages, one on either side. They are fixed to the body mass anteriorly, but are free posteriorly, and are capable of considerable dorsal and ventral rotation. Eight club-shaped filaments were counted in either row at this early stage. Each filament is ciliated and perforated by a tube which expands dorsally into a canal connecting the tubes of the several filaments. The filaments are entirely free and separate from one another excepting on their dorsal border and are not bent back upon themselves on their ventral margins as they are in later stages. Each filament represents a hollow bag, or pouch, in which the blood is aerated by water kept in constant motion by the active cilia. This stage of development of the gills is exactly comparable to that figured in the young of *Mytilus* by Lacaze-Duthiers (41). The condition is also comparable to that described by Mitzukuri in the adult of *Nucula* excepting that in that genus a pair of filiferous branchiæ exist on either side. After tracing the further development to the adult condition in *Ostrea* it will be seen that the gills of the other Pelecyпода described are only modifications of this simple early type.

V. OSTREA: DEVELOPMENT OF THE SOFT PARTS.

THE SPAT.

At the close of the period just described, the young oyster enters on stages of growth both in the soft and hard parts which are rapidly approaching the conditions characteristic of the family to which it belongs. They are stages distinctly post-embryonic and I shall consider them as the nepionic or babyhood stages.¹

The young oyster, Pl. XXIV, figs. 1-2, growing on a glass slide, was kept alive in a

¹ For a discussion of the nomenclature of stages *vide* section III.

beaker of sea water for four days. When twenty-four hours older than the figures cited, a good deal of spat growth had taken place; the velum had disappeared and the anterior adductor was difficult to discern, but I think still existed in a position much nearer the hinge margin than in figs. 1-2; the muscle had therefore revolved dorsally. The posterior adductor had not changed much in its position; but the palps had revolved dorsally. The animal was yellowish-green as on the previous day, and the mantle border was wide and actively extended and retracted. The action of the parts was more clearly seen when viewed from the left side through the glass to which it was attached than from the right upper side. From this view many observations were made. The gill filaments at the end of twenty-four hours were not yet joined to one another on their ventral margins as in later stages.

When the same specimen was forty-eight hours older than Pl. xxiv, figs. 1-2, no anterior adductor muscle was seen. The posterior adductor from its earlier position had moved ventrally so that it lay near the border of the prodissoconch valves. The palps had revolved dorsally so that they were situated near the hinge line, but were directed ventrally; a fact to be discussed later. I did not see the radial muscles of the mantle visible in later stages, but they doubtless existed; no marginal tentacles were yet developed. The rhythmical pulsating body, noticed on the first day in the umbo of the left valve, had disappeared or become hidden in the increasing liver follicles. No heart was discovered on the dorsal border of the adductor, where it is later found. The liver was greenish brown, not light green, as at first.

Pl. xxiv, fig. 3, is from the same specimen three days older than figs. 1-2. The spat shell has grown considerably, the posterior adductor has moved to a more ventral position than it occupied forty-eight hours after attachment, and the palps have moved farther dorsally. The gill filaments are now connected on their ventral margins by cross connecting bars, and this is the beginning of the intricate system of cross connecting network, characteristic of the adult ostrean gill. The filaments in young and adult *Pecten* are joined by interlocking but separable cilia, similarly to those of *Mytilus* as described by Peck, but the connection in *Ostrea* is a complete organic union brought about by the concrecence of fleshy processes from the margins of adjoining filaments. The cross bars begin to be developed between the filaments in the anterior portion of the gill and from that region are formed posteriorly in a serial manner between successive filaments. In oysters up to 2.2 mm. in height only a single series of cross bars exist and those are on the ventral margin as in Pl. xxiv, fig. 3. The ends of the gill filaments in the spat, fig. 3, are recurved and joined by concrecence at their tips with the recurved filament tips of the opposed gill-lamella. This is understood by comparing the diagrams of the gills of developing *Ostrea* of this stage, Pl. xxiv, fig. 7, with those of an adult *Pecten*, Pl. xxiv, fig. 12. The contiguous surfaces of the direct and reflected portion of the filaments are not organically connected at this early period, so that each gill-lamella represents a hollow cavity bordered by its filamentous walls and a condition similar to this has been observed in adult *Perna*. The two gills are of about equal size at this period. Horst states that in young *Ostrea edulis* the gills are filamentous, joined only at the bases and tips; and he compares this condition with Lacaze-Duthiers' (41) well-known observations on *Mytilus*.

We will now consider an oyster, Pl. xxiv, fig. 4, considerably older than our last figure. Ryder (63) published a figure and description of an oyster somewhat younger than this and yet older than my Pl. xxiv, fig. 3. He compared the anatomy of his figure with that of Professor Huxley's figure (my fig. 25, p. 300) and demonstrated serial connections between these and the adult. Pl. xxiv, fig. 4, illustrates a young oyster of the spat stage growing on a glass slide, on August 6, 1888. The single adductor muscle occupies a sub-central position similar to that of the adult. The palps have revolved dorsally and assume a position intermediate between that shown in Pl. xxiv, fig. 3, and that characteristic of the adult, Pl. xxv, fig. 12. They differ from the adult in that the outer pair of palps forms a hood above the mouth which opens downwards and not as directly forwards as in the adult. Both these differences are discussed by Ryder (63). Four palps exist, but they are marked by few (five) furrows on their surface, instead of a great number as in the adult. Ryder observes this difference, and says that though few in the young he has counted over a hundred furrows on one side of the lower palp of an adult.

The heart is situated in a pericardial cavity above the adductor muscle, as in adults. From ninety to one hundred and ten heart-beats per minute were counted. This is a very high number, as Professor Ryder (64) notes that in the adult the heart-beats probably do not exceed twenty per minute. A large pulsating artery, *v*, passes to the mantle border where it is confluent with the posterior tips of the gills, and lesser ramifying arteries bifurcating frequently are spread over the mantle in every direction. These are not shown in the figure as they would confuse other details. The blood corpuscles traversing the arteries may be readily seen through the thin shell as indicated by arrows and, when the heart is beating rapidly, the blood may be seen returning to the heart through the canals on the dorsal border of the gills. It passes out from these canals through the foramina *c* and *d*, and also from between foramen *d* and a point nearer the anterior tips of gills. At *d* the afferent and efferent vessels are connected and though most of the blood from the gills passes into the heart, some corpuscles may be seen joining the efferent current and flowing into the large artery, *v*, which supplies the mantle border.

This specimen growing on glass afforded excellent opportunity to study the gills. The filaments of the two gills, *A*, *A'*, Pl. xxiv, fig. 4, are connected by several rows of cross bars, instead of only a single row on the ventral margin. (Compare with Pl. xxiv, fig. 5.) An oyster, 6 mm. high, was observed to have five cross filaments in the larger gills. The two first gills originated simultaneously as far as known. They began as tubular disconnected bags, as described; by the conerescence of lateral fleshy processes and of the inwardly grown recurved tips of the filaments, their present form, which is diagrammatically shown in Pl. xxiv, fig. 8, has been built up. But this accounts for only two gills and there are four in the adult; the development of the last two gills has not been previously studied, though Ryder (63) states that in very young spat only two are present. When first studied on the sixth of August, the young oyster, Pl. xxiv, fig. 4, besides the two larger gills, *A* and *A'*, had a third very short gill, *B'*, on the right side; but no corresponding, fourth short gill on the left side. The gill *B'* was continuous along the margin of the adjoining gill *A'* for its whole extent. It originated from the same base as did *A'* for the outer border of *A'* was first formed, the inner border be-

ing the reflected portion and of later growth. This will be better understood by comparing the diagrams of the gills of *Ostrea*, figs. 6-9, with those of *Anomia*, fig. 11, and *Pecten*, Pl. xxiv, fig. 12, where the origin and relation of separate gills and gill folds are perfectly clear. The newly formed gill *B'* was composed of the same number of filaments as was the well developed gill *A'*. In dissecting similar specimens it was found that the tips of the filaments of the gill *B'* were already folded back upon themselves, but they are reflected outwardly instead of reflected inwardly (toward the median line of the body) as is the case with the filaments of the first formed gills (again compare with the diagram of gills of *Pecten* and *Anomia*). After an interval of two days, a fourth gill, *B*, shown diagrammatically in Pl. xxiv, fig. 8, appeared on the left side on the basal margin of *A*. It began as a minute bud-like process and grew as already described for gill *B'*.

In other specimens up to 4.75 mm. in height, a third gill, *B'*, had begun to develop on the right upper side as in Pl. xxiv, fig. 4, but no fourth gill had yet appeared on the left lower side. Oysters of 1 cm. in height had all four gills developed, but in disproportionate degrees. The right outermost was short, the right innermost long, the left innermost longer still, and the left outermost (the last formed) very short, as in the diagram, Pl. xxiv, fig. 8.

First, it is noteworthy that those gills, which are to form the right and left outermost gills of the adult, appear much later than the two innermost gills. Secondly, it is a remarkable and interesting fact that a considerable time elapses between the origination of the right outermost gill *B'* and the left outermost gill *B*. Stoliczka, in his "Cretaceous Pelecypoda," on page 2, says, "I have examined one or two animals of almost every family of the Pelecypoda, and in all I found that there are at least two gill-lamellæ present on either side,—never a single one, though they are often unequal and one of them sometimes, as in the Tellinidæ, nearly obsolete."¹ The late appearance of the third and fourth gills in *Ostrea* may have phylogenetic significance, but the irregularity of their appearance is probably due to other causes, perhaps due in some way to the pressure exerted on the parts as the oyster lies on the left side in its adopted habit of fixation.

Viewing our specimen from the left side through the glass to which attached, it was found that the dorsal margins of the several gill-lamellæ were not superimposed; the united borders of gill *B'* and the outer lamella of gill *A'* were near the middle line of the valves. The reflected borders of *A'* and *A* united to form a margin nearer the ventral edge of the shell than the previous gill margin. The outer lamella of *A* and the new gill *B*, when formed, made a united border still nearer the edge of the shell. The result of this want of juxtaposition was that, when viewed from the right side, fig. 4, Pl. xxiv, the gill *A* looked much larger than *A'*, because it extended nearer to the margin of the shell. In degree this was untrue, though as a matter of fact *A* is somewhat larger than *A'*. Dr. Pelsener, in his report on Lamellibranchiata in the Challenger Reports, gives a very clear figure showing the condition and relation to one another of the gill filaments in a large number of genera.

The course of the alimentary tract has been traced in the young oyster by Ryder (63),

¹ According to Dall (16), a single gill-lamella, composed of separated filaments, exists on either side in *Dimya*. He

briefly discusses the relations of the gills and classification on this basis in Bull. Mus. Comp. Zool., Vol. xviii, 1889.

but it may not be amiss to repeat the observations as my specimens, growing on transparent glass, were very clear. In Pl. xxiv, fig. 4, the dotted outlines of the alimentary canal are those portions not visible from the right side, but seen when the oyster was viewed from the left side through the glass microscope slide to which it was attached. From the upper part of the hood-shaped palps a short œsophagus, α , leads directly into the stomach, st . The stomach, embedded in greenish-brown liver, has a circuitous outline especially on its ventral border. The intestine leads from the posterior end of the stomach and extends in a nearly direct line to a point half way past the adductor muscle. It then takes a sharp bend and, returning on itself, curves and follows the dorsal outline of the body; again turning when near the umbos, it follows the outline of the body and passes to the left of the œsophagus. It is then produced posteriorly in a curving line, passing to the left at the two points where it crosses the earlier portion of its own track and emerges from the liver mass just above the heart. It passes outside of the heart and wrapping itself around the adductor muscle terminates in close relation to that muscle. This course of the alimentary canal is identical with that figured by Ryder (60), in an adult, excepting that in the adult the œsophagus is directed more anteriorly than in the spat. The fæces, of a peculiar, nearly horse-shoe shape,¹ pass from the intestine in small particles and are carried from the cloacal space by the excurrent water from the gills through the opening, s , Pl. xxiv, fig. 4, formed by a sinuosity of the border of the right valve. All water from the body passes out through this opening, as indicated by arrows, and the mantle is retracted to allow of its passage.

A special excurrent passage is characteristic of younger and older spat than the one described (Pl. xxv, figs. 5-6); but no trace of it has been found in the adult. The sinuosity of the right valve is apparently due to the constantly retracted condition of the right mantle border at this point. It is constantly retracted to admit of the passage of the excurrent water and being so retracted, as a necessary result, the shell is not built at this area as rapidly as at other places where the mantle is fully extended. It might be considered that the peculiar excurrent opening was due to the mechanical conditions under which the oyster lives, an opening being necessary on account of the close relation of the shell to the object of fixation, and it is possible that this is the case; but against it may be urged the fact that no such character is found in *Anomia* which is subject to similar conditions. I think that this excurrent passage and the correlated sinuosity of the right valve are of hereditary significance. Examining the fossils, we find a similar sinuosity of the left and right valve characteristic in marked degree of the genus *Gryphæa*; it is also found frequently in *Exogyra* and in many fossil members of the *Aviculidæ*, from which last group the *Ostreadæ* were doubtless evolved.²

As in the case presented, many peculiarities of the form of shells can doubtless be elucidated by a study of the soft parts and life-habits of the animals. The byssal notch, ridges of large siphonated forms as the *Myidæ*, and siphonate processes of *Gasteropods* are examples of such characters, many of which are specially studied in this paper.

¹The horse-shoe shape is the form of the cross section of the fæces and owes its origin to the peculiar form of the intestine Ryder (60).

²In section VII, it is stated that *Gryphæa* and *Exogyra* are probably aberrant members of the *Ostreadæ*, not typical

forms in the line of evolution of the group. I do not think this militates against what is above stated. *Ostrea* has an excurrent sinuosity of the valves similar to that found in *Gryphæa* and *Exogyra*, in all, inherited (if at all) from far-off ancestral groups.

The mantle borders of Pl. xxiv, fig. 4, are free throughout their extent, with the exception of a small area near the umbos, where the borders of the two folds are confluent. The margins are thickly set with tentacles which are slightly pigmented with black. When undisturbed and quietly feeding, the mantle stretches out to the margin of the shell on all sides and even protrudes considerably beyond it. It moves actively, being constantly retracted and extended by the radial muscles shown in my figure and described by Ryder (63). The radial muscles are best seen from the left side when the spat is viewed through the glass to which attached, as the lower valve is thinner and less pigmented than is the upper right valve. The marginal tentacles are constantly in motion, being continually elongated and retracted. When elongated they are used with a tentative, feeler-like motion, and if irritated are capable of extreme prolongation. The gills and palps move frequently and suddenly. The adductor muscle in Pl. xxiv, fig. 4, is seen to be composed of two parts, as is that of the adult, Pl. xxv, fig. 12, and a condition of the adductor similar to that of *Ostrea* is seen in *Perna*.

During later stages of growth the soft parts rapidly assume the form, structure and position which they occupy in the adult, Pl. xxv, fig. 12. The mouth parts are revolved towards the umbos and the anus and adductor are revolved in the opposite direction, towards the free ends of the valves. The gills increase in complexity by the development of cross partitions within the gill chambers, between the contiguous faces of the direct and reflected portions of each gill lamella. These partitions form walls joining gill filaments and separated from succeeding walls by eight or ten filaments not so joined. Their existence gives rise to the folds characteristic of the adult oyster's gill. Large water tubes are thus formed, each tube bordered by eight or ten gill filaments on either side with their network of cross bars.

An epitome will now be given of the changes by which the adductor muscles of the young oyster become transformed into those of the adult and the relation of these changes to what exists in other adult Pelecypods is discussed. The embryo first passes through an early single-muscled stage, fig. 25, p. 300, in which the single adductor is the equivalent of the anterior adductor of dimyarians. This stage, as stated I believe, is a typical early stage of all Pelecypod embryos.¹ Later, the oyster has two adductors, Pl. xxiv, figs. 1-2, entitling it to ancestral kinship with dimyarian Pelecypoda. Finally the anterior adductor is lost, and the remaining posterior muscle is alone retained.

In the embryonic oyster, fig. 23, p. 299, the mouth and anus are closely approximated on the ventral aspect of the body. Passing to figs. 24 and 25, pp. 299-300, the anterior adductor muscle has developed, and the anus has revolved dorsally. In Pl. xxiv, figs. 1-2, the posterior adductor has developed on the ventral side of the intestine, which wraps around that organ as in later stages, and in all adult Pelecypods. In the last figures the velum, interposed between the anterior adductor muscle and the mouth, prevents the mouth revolving dorsally as it otherwise might have done. Passing to Pl. xxiv, fig. 3, the mouth has revolved dorsally similarly to the anus, and lies nearer the umbos than in previous stages. However, as noted by Ryder (63) in his studies, it still opens downward and not as directly forward as in the adult. In Pl. xxiv, fig. 4, the mouth lies still nearer to the umbos of the valves and from this stage to the adult, Pl. xxv,

¹ Vide p. 280, and section xv.

fig. 12, where it immediately underlies the umbos, and opens toward them is merely a series of mechanical stages. Correlatively with the dorsal revolution of the mouth the anterior adductor muscle has disappeared in the growing oyster.

In the dimyarian stage of the young oyster, Pl. xxiv, figs. 1-2, the relative position of the axis of the body to the hinge axis of the shell¹ resembles that of adult typical dimyarian Pelecypoda,² Pl. xxv, fig. 9, where the hinge is dorsal, free edges of the valves ventral, the mouth and anus lying at either end of the equal valves, so that the antero-posterior axis³ is nearly parallel to the hinge axis. In the adult oyster, Pl. xxv, fig. 12, this relation is different. The mouth lies close up under the hinge line, marking this as the anterior end of the shell. The free ends of the valves are at the posterior extremity, the gills lie on the ventral side, and the intestine on the dorsal.⁴ The antero-posterior axis passes nearly through the umbos and centre of the valves and at an angle of about ninety degrees from the hinge axis.

To bring about the adult condition the antero-posterior axis has therefore revolved through an angle of about 45° from the position it had in the dimyarian stage. In this revolution the anterior adductor has disappeared and the posterior adductor has become sub-central, thus occupying the functionally most effectual position. In other monomyarians, as *Pecten* and *Anomia*, Pl. xxix, figs. 1-2, the mouth closely underlies the umbos, which are in the median plane of the shell; thus the relations of the antero-posterior axis to the shell are similar to those of *Ostrea*.

In heteromyarians, as *Mytilus*, *Modiola*, Pl. xxv, fig. 10, *Perna*, Pl. xxv, fig. 11, and *Avicula*, a transitional series may be studied in which the relations of the axes are changed from what exists in the typical dimyarians, such as *Mya*, Pl. xxv, fig. 9, to what we find in the single-muscled group, as *Ostrea*, Pl. xxv, fig. 12.

In the clam, *Mya arenaria*, fig. 9, the adductor muscles are at either end of the longer axis of the shell, the mouth lies close behind the anterior adductor, the anus overlies the posterior muscle and the umbos lie dorsally. The antero-posterior axis is nearly parallel to the hinge axis. It is seen that in *Modiola*, Pl. xxv, fig. 10, the mouth and anterior adductor have revolved dorsally, so that they lie nearer to the umbos than in the clam. Similarly the posterior adductor and anus have revolved in the opposite direction, and occupy a position much farther removed from the hinge line than in the clam. The antero-posterior axis lies at an angle of about 25° from the hinge axis. In *Perna ephippium*, Pl. xxv, fig. 11, the mouth lies close up under the umbos, but the umbos are not in the median plane of the shell. No anterior adductor was found, but it probably exists in closely related species.⁵ The posterior adductor and anus are still further re-

¹The hinge axis refers to an ideal line drawn through the hinge area, and coinciding with the axis of motion of the valves, as shown in Pl. xxv, figs. 9-12, inclusive.

²I say resembles because the mouth does not closely underlie the anterior adductor muscle, as the velum intervenes, and therefore the comparison is not exact, though to all intents and purposes the comparison is perfectly correct.

³The antero-posterior axis, as shown in Pl. xxv, figs. 9-12, is considered as passing through the mouth and middle of the posterior adductor muscle and nearly or quite coinciding with the termination of the intestine.

⁴The fact that the umbos in the oyster are at the ante-

rior end of the body has already been pointed out by several authors, and Hyatt (28) figures an oyster drawn over a clam to show their relations. Ryder (63), on page 787, notes the rotation of nearly ninety degrees that must take place from my fig. 25, p. 300, after Huxley, to bring about the adult relation of parts.

⁵Mr. Purdie, of New Zealand, notes that *Mytilus latus* has no anterior adductor, while two otherwise closely related species *M. edulis*, and *M. magellanicus*, have anterior adductors. In *M. latus* the loss of the anterior muscle is accompanied by a movement of the one existing muscle inwards, nearer the central plane of the valves, where its mechanical action is more effectual.

moved from the hinge line than was the case with *Modiola*, and the antero-posterior axis lies at an angle of about 50° from the hinge axis.

A revolution of the axes similar to that traced in oysters, and in the above serial groups, may be seen in *Mulleria lobata*, Pl. XXVI, figs. 5-7, a widely separate genus. According to Adams and other authors, it has two muscles when young; but, when fully grown, one muscle. The anterior muscle has disappeared, and the posterior, which is retained, lies in the middle lower portion of the shell, in a position closely similar to that of an oyster. This case is particularly interesting, as the change takes place much later than in the oyster; for the two-muscled stage is not an embryonic one, but is of a much later period of development. In *Ætheria*, a near ally, the two muscles are retained throughout life, in a partially revolved position. *Tridacna* is another genus having but a single adductor muscle in the adult, and that muscle is the posterior. According to Woodward's figure the single muscle is in a sub-central position and the posterior retractor of the foot occupies its common point of insertion close to the dorsal aspect of the adductor. The mouth and palps have revolved dorsally so that they lie close up under the umbos as in *Ostrea*, marking this as the anterior end of the valves, and a large byssus by which the animal is attached is protruded through a notch in the valves immediately below the umbos. The antero-posterior axis lies nearly perpendicularly through the umbos and middle of the valves. The revolved position of the axes of the soft parts in *Tridacna* is not accompanied by any marked changes in the form of the shell excepting the position of the byssal notch. Allies of *Tridacna* are typical dimyarians and it is doubtless dimyarian when young.

The theory of the revolution of the axes explains the changed position of the axes and adductor muscles on purely mechanical grounds. It is found in widely separate genera of Pelecypoda that the revolving of the axes is accompanied by a reduction and final loss of the anterior adductor as it moves into a position close to the hinge area where its mechanical action is slightly if at all effectual in closing the valves. At the same time the single posterior adductor increases in size as it moves into a sub-central position where its action is most effectual. The revolution of the axes in Pelecypods, relatively to the axis (hinge) of motion of the valves, is therefore seen to be closely correlated with the reduction and final loss of the anterior adductor, together with the increase and final exclusive retention of the posterior. This theory substantially as here presented was published in my preliminary paper. While that paper was in press, a paper was published by Dr. Benjamin Sharp in which he presents a mechanical theory for the loss of the anterior and retention of the posterior adductor muscle in Pelecypoda, which is quite similar to that of the revolution of the axes.

It is a very noticeable fact that oyster spats attached to various foreign bodies do not lie with their axes arranged in any special direction. Different individuals attached to the same stone or shell, may have their axes at every angle of deviation, in the plane of the surface of attachment, as compared with one another. I have never seen them arranged with any reference to the resistance of prevailing currents. On the other hand, *Anomias* and *Crepidulas* are sensitive to prevailing currents. Large numbers of *Anomias*, attached to a single block, will very commonly be found with their axes parallel and headed one way (see discussion on development of *Anomia*, section XIII), and *Crepi-*

dulas, Pl. xxiii, fig. 22, may be found piled on one another to the height of several inches, each individual with its axes in the same vertical plane. These comparisons go to prove what was claimed earlier, that calcareous fixation of the oyster's lower valve took place when it became attached. It is almost certain that if any form of prehensile attachment had existed for an appreciable time, we should at least occasionally find evidence of the arrangement of the shells in the line of least resistance to currents.

VI. OSTREA. DEVELOPMENT OF THE SHELL.

In the study of the soft parts it is shown that the shell of the oyster develops from a primitive structure, the preconchylian gland, which is found not only in other genera of Pelecypoda, but in other classes of mollusca as well. According to Horst, a simple unpaired-cuticular membrane, my fig. 22, p. 297, the product of the cells of the shell-gland precedes the paired calcareous shell.

The two valves of an adult oyster are together homologous with the single valve of adult Cephalous molluscs (see p. 281). In both, the shell originated from similar structures, one as a single and the other as a paired organ. The adult shell of Cephalous mollusca is termed a conch. Therefore, in view of its homology and strikingly different double character, I have suggested (36) the name *dissoconch*¹ for the shell of an adult oyster and similarly the same terminology is applicable to the shell of other Pelecypoda.

The protoconch of Professor Owen, in Cephalopods, figs. 1-8, p. 292 and Pl. xxiii, figs. 15-16, is the early cup-shaped shell which precedes the conch, or true shell. A spirally twisted protoconch in Gasteropods,² Pl. xxiii, figs. 19, 21, 23, and a saddle-shaped periconch (protoconch) in Scaphopods, Pl. xxiii, figs. 13-14, may be also found as an embryonic shell preceding the conch or true shell of these groups (see section III). It will be seen from the study of *Ostrea* that the true shell, that which characterizes the adult, originates with the introduction of the spat stage, Pl. xxiv, figs. 19-21 and Pl. xxv, figs. 1-7. The earlier shell, Pl. xxiv, figs. 17-18, is strikingly different. It is the completed shell of the embryonic stages, and as shown in previous studies, it has developed from structures closely similar to those found in Cephalous molluscs. The embryonic shell of *Ostrea*, therefore, is distinctly the homologue of the protoconch and periconch. In the oyster, however, this shell is not single- but double-valved and, therefore, deserves a distinct name. As it precedes the *dissoconch* or true shell, I have suggested (36) the name *prodissoconch*³ or early, double shell, for the first-formed shell of the oyster. A *prodissoconch* or embryonic shell, strikingly different from the succeeding *dissoconch*, is figured in this paper in many widely separate genera of Pelecypoda (see Pls. xxiv to xxx and cuts in the text) and it may be safely considered as characteristic of the class.

The shell of oysters, at different periods of growth, presents striking dissimilarities. There are four well-marked stages of growth: (1) phylembryo, early embryonic stage; equivalvular, with a straight hinge line; (2) completed *prodissoconch*, symmetrical fry stage, with a curved hinge line and high umbos developed; (3) nepionic (spat) stage,

¹ Δισσόσζ, double; Κόγχη, shell.

² Πρό, before.

³ See footnote, p. 292, and discussions in section on Classification of Stages of Growth and Decline.

with a flat, lower left valve and convex, upper right valve; (4) adult, flat, upper right valve and concave, lower left valve.

The early prodissoconch or phylembryonic stage of *Ostrea edulis* is equivalvular, nearly discoidal and flattened into a straight line at the hinge area. On the hinge line, minute interlocking teeth are visible when viewed from the dorsal side. Embryonic shells of *Ostrea edulis* of this stage are represented in Pl. xxiv, figs. 13-16. They were removed from the gills of the parent and sent out as preparations by a London dealer in microscopical supplies. The age is similar to fig. 25, p. 300. The valves are saucer-shaped, and are marked by concentric lines of growth closely approximated dorsally, but farther apart ventrally and anteriorly, so that the centres of calcification are already pushed posteriorly by the growth that has taken place, as seen in figs. 13 and 15, viewed from the left and right sides respectively. By polarized light the shell gives the characteristic lines of crystallized carbonate of lime. A straight hinge line seems to be characteristic of the phylembryonic stage of Pelecypoda before the development of umbos (see section xv). As examples, I would refer to embryos of *Ostrea*, Pl. xxiv, figs. 13-16, *Anodon*, *Cardium*, *Modiolaria* and *Montacuta*, Pl. xxiii, figs. 7-11, also to Hatschek's figs. 19-21 of developing *Teredo* and Ryder's (62) figure of an embryonic *Ostrea virginiana*.

The valves of the phylembryonic stage of *Ostrea edulis*, Pl. xxiv, figs. 13-16, have scarcely any umbos developed, whereas our next stage of shell development has prominent umbos. The completed prodissoconch of *Ostrea virginiana*, Pl. xxiv, figs. 17-18, has deeply concave valves which are nearly equal. The lower left valve is, however, somewhat larger and deeper than the upper right valve, fig. 18. The umbos are highly developed and are always inclined upward at a high angle, as the shell is invariably attached by the extreme border of the left valve. The umbos are directed posteriorly as shown in the studies of the soft parts, Pl. xxiv, figs. 1-2, and they invariably point to the left of the observer viewing them from above, a necessary consequence of their being attached by the left valve.¹ (For further discussion of the fixation of the oyster by the left valve, see section iv.) Coincident with the development of high umbos, the early straight hinge line, seen in the phylembryonic stage, is lost and is superseded by one of a gentle curvature. The prodissoconch is the completed shell of the embryonic free-swimming veliger period, and the young oyster becomes attached permanently at the close of this period, the fixation consisting of the soldering of the ventral margin of the left valve to the object of support.



FIG. 26. Completed prodissoconch of *Ostrea edulis*, attached by border of left valve in an almost upright position (after Horst).

The completed prodissoconch of *Ostrea edulis*, fig. 26, differs from that of our species, according to Horst. The umbos are less developed than in our species, but they are directed posteriorly. Teeth, also, are mentioned on the hinge line at this stage and earlier by both Horst and Lacaze-Duthiers, whereas in our species no teeth have been observed by either Ryder (63) or myself. The histological structure of the shell, as described by Huxley and Horst, is similar to that of our species. Specimens of *Ostrea edulis* kindly sent to me by Dr. Horst show unmistakably the teeth and other features described.

¹ Professor Ryder informs me by letter that he has never seen an exception to this nor have I, though I have

sought for umbos pointing to the right.

The prodissoconch of *Ostrea virginiana* is homogeneous and laminar in arrangement, "not prismatic" as in the immediately succeeding stages of spat growth as described and figured by Ryder (62). It is composed of lime infiltrating an amorphous matrix of conchyolin, as shown by treatment with acid. One of the marked characters of the prodissoconch is the uniformity of shape and size found in different individuals, it not having the ostrean tendency to variability noticeable in later stages. The height of the fully developed prodissoconch is about $\frac{1}{10}$ of an inch. The left attached valve turned over and viewed from the lower side is seen to be exactly like the right free valve in appearance. It is not flattened nor are there other indications to mark where it was attached, so that this attachment is evidently of a very superficial and delicate nature.

A prodissoconch identical, or very closely similar, to that found in *Ostrea virginiana* has been found in many species of the Ostreadæ. Ryder (62) has observed it in four species: *Ostrea equestris*, Say, from Florida; *O. conchaphila*, California; *O. cucullata*, Viti Islands, Pacific; and *O. peruviana*, Peru. I have observed it in undetermined oyster spats, from Cuba, and from the chamber of a *Nautilus pompilius*, from the Pacific. I also found ostrean prodissoconchs in the following: the spats of tertiary oysters from Carolina; *Gryphæa vesicularis*, Lam., Cretaceous, found in both European and American specimens; *G. calceola*, var. *nebrascensis*, M. & H., Pl. xxiv, figs. 23-24, from the Jurassic of Wyoming Territory, specimen number, 1881, U. S. National Museum; *Exogyra conica*, Cretaceous, Europe; *E. columba*, Lam., Cretaceous, Europe; *E. arietina*, Cretaceous, America; and *E. costata*, Say, Cretaceous, America. Of this last species abundant very young specimens, which I collected at Delaware City, Delaware, showed the typical early prodissoconch.

From the number and wide distribution of the species, it cannot be doubted that the prodissoconch found in *Ostrea virginiana* is characteristic of the Ostreadæ. The teeth noted above in the prodissoconch of *O. edulis* is the most striking difference that has been found in the prodissoconch of the family.

There is, in the prodissoconch and spat stages of the oyster, an organic conchyolin attachment of the shell itself, thus described by Ryder (62): "The cementing material seems to be the organic matrix of the shell which forms a perceptible layer on the outside of the valves, and which constitutes the epidermis or periostracum of the oyster." In the prodissoconch, as well as spat stage, the cement is so firm that, as Ryder says (62), the shell may be broken before it can be removed. To prove that this is an organic cement, if we put a drop of water on a dead, young shell and allow it to remain a short time, it can be readily picked up on the point of a knife. Quite large spat may be removed when dead (*i. e.*, the organic matter inert) by soaking or boiling. Treatment with acid, on the other hand, does not loosen the hold of the shell. Quantities of young spat die during the summer, yet few dead shells are found on cultch, because soon after death the organic cement decays, is dissolved, and the shell falls off. Professor Huxley notes that the European oyster separates naturally from unfavorable objects of support; and that the separation takes place naturally at an early stage can be seen markedly in many fossil members of the family. Conversely, the calcareous plug of *Anomia*, which is fixed to the object of support by a purely calcareous union, remains indefinitely after the death and separation of the individual to which it belonged. All the evidence is there-

fore in favor of the assumption that the cement by which the oyster is attached is wholly organic.

With the introduction of the spat stage, a fundamental histological difference arises abruptly in the structure of the shell of *Ostrea virginiana* as in *O. edulis*, fig. 27. As stated above, the prodissoconch consists of lime infiltrating an amorphous matrix of conchyolin, but in the initial spat stage the first layer of shell of the right valve is deposited in a "tessellated or prismatic" manner in a horny matrix, as described and figured by Professor Ryder (62, 64). Soon after the formation of the spat stage, the subnacreous, white porcellanous layer begins to be deposited on the yellowish-brown, prismatic layer, first making its appearance as irregular blotches in the centre of the valves. These two layers continue throughout the rest of the life of the oyster, and together, though in disproportionate degree, build up the massive adult shell. The prismatic layer always remains thin, as may be readily seen by sections, or by treating an adult with acid, when the remaining conchyolin of the prismatic layer will separate from the overlying subnacreous layer like a dissected skin.

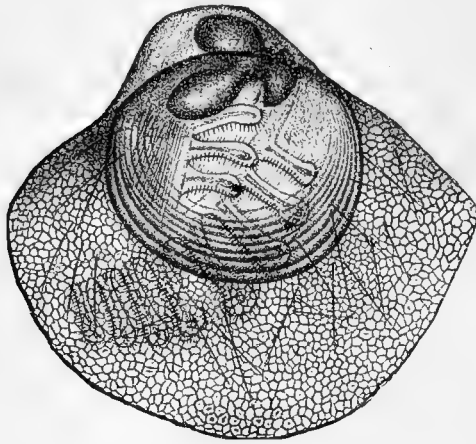


FIG. 27.

FIG. 27. Young *Ostrea edulis*. The prodissoconch is composed of homogeneous and the early dissoconch of prismatic cellular tissue.¹ The gills are filamentous.

FIG. 28. Fragment of border of upper valve, enlarged to show the prismatic structure.

FIG. 29. Fragment of lower valve (after Horst).



FIG. 28.



FIG. 29.

It is a remarkable fact that in young *Ostrea virginiana*, the prismatic structure is typical of the upper right valve alone; the lower valve presenting a fine granular structure, as in *O. edulis*, fig. 29. In later life in *Ostrea virginiana* and some other species, a very thin layer of prismatic tissue may be found in the left valve though it is for the most part eroded away, but the same layer is thicker and therefore better preserved in the right valve. The prisms of the right valve of the adult oyster are not as perpendicular to the surface as in the young, fig. 27. There-

fore in horizontal section the outline of the prisms presents oblique rather than hexagonal faces. A similar obliquity of the prisms may be seen in *Solemya mediterranea*.

The nepionic or infant stages of molluscs begin according to the classification of stages adopted with the formation of what Professor Owen called the apex of the conch, or true shell. It is shown that the spat marks the beginning of the dissoconch (true shell) in *Ostrea*; therefore the spat is considered as the nepionic period.² In my preliminary paper I said the spat of *Ostrea virginiana* is divisible into five stages which were described at some length. I also said that they are more or less clearly marked in every

¹The relations of structure of the prodissoconch and dissoconch are the same in *Ostrea virginiana*, also in *Perna*, *Pecten* and *Anomia*, as described in the text.

²In my preliminary paper this same period was consid-

ered as the "silphologic" period. In a footnote to this paper Professor Hyatt has given up the use of the term silphologic, and has supplied in place of it the term nepionic (*vide p.* 290).

regular growing, unworn, young specimen. There are often well defined stages indicated as arrests of growth in the early growth of the spat; but I must retract the statement that there are typically five and that they are always more or less clearly marked in regular, unworn, young specimens. Frequently no indication of later spat stages are present, and they cannot be considered as constant. To remodel my conclusions and statement: The spat stage in *Ostrea virginiana*, as a whole, is frequently marked by stages of growth. Stages are characteristic of the earliest spat growth and as many as five have been found, but often no more than two or three are indicated. To study these stages specimens should be sought growing in protected places, as the wear of sand and waves destroys their demarcation rapidly. Some spat found in the inside whorls of dead *Sycotopus* shells and others, secured on glass in drain pipes and on inverted flower pots, retained the markings clearly.

The spat growth begins along the ventral margin of the prodissoconch valves Pl. xxiv, figs. 18-21 and Pl. xxv, figs. 3-4, and throughout life the most rapid growth is in this direction. The growth rapidly pushes up the sides of the valves, and between the hinge areas of the latter, Pl. xxv, fig. 3, lifting them apart and separating them by interstitial growth. A little to the right of the umbo of the lower, left prodissoconch valve, as seen from above, in the initial stages of spat growth, is a notch which indicates the beginning of the cartilage pit of the lower valve. This is seen clearly in Pl. xxiv, fig. 19. It is necessary to describe the left and right valves separately. The upper, right valve, Pl. xxiv, fig. 20, is continuous with the prodissoconch valve and follows the curve of that stage though in a lessening degree. It spreads out laterally on the hinge line in a descending curve, and on the margin overhangs the lower valve by a considerable amount, Pl. xxiv, fig. 21, as it continues to do while the shell is flatly related to the object of fixation. The same overhanging of the upper valve may be seen in young *Pectens*, Pl. xxviii, and *Anomias*, Pl. xxix. The lower left valve of the young oyster, Pl. xxiv, fig. 21, starts as does the upper, following the curve of the early valve. When this curve has been followed for an extremely brief period, the valve suddenly flattens and becomes closely related to the surface of attachment. The result is, that a slight groove runs around the border of the spat valve, beyond which it is abruptly continuous with the flat later growth as mentioned by Ryder. I have, however, to note a peculiar and significant exception. Sometimes, instead of becoming flat and closely related to the object of attachment, the spat valve is continuously curved throughout its early growth, and not at all flattened. It then resembles the upper valve in shape. This curved shape is held, as far as observed, only on rough objects of attachment. Seeking for such material on rough stones and shells, one will always find some valves more or less curved in their earliest stages. This is interesting, as showing the modifying influences of environment on a very young stage, where heredity might be supposed to fashion the form with overpowering force. Further notes on this character are given when discussing *Exogyra*, section VII.

When the spat shell has attained the height of 0.8 mm. to 1.2 mm., frequently a well defined stage or period of growth is marked by an interruption in the lines of growth as shown in Pl. xxv, figs. 1-2. This indicates what is considered as the close of the first nepionic stage. In the shell growth succeeding the first nepionic stage the upper valve,

fig. 1, is in form a continuation of the first stage. The lower valve spreads out over the object of attachment by wing-like extensions of its anterior margins, and makes a shoulder on its anterior border by its increased growth, where it comes in contact with the outer limit of the first stage, fig. 2, and similar shoulders mark the periods of growth of later stages in the lower valve, Pl. xxv, fig. 6. The lower valve may remain curved, as in the first nepionic stage, for a limited extent. When the spat has attained the height of from about 1.4 mm. to 2.4 mm., another stage is frequently marked by an interruption in the shell growth as shown in Pl. xxv, figs. 1-2, which illustrate the first and second stages of the nepionic or spat growth. After the second stage, as described, other stages may be found in the spat growth. They are marked as arrests in the regularity of shell growth and in the lower valve shoulders are formed by their contact with earlier stages as shown on the hinge border in Pl. xxv, fig. 2. In all, five stages have been observed; but the number and the later stages cannot be considered as characteristic as the first two stages are.

After the close of the second spat stage the shell is still even and rounded in outline, as the convolutions and distortions common in oysters do not often begin till growth has considerably advanced. The lower valve spreads out over the object of attachment, and leaf-like layers of shell deposition may be seen spreading beyond the limits of the hinge line, as growth continues, as shown in Pl. xxiv, fig. 19, and Pl. xxv, fig. 5. The upper valve in regular growing specimens frequently departs from the form which is observed in the earlier growth, Pl. xxiv, fig. 20, and spreading out laterally becomes more wing-like on the margin than in any earlier stages, Pl. xxv, figs. 5 and 7. These wing-like productions of the spat growth were pointed out and figured by Ryder (60). In describing such stages he says: they are ". . . . handsomely rounded in shape, not unlike a scallop in form, which they simulate still more by the lobes which they develop on the shell on either side of the hinge." This scallop-like form, shown in Pl. xxv, fig. 7, is quite likely due to the irritating action of a foreign body on the extended mantle border of the left valve, or it may be due to the opportunity to make more secure the fixation by deposition of lime in this direction. In spat growth the free ends of the valves often change the direction of their growth to the left or right of the median line. By this change the umbos may be revolved so that they often point in the opposite direction from that which they would have otherwise assumed, as noted by Ryder (65). A twist in the direction of growth as described is characteristic of the fossil genera, *Exogyra* and *Gryphæa*, in which the variation is always to the left of the median line viewed from above. The young oyster when it twists to the left resembles very much a young *Exogyra*; but when the twist occurs in the opposite direction, or to the right, as frequently occurs, this close comparison cannot be made. The right valve of the spat has a sinuosity, *si*, Pl. xxv, fig. 5, which is related to the excurrent flow of effete water as described, p. 307.

Throughout the period of spat growth the young oyster shell has an approach to the rotundity characteristic of the early spat stages. The attached valve is flat and the free convex, but when the oyster projects beyond the object of fixation this relative form of the valves is changed and the condition characteristic of the adult, Pl. xxv, fig. 8, is brought about. The attached valve becomes deeply concave or spoon-shaped and the free valve conversely becomes flat, as pointed out by Brooks and Ryder. At the close

of the spat period if the shell does not project freely from the object of fixation, then the relative shape of the valves characteristic of the spat is retained, the attached valve still spreading over the support, is flat, and the free valve is convex. In such forms the true spat period is marked as a smooth rounded convex area at the umbos.

In young *Ostrea virginiana* spat, as noted by Ryder (60), bands of purple color radiate from the hinge line, widening toward the free edges of the valves; but these coloration bands are in the prismatic layer and are therefore limited to the upper right valve. In none of the oysters growing on glass, have I seen color bands in the lower valve, which is nearly or quite white; in later growth, however, faint traces of color bands may be occasionally seen in the left valve. I found spat in the living chamber of a *Nautilus Pompilius*, when unpacked on arrival from Singapore, and these are similar to the spat of *O. virginiana*, showing similar prodissoconchs and nepionic stages, but no coloration bands, the upper valve being yellowish-white. The early spat growth of *Ostrea edulis*, fig. 27, p. 314, is very similar in form to that of *O. virginiana*, Pl. XXIV, fig. 20, but I have not had specimens for a comparison of later stages.

VII. GRYPHÆA, EXOXYRA AND ADULT OSTREA, WITH A CONSIDERATION OF THE MECHANICAL ORIGIN OF THE OSTREAN FORM OF SHELL.

The genus *Gryphæa* is described as free or attached in the young, yet I have not been able to find a species in which it is free at a very young stage. All the species studied have a flat area in the lower valve and a curved area in the upper valve at the umbos, corresponding to the condition found in the attached spat stage of the oyster. *G. arcuata* of the Lias is commonly considered as free, yet I have found well preserved specimens, Pl. XXIV, fig. 22, in which the lower valve is flat at the apex, where it was attached when young, and correspondingly the upper valve has a small convex area at the umbo, as noted by Sowerby. Flat areas of attachment have also been found at the umbos of two other highly arcuate species, namely, *G. calceola*, var. *nebrascensis*, M. & H., Pl. XXIV, figs. 23-24, from the Jurassic of this country, and *G. pitcheri*, Morton, from the Cretaceous of Texas.

The area of attachment in many species of *Gryphæa* is uniform in size, indicating that the shell dehisced at a very definite period from the object of attachment. In fact, highly arcuate forms must have separated early, as the involute form could not have been developed unless the shell was free. Other species were attached for a very variable period, as is seen by the differing size of the flat area of the lower valve and corresponding curved area of the upper. This is well shown in any large collection of the European form of *Gryphæa vesicularis* from the Cretaceous, where the arcuateness of the adult varies inversely as the length of period of attachment.

Exogyra, also, is said to have been free or attached; but here the case is somewhat more complex. Take, for example, the typical *E. costata*, Say, of the Cretaceous. Specimens are found in which a flat area at the apex of lower valve distinctly shows them to have been attached when young, but rarely are adults found with the object of early fixation still clinging to them, showing that as in *Gryphæa* and many oysters, they separated naturally. Other specimens are found which, upon most careful examination, show no

flattened area on the lower valve. I have noted that *Ostrea* may in its early nepionic period be attached, and yet not conform to the object, or become flattened at all, so that if it could have separated at the close of this period, the adult would show no sign of early fixation. This is what apparently took place in specimens of *Exogyra* which show no flat area. In such there is no proof that they were not fixed during the young stages, but merely that they debisced before the shell conformed to the outline of the object of support. Some individuals may be attached for a considerable extent, and a specimen in the American Museum in New York has an area of attachment measuring 11 cm. in its greatest length. This species is also very variable in the degree of costation. Aged specimens, as noted and figured by Whitfield, often lose the ridges and become quite smooth. I have seen many specimens in which the lower valve was first smooth, then costate, and later smooth again, or the reverse of this order. In a large collection one may find every gradation between the highly costate type, known as *Exogyra costata*, and the smooth type without costations known as *E. ponderosa*, Roemer. The relations of these species is about the same as that which exists between *Ostrea virginiana*, Lister, and *O. borealis*, Lam., which Verrill unites under the former species, as he says they may easily be connected by all sorts of intermediate forms.

In the Ostreadæ there is a striking peculiarity of the adult which has not been considered in its full significance, so far as I am aware. *The two valves are unequal, one being concave and the other flat; but they are not only unequal, they are very dissimilar, as different as if they belonged to distinct species in what would be considered typical forms.* This character of the shell is due, I believe, to the mechanical conditions of direct cemented fixation acting upon a Pelecypod shell, and is of great value in considering the systematic relations of attached groups as I shall attempt to show in the following pages.

As examples amongst the Ostreadæ, showing dissimilarity of the two valves, we may take *Ostrea edulis* of Europe, *O. compressirostris*, from the Eocene of this country, and *Exogyra costata*, from the Cretaceous. In these species the lower valve is plicated, and the upper smooth, and regular-growing, without plications. The examples could be multiplied extensively, but these suffice to give my meaning. In consulting Coquand's finely illustrated monograph of Cretaceous oysters, examples of this difference of the two valves will be found in many species. This is a highly interesting feature, as it is a *case of inherited or acquired characteristics, finding very different expression in the two valves of a group belonging to a class typically equivalvular.* As might be expected, variations from the rule are occasional as in *Ostrea marshii*, *O. larva*, etc., where the two valves are more closely alike. Dissimilarity is nevertheless the rule. The upper valve may bear characteristic features not found in the lower valve. As an example we may mention *Gryphæa vesicularis* of the Cretaceous, in which the upper valve in both European and American specimens is marked by radiating depressed lines. Similar radiating lines may be found in *G. dilatata* from the Jurassic, and indications of them have been observed in other species. These lines are a feature which would probably be of value in tracing the serial connections of the several species possessing them.

The differences in the two valves may be observed in species of Spondyli, especially those in which the right, attached valve is very ostreaform, while the free, left valve is

less modified, as shown in *Spondylus hippuritarum*, d'Orb., Pl. xxvi, fig. 1. We would also refer the reader to M. d'Orbigny's plates 450 to 461 of Cretaceous Spondyli, especial attention being called to his figures of *S. histrix*, Goldf., in which the attached valve is rough and o-streaform, whereas the free valve is evenly plicated and smoother. Striking differences in the features of the two valves may be seen in the Rudistæ as shown in *Radiolites fleuriauxa*, d'Orb., Pl. xxvi, figs. 11-12, in which the lower attached valve is irregularly cornucopia-shaped, whereas the upper free valve is comparatively regular growing, flattish and plicated. The young of this species and several species of Hippurites studied resemble an Exogyra (compare the figures cited with the adult and young of *Caprotina semistriata*, Pl. xxvi, figs. 10 and 20). Because the young of these aberrant forms resemble an Exogyra, I do not wish to imply any genetic connection with that group. I state later, p. 322, the conviction that the ostrean form is induced by the condition of fixation, and the similarity to an Exogyra in the young of the Rudistæ and Chamidæ is believed to be due to the similar conditions of a fixed cemented habit common to both groups, and not as expressing any affinities. This is a point which must be understood, as in this paper high importance is attached to the form of young shells in tracing genetic relations.

Aberrant forms of the Chamidæ are shells which show in a high degree differences in the attached and free valves. *Caprinula boissyi*, d'Orb., Pl. xxvi, fig. 8, from the Cretaceous of Europe is a remarkable form; the attached valve is deeply conical with perpendicular rugæ, whereas the free valve is spirally twisted, without plications and resembles a typical Diceras. *Caprotina semistriata*, d'Orb., Pl. xxvi, fig. 10, is another form not less remarkable in the striking dissimilarity of the two valves. In this species the attached valve is arcuately conical with perpendicular rugæ and showing at its base a spirally twisted tip as in *Radiolites*, Pl. xxvi, fig. 12. The free valve is of a simple concave form, not at all aberrant and not presenting the rugæ seen in the attached valve. A very young specimen of *Caprotina semistriata*, Pl. xxvi, fig. 20, was found attached to the base of a colony of this species in a specimen in the Museum of Comparative Zoölogy. This young *Caprotina* resembles an Exogyra, taking for comparison a young *E. costata* or an adult *E. spiralis*, Goldf. The attached valve is highly twisted and the free valve convex showing little twisting as in Exogyras. The specimen was too much worn to show lines of growth, but in the figure they are inserted where I think they would appear if not eroded, in order to render the form and its relations to the adult clearer. That they are fairly represented will be evident upon a comparison with similarly twisted shells where they are preserved. As the attached valve in *Caprotina*, Pl. xxvi, fig. 20, grows from its early twisted condition to the deeply conical condition found in the adult, Pl. xxvi, fig. 10, the lines of growth gradually and progressively assume a more and more horizontal position until in the adult they are nearly or quite horizontal and the attached valve has lost the twisted condition characteristic of the younger stages. The outgrowth from an early twisted condition of the attached valve to an adult deeply conical condition, as just described, doubtless took place in the development of *Caprinula boissyi*, Pl. xxvi, fig. 8, and the change may be seen in *Monopleura marcida*, White, Pl. xxvi, fig. 9. In Dr. White's paper (74) the same feature and the modification of attached shells are very well shown in many species.

Our examples of differences in the two valves amongst attached Pelecypods might

be carried further and for such inquiry we would refer to published works on conchology and palæontology. Believing that the inequivalvularity of the above genera is due to the conditions of environment acting on a bivalve shell, I would refer to species of attached Brachiopods in which is found further proof of the correctness of the conclusion. *Davidsonella rugosa*, Pl. xxvi, figs. 14-15, the Cretaceous, is soldered to an object of support by the lower valve, and here, as in the above cases of Pelecypods, the attached valve, which is rugose and concave, is strikingly different from the upper valve which is flattish and smooth. The same feature is shown in species of *Strophalosia* recently discovered and shown me by Dr. Beecher. *Productus proboscideus* of the Carboniferous has a tubular highly modified attached valve and a nearly normal free valve¹.

In the various genera considered, *the free valve is that which is least modified and nearest resembles the form existing in both valves of less aberrant related genera. It is the attached, cemented valve, which is highly modified and so much so as by itself in some cases to be with difficulty recognizable as belonging to the Pelecypods.*

In the shell of *Ostrea virginiana*, Pl. xxvi, fig. 13, there are lenticular cavities in the hard subnacreous portion which are filled with a soft, white, chalky deposit. These cavities are also noticeable in many fossil oysters and Gryphæas. In *Exogyras* they are commonly very large and abundant, especially near the umbos where shell growth takes place rapidly and to a great thickness. *Exogyra costata* shows these cavities well, and they are highly developed in *Exogyra aquila*, Goldf. and *E. couloni*, d'Orb. from the Cretaceous of Europe. Not infrequently the cavities in living and fossil shells will be found filled with mud, and in such cases it is evident that the shell roofing was formed to include the mud; being caused by the irritating action of that substance on the overlying mantle. Specimens of *Mya arenaria*, which have included mud in this fashion are frequent, although this shell never builds true camerated structure. The shallow chambered structure of the oyster was noticed by Professor Owen (50, 51) and was compared by him to similar conditions in the shell of *Spondylus*, *Ætheria* and some univalves. Professor Woodward (77) compared the structure of the oyster also with camerated structure in species of *Teredo* and *Caprinella* which he figures. This last genus is remarkable for the regularity and size of its chambers which truly resemble analogous structures in Cephalopods. Owen (50) notes the fact that *Spondylus* and other bivalves, which have camerated structure, are cemented to extraneous bodies by the shell. I have not made an extensive study of this subject; but what has been made, leads to the conclusion, that this statement may be safely reversed and we may say, that *bivalves which are cemented by one valve to extraneous bodies have a tendency to produce a camerated structure of the shell* which is not found in free forms. Thin shelled, cemented Pelecypoda, such as *Dimya*, quite likely would not show cameration, but amongst other groups it is general, whereas no free locomotive forms of Pelecypods, however thick the shells, have been found to possess such structure.²

¹In the developing shell of *Vermetus radricula*, fig. 9, p. 294, I have observed in well-preserved specimens that the shell is evenly spiral and regular growing while young and unattached. As soon as attached, however, the irregular loosely spiral features characteristic of the adult are introduced and are retained throughout subsequent growth.

²It is important to notice that fossil corals of the *Tetracorolla* type have a highly developed camerated structure. So similar is their appearance in their regular chambering that they may often be compared to chambered Cephalopods especially of the *Cyrtoceras* type which they simulate by their arcuate form. They also bear often a striking resemblance both in external and internal form to

In adult *Ostrea virginiana*, the left valve is concave, and the right flat, when growing naturally, the left valve being lowermost; and Ryder notes that the same relative shape is held by oysters which grow vertically in crowded beds. Oysters frequently attach themselves to the lower side of objects, so that the left valve is uppermost, and right valve lowermost, the reverse of the common position, Pl. xxv, fig. 8, and here again the normal relative shape of the valves is maintained, the left valve concave, the right flat. The shell of the oyster is so variable that we should expect it to be especially susceptible to varying conditions of environment; yet these strikingly different positions produce no change in the resulting form. Whatever the cause of the typical form of the group, the changed relations brought about by inversion, or other positions assumed by the growing valves, are insufficient to modify greatly the form of a modern individual, where hereditary or other influences bind the shell within the limits of its typical form.

Professor Hyatt (29) has published the view that the *attached supported* valve of fixed bivalve shells is the larger, the element of gravity being the active factor according to his ideas, and he ascribes the form of the oyster and similar shells to such conditions of environment. My conclusions on the form of attached Pelecypod shells, although somewhat similar, differ from those of Professor Hyatt. The conclusions, as presented in these pages, are that the form of fixed Pelecypoda is due to the condition of *cemented fixation*; whereas he assumes that the form of inequivalvular bivalves is due to *support*, the shell being free or not as the case may be. The two views are therefore based on different grounds of consideration, which should be borne in mind in a comparison of our studies.

The family of the Ostreidæ is characterized throughout by being attached, at least when young, by the left valve, as shown in Pl. xxv, fig. 8, and Pl. xxvi, fig. 13. The left attached valve is typically, deeply concave, of rough, irregular growth and comparatively thick. The right free valve, on the other hand, is flat or flattish, thinner, and less irregular. To perceive the truth of this statement it is necessary to look over a collection of the Ostreidæ, or in default of it some of the illustrated monographs, as Coquand's or White's. It will then be seen that all typical forms are referable to this description in a more or less marked degree. I say more or less marked, because some species, especially among the Alectryonia division, have right (free) valves which are comparatively like the left valves; but on careful study one finds that it is only a matter of degree and that they are actually less concave and generally less irregular than are the left attached valves.

The systematic position of the family to which the oyster belongs has long been a perplexing problem to the naturalist; the asymmetry and irregularity of the valves has rendered them a group difficult to characterize and of uncertain systematic position. The late Mr. Tryon in his work on Conchology says: "The union of the Ostreidæ

the attached valve of Hippurites. *Culceola sandalina*, an operculated coral, has a deep thick attached valve and flattish thinner free valve; bearing thus considerable analogy to the effects produced in bivalve molluscs by cementation. *Beatricea*, a fossil of uncertain affinities, has well-marked camerated structure. In all these attached forms there is an irregularity of growth and cam-

eration strongly recalling the similar structure induced in Pelecypods by the condition of cemented fixation. Woodward (77) suggested that septa and other forms of cameration in Molluscs are induced by the mechanical necessity of cutting off the rear unoccupied portions of the chamber of a shell as the animal is urged forward by the growth taking place on the free edges of the living chamber.

and Pectinidæ, as proposed by the authors of the 'History of British Mollusca,' has not proved satisfactory. The genus *Ostrea* stands quite alone, and distinct from all the Pectinidæ in the structure of its gills, which are like those of *Avicula*, and by resting on its left valve. The shell also is more nacreous than that of the scallops." Another leading naturalist, Dr. C. A. White, in a recently published monograph of the Ostreidæ of North America, says: "To what primary cause this asymmetry among the Ostreidæ is due, it is, with the present limitation of our knowledge, impossible to say; but it is certainly a characteristic of the whole family, including all its genera and its fossil as well as living forms."

My studies of the Ostreidæ, and other Pelecypoda as well, have brought me to a conclusion in regard to the origin of the peculiar forms we have here to deal with, which is that the ostrean form is due to the *conditions of a direct cemented fixation, acting upon a Pelecypod shell*. Given such conditions, and a closely similar form is the result in widely separated genera of this class, as I shall attempt to show. The form which is claimed as the result of the conditions of direct, cemented fixation is a concave attached valve; a flatter free valve, commonly much thinner than the attached valve; an irregularity and asymmetry of growth tending to the displacement of characters normally found in near allies of the subject under consideration, and as a general thing a camerated structure of the shell. The fullest modification in this line of variation is the production of a shell in which the attached valve is cup-shaped, conical, or sub-cylindrical as seen markedly in the Chamidæ and Rudistæ. In this group all the transitions may be traced from a simple ostreaform or exogyriiform shell to the most highly modified conical type. A further result of the modified condition induced by fixation and which I consider perhaps the most interesting of all, is the fact that the attached valve is the most highly modified; the free valve being the least modified and retaining more of the ancestral characteristics, *enabling one through it to trace the genetic connections of the group, evidences of which may be completely eradicated from the attached valve*. If the ostrean form is due to the conditions of direct fixation, then all or nearly all Pelecypoda which have one valve cemented to a foreign body for a longer or shorter time should be ostreaform or modified in this line of variation.¹ First, fixed forms will be considered as

¹The Rudistæ are conical or cup-shaped Pelecypods with a superficially marked radial symmetry. So striking is the radial feature that they have been classed with the corals or Cirrhipeds, and the term radial is combined frequently in generic and specific names of the group. *Barretia monolifera*, described by Woodward (78), is highly radial, and infoldings of its thin walls closely resemble the radial septa of corals. In other animals which are permanently attached by calcareous fixation as corals, some worms, and Brachiopods, Cirrhipeds and others we find closely comparable forms in which radial symmetry is a marked feature. When similar forms are built up on different lines of descent, there is strong evidence that common forces acting on all alike have induced the resulting form.

I suggest the following as a possible explanation of the cause of these markedly similar forms, and would say that I have a great deal of evidence on the question but it must be reserved for a future publication. The

equal impact of moving water on all sides of an attached growing organism it seems would cause an equal effort of resistance on all sides, and therefore induce an equal growth on all sides, thus producing a form circular in section at any one horizon and sub-conical, cup-shaped or globose in its entirety as are all the attached forms which we are considering. To strengthen the walls of a round organism, the wall might be thickened by solid accumulation, by vesicular formation or by perpendicular partitions arranged at right angles to the supported wall. Such mechanical supports are characteristic of attached Cœlenterates, Rudistæ, Cirrhipeds, and some Vermes. As all sides of the periphery of an attached organism are equally exposed to food-supply, danger, etc., the organs, as tentacles, nerve-centres and eyes, would gradually tend to become situated at all points on the periphery, or radially. It is well known that the external parts of an animal are more easily modified than the deeper-seated parts. It is also known that the modification of deeper-seated parts may be

proof of this fact and then special cases will be considered which show the relation of cause and effect.

The genus *Spondylus* is attached by the right valve. It has a concave right valve, flatter left and a highly developed cambered structure. The growth is irregular, spinous, uneven, and the lower valve is often highly ostreaform as shown in *Spondylus hippuritarum*, Pl. xxvi, fig. 1. The group is called spiny oysters from the typical spiny growth and ostrean form. In the Challenger Report, a species is described as *Spondylus ostreoides*, Smith, so named, on account of the close similarity to a small oyster, the features of comparison being marked in both valves. *Plicatula*, a genus nearly related to *Spondylus* and attached by the right valve, is also highly ostreaform. This genus, as is the case with the *Ostrea*, becomes attached at the close of the prodissoconch stage, as shown in Pl. xxvii, fig. 5, and the ostrean characters are assumed at that period of development.

The *Chamida* as a group are characterized by ostrean features, though departures in degree rather than in kind are seen in several genera. The genus *Chama* has typically a deep, irregular, thick, attached valve and flatter, thinner, free valve. A Tertiary species is named *Chama grypheata*, on account of its close likeness to the genus *Gryphæa*. *Chama* constitutes one of the best proofs that the condition of fixation causes the form of the valves, because some species are attached indifferently by the right or left valve, and in both cases the resulting form is the same, a deep attached and a flatter free valve. *Chamostrea albida*, Pl. xxvi, fig. 2, which is attached by the right valve, is almost indistinguishable in external characteristics from many forms of *Exogyra*. The aberrant forms of the *Chamida*, as *Caprinula*, fig. 8, *Monopleura*, fig. 9, and *Caprotina*, fig. 10, Pl. xxvi, also similar allied genera, are forms which may be considered as extremes of variation due to fixation. The attached valves are deep and mostly cornucopia-shaped, often highly irregular and asymmetrical, whereas the free valves, though frequently modified, are yet not different from what is often met with in genera of unattached Pelecypods. In these peculiar genera it is the free less modified valves and extreme young to which we must turn in studying the relationships of the groups. In occasional species the attached valve is not deeper than the free valve, which is the larger and deeper of the two. Such forms are exceptional, as in all other

progressively produced from without inwards (example: development of internal from external skeletons in fishes), or *centripetally* as I would call it. To return, if we have an attached animal that is round, with some organs arranged on the periphery (a very common case), then further modification or development of such organs or parts would tend to be produced *centripetally or radially*, for the centripetal variation of a round form equally exposed to modification on all sides, would, as a mechanical necessity, be radial variation. In the Hydrozoa there is strong proof of the correctness of this view. Passing from *Photohydra* to *Hydra*, to the hydroid stage of *Aurelia*, then to the free medusoid stage of *Aurelia* and other *Discophores*, we find progressively a more and more perfect radial symmetry built up centripetally. Passing to free swimming Hydrozoa, as the *Ctenophores*, radial symmetry is eradicated, and an almost complete bilateral symmetry adopted by the

adult. A similar line of comparison may be made in the development of corals. Cirrhipeds in the shell show a very complete radial symmetry especially seen in *Coronula*.

Many permanently attached forms of bilateral classes of animals assume a considerable degree of radial symmetry and, conversely, many free locomotive genera of radiated animals assume a considerable degree of bilateral symmetry. As bilaterality is a feature induced and progressively built up by the conditions of free locomotion, it is believed that radiality also is induced and progressively built up by the conditions of permanent fixation with its attendant influences of environment.

Many animals are attached by more or less fleshy processes from the body, as *Brachiopods* by a peduncle and *Pelecypods* by a byssus, but these do not adopt a round form, as do those groups which are attached by a more permanent calcareous fixation.

fixed Pelecypods that I know of, the normal condition of a deeper fixed valve is maintained. However, the relative size of the fixed and free valves is a factor, which may be subject to variations without impairing the general conclusions as to the effects of fixation.

The Rudistæ is a group having an enormously developed attached valve of highly irregular growth and a flattish free valve. The free valve may be of a form similar to that found in unattached normal Pelecypods, while the fixed valve is most irregular as shown in *Radiolites fleurbausa*, Pl. XXVI, figs. 11-12. Commonly, however, the free valve of the Rudistæ is radially plicated in the adult and differs widely from any normal form of Pelecypod shell. This extreme variation marked in both valves is accounted for as a case in which the conditions of fixation have produced the extremes of modification (see note, p. 322), affecting the free as well as the fixed valve, instead of the latter principally, as is the normal case.

Dimya is a genus of rare and little-known Pelecypods. The shell is irregular ostreaform and attached by the beak of the right valve which is deeper and larger than the other. We fail to see any important characters of anatomy (described in *D. argentea* by Dall) which would connect it closely with *Ostrea* to which it has been compared by writers. From my view, whatever the affinities, its ostrean form of shell is due to the conditions of fixation.

The Mulleriaceæ comprising the genera *Mulleria*, *Ætheria* and *Bartlettia* is a division of the Unionidæ, which in the adult condition resemble oysters. *Mulleria lobata*, Fer., is so remarkably like an oyster that it has been called the fresh-water oyster. In the Monomyarian adult, Pl. XXVI, fig. 5, the shell is rough and irregular, with a deep attached and flattish free valve, and a specimen in the Museum of Comparative Zoölogy is indistinguishable in shape from forms commonly found in *Ostrea virginiana*. The shell as in *Ætheria*, also has a finely camerated or blistered structure. The young shell of *Mulleria*, Pl. XXVI, figs. 6-7, is Anodon-shaped, equivalvular and dimyarian as described by authors. In this genus we have the important feature of an Anodon-shaped shell, losing its symmetry and becoming irregular and ostreaform as soon as attached.

Hiinites is an important genus in our considerations. In the young it is free and pecteniform, but in the adult is attached by the right valve, is irregular and more or less ostreaform. So close is the likeness to an oyster that in the synonymy of the genus it has been named *Ostrea* and *Ostracites*. *Hiinites cortesi*, Defr., Pl. XXVI, figs. 3-4, from the Tertiaries, illustrates clearly the characters found in the young and adult shell. We will consider the two valves separately. In the young nealogue period the right valve, fig. 3, is purely pecteniform. It has well developed ears, a deep byssal sinus, and an evenly plicated shell which at this stage is nearly or quite equivalvular. At a definitely marked period, as shown in the figure, the valve becomes attached to a foreign body by a cementing fixation of the shell. With this change in condition, a most marked change in form immediately takes place. The shell grows irregularly, losing the evenness and in considerable degree even the existence of the plications marking its nealogue period. While the early nealogue shell was but slightly concave and pecteniform the adult fixed valve is deeply concave and highly ostreaform. The byssal notch, which is a marked feature of the nealogue stage, is filled up and completely wiped out of existence by the irregular ostreaform growth. The left free valve, Pl. XXVI, fig. 4, in the nealogue stage,

is even and regularly pecteniform like the right valve. When the right valve becomes attached, the left valve affected somewhat by the same conditions loses much of the regularity and evenness of marking characterizing its nealogue period, but it never becomes as irregular in growth and ostreaform as does the right (attached) valve. Hinnites is marked therefore by a byssated pecteniform stage followed by an attached ostreaform stage. The transitions described in *Hinnites cortesii*, I have also observed in the living species *H. gigantea*, Gray, and *H. sinuosus*, Gmelin.

Ostrea we have shown becomes attached at the close of the prodissoconch period, and the same is true of Plicatula (see section XI); as soon as attached both these genera, as in Hinnites and Mulleria, assume the irregular ostrean form of shell, losing entirely the symmetry in the valves of the early unattached period.

Pernostrea, a Jurassic genus, is of interest in these studies. According to Stoliczka the shell is "rounded or oval, solid, more or less tumid, inequivalve, the left valve being in adult specimens attached; structure lamellar, resembling that of Perna . . ." Again Stoliczka says: "This genus forms a connecting link between Melina (Perna) and Ostrea, differing from the former especially by its sessile habitat, absence of a byssal sinus and strongly excavated muscular scar; from the latter by the presence of separate ligamental grooves. Externally Pernostrea is barely distinguishable from Ostrea." From our point of view, the ostrean form is due to the condition of fixation. Therefore Pernostrea is like Ostrea because it is cemented to foreign bodies. I have shown that in Hinnites, Pl. XXVI, figs. 3-4, the byssal notch disappears as soon as the shell becomes soldered to an object of fixation, as the byssal attachment at that period is abandoned and the shell assumes an irregular ostrean growth. Therefore the disappearance of a byssal notch in Pernostrea is another character fairly attributable to the condition of cemented fixation. In the species of Perna in Pl. XXVI, figs. 16-18, we find that from the typical form of this genus having a long hinge area and many cartilage pits, fig. 16, a series may be traced to a form with few cartilage pits and wing-like productions of the shell, fig. 18. If we should carry this reduction of the cartilage pits still further till only one remained while still retaining the wing-like productions of the shell we should have a form similar to the nearly allied genus Malleus. Still more to the point is the fact that in studying young Perna I have found that at first only one cartilage pit exists, which is triangular in outline and oblique in position as in Meleagrina, Malleus and Ostrea. It seems that there is no difficulty in a single cartilage pit being derived from many cartilage pits; so, that other points being considered, Pernostrea may very properly be considered as intermediate in form between Perna and Ostrea. As Pernostrea is known only in the Jurassic, and true oysters are known from older formations, it is best to consider Pernostrea not as in the line of ancestry of the Ostreadæ, but as a separate branch from Perna parallel to the branch on which the Ostreadæ evolved as discussed at the close of this section and in section XVI.

In looking back to the earliest known oysters, we find that they are very typical, inequivalvular ostrean forms. M. Barrande's *Præostrea bohémica*, Barr., a form which seems referable to the oysters, is based on isolated valves attached by the umbo of apparently the left valve. His Pl. 111, fig. 2, is an upper free valve and bears at the extreme tip a rounded, very marked early stage which resembles the ostrean prodissoconch as

described and figured in this paper. Whether this comparison can be properly made can only be ascertained by a study of the specimen. *Præostrea* is from the formation, E. 2 and 3, *Système Silurien*, a period equivalent to a portion of the Upper Silurian. If a true *Ostrea*, it is the earliest appearance of the group yet recorded. Professor L. de Koninek figures a form from the Carboniferous as *Ostrea nobillissima*. His figures resemble a *Perna*, and are very much the form we might expect if that genus, or a similar one (as *Perna* is not known before the Trias), should have become attached. *Ostrea patercula*, Winchell, from the American Carboniferous, appears to be a true *Ostrea* and has the typical form of the genus.

As it is shown that the ostrean form is due to the conditions of fixation, these early and questionable species have to be looked at sceptically, as any Pelecypod adopting a fixed habitat might assume a form which in isolated specimens could well be taken for an oyster. The paucity of the Permian and Triassic formations gives but little evidence concerning the early history of the *Ostreadæ*, but in the Jurassic the family is well developed, and from that time on there are abundant species and individuals for study.

In the early Jurassic, *Exogyra* and *Gryphæa* are developed as well as typical *Ostreas*, and the question comes up as to which is to be considered the typical, least modified form of the family. I show (below) that *Ostrea*, the type of the family, is connected with *Perna*, or *Perna*-like forms, by important characters of anatomy and shell structure. It has been shown that the attached valve is that which is most modified in all Pelecypoda which solder one valve to a foreign body. Therefore, the same line of reasoning may be followed, and as *Ostrea* is near to *Perna*, *Exogyra* and *Gryphæa* should be considered as extremes of variation in the *Ostreadæ*. They are extremes of the *Ostreadæ* as *Caprinula*, Pl. xxvi, fig. 8, and *Monopleura*, Pl. *id.*, fig. 9, are extremes of the *Chamidæ*, and in the same line of variation. The almost simultaneous appearance of the three genera of the *Ostreadæ* in marked abundance in the early Jurassic is probably due to the recognized law of quick development of new types of animals, together with the fact that the Trias and Permian are formations bearing few fossils, so that what *Ostreadæ* did exist in those periods have been but fragmentarily preserved.

After our studies in previous chapters and the present discussion of shell form we are in a position to consider the probable ancestry of the *Ostreadæ*. The anatomy of *Ostrea* bears a close similarity to that of *Perna*. The gills of the two genera bear a close resemblance.¹ The palps, heart, adductor muscle, position and termination of the in-

¹Dissecting *Perna ephippium* I find that the dorsal border of each pair of gills presents the cross connecting lattice-like meshes characteristic of *Ostrea*. In some specimens the two pairs of gills are separate from one another throughout their extent, as represented in Pl. xxiv, fig. 10, whereas in other specimens the two median gills are connected by concrecence at their dorsal border thus uniting the two pairs of gills, as in *Ostrea*. The degree of concrecence varied in different specimens which possessed it; the gills being united for their whole extent or only posteriorly. That such a difference as this should exist in what is commonly considered a fundamental character is peculiar and should be studied on fresh specimens (mine being alcoholic). In a young *Meleagrina*, I find the two pairs of gills separate, though Woodward says they are

united behind the foot. Probably he refers to the adult. In an *Avicula* also, I find the two pairs of gills separated throughout their extent. In both *Avicula* and *Meleagrina* the characteristic lattice-like meshes connect the lamellæ of either pair of gills on their dorsal border as in *Perna* and *Ostrea*. The anatomy of *Meleagrina* and *Avicula* as far as ascertained from my rather limited material is as near to that of *Ostrea* as is the anatomy of *Perna*, and it may be that *Ostrea* is a direct branch from *Avicula* rather than from *Perna*. I have adopted the latter view because the shell of *Perna* approaches nearer to *Ostrea* than does the shell of *Avicula*, and because in *Pernostrea*, an unquestionable branch from *Perna*, we find a form almost identical with *Ostrea*.

testine and mantle border are also closely alike in *Perna* and *Ostrea*. In *Ostrea* the foot is wanting, but probable remnants of it are preserved as the pedal muscle mentioned by Dall, *pd*, Pl. xxv, fig. 12. The prodissoconch of *Ostrea* is strikingly like that of *Perna*. In both genera it is an oval, nearly or quite equivalvular shell with umbos directed posteriorly. In both it is composed of homogeneous lime, and shows fine concentric lines of growth. The succeeding dissoconch in both *Ostrea* and *Perna* is strikingly different from the prodissoconch. In *Perna* it is composed of an external laminar prismatic cellular layer with internal nacreous layers. In the oyster the right valve has an external thin laminar prismatic layer, the bulk of the valve being composed of sub-nacreous tissue. The left valve, on the other hand, in the young, is composed wholly of sub-nacreous lime, not having the typical prismatic layer (*vide* p. 314). This absence or extreme reduction of the prismatic layer in the left valve of the oyster may be due to the modifying influence of fixation or to other causes, for in young *Pectens* a prismatic layer is found in the right valve although wanting in the left.

Having seen some important likenesses of the two genera, *Perna* and *Ostrea*, let us examine the differences and see if they can be accounted for. *Ostrea* is attached; this habit is acquired by many Pelecypods in widely separate groups. The loss of the foot and accompanying byssal notch in *Ostrea* is easily explained as the result of fixation, for such a reduction and disappearance are described in attached Hinnites, Pl. xxvi, figs. 3-4, *Spondylus*, Pl. xxvii, fig. 4, and *Pernostrea*. The shell of *Ostrea* is inequivalvular, of rough, irregular growth, especially marked in the lower valve, which is deeply concave; the sub-nacreous tissue is characterized by a shallow camerated structure. This form and the cameration we have shown are the result of the conditions of fixation acting on attached Pelecypod shells. *Ostrea* has but one cartilage pit in the middle of the line of ligamental tissue connecting the valves, whereas *Perna* has many pits situated on such a line of tissue, Pl. xxvi, figs. 16-18; but this character is variable in *Perna* and in the young only a single pit exists, figs. 30, 31, p. 329. The nepionic period, as shown in many genera in this paper, is of value in tracing relationships which are with difficulty or not at all traceable in the adult. Therefore we naturally turn to the nepionic period of *Ostrea*. I have not been able to trace connections between the nepionic stage of *Ostrea* and similar periods in *Perna*, but it is to be remembered that *Ostrea*, even at this early period, is already attached and highly modified, so that close comparisons are not to be expected. All differences seem referable to details, which are explicable on established bases of argument. We feel justified, therefore, in supposing that *Ostrea* is a close ally of *Perna*, the differences between the two genera being largely explained by the effects of the changed conditions of environment acting on the genus *Ostrea*. *Ostrea* probably descended directly from *Perna* or from a close common ancestor of the two genera, and by soldering its shell to a foreign body at the close of the prodissoconch period has by this means eradicated from the shell, features which might otherwise render the young referable to *Perna* in form.

VIII. PERNA, AVICULA AND NEAR ALLIES.

Seeking on masses of *Perna ephippium*, L., preserved in alcohol, a number of young specimens were secured, which had the embryonic shell well preserved. The young were

attached by a byssus as are adults, and it was due to this fact that they were collected at the same time with the adults.

The prodissoconch of *Perna*, as shown in Pl. xxvii, figs. 1-3, and Pl. xxviii, fig. 11, is very closely similar to that characteristic of *Ostrea*, the umbos are directed posteriorly and the histological structure is homogeneous and laminar. The succeeding dissoconch is sharply marked off from the prodissoconch by the shape of the shell and by the fact, as in *Ostrea*, that it is composed of lime deposited in a prismatic manner in a conchyolin matrix. These two characters are features as clearly marked and as striking in the young of *Perna* as they have been shown to be in the young of the oyster, fig. 27, p. 314. The byssal notch of *Perna* originates in the initial stages of the dissoconch, as shown in Pl. xxvii, figs. 2-3, viewed from the right side. It is a fact to note in our comparative studies that there is no indication of a byssal notch in the prodissoconch valves of *Perna*; and the same is true of the prodissoconchs of *Spondylus*, Pl. xxvii, fig. 4, *Avicula*, fig. 33, p. 330, and *Pecten*, Pl. xxvii, figs. 8-9, all tending to prove that the embryos lived a free locomotive existence as did *Ostrea* up to the close of the prodissoconch period and crawled, if at all, on the ventral border of the valves. As viewed from the left upper side the young shell of *Perna*, Pl. xxvii, fig. 1, is auriculate, but shows no indications of the byssal notch; as in the lower right valve, Pl. xxvii, figs. 2-3, the same being true of young *Pectens*, Pl. xxviii, figs. 9-12. This is attributed to the fact that it is the right valve which is most affected by the presence of the byssus, for that organ in mooring the animal to its habitat passes over the edge of the right valve, as the animal lies on the right side.

The degree in which a special notch exists for the extrusion of the byssus and foot appears to bear a direct relation to the position of the axes of the body as compared with the hinge axis of the shell (relation of axes to the shell, see p. 309). In byssated Pelecypods which have the anterior portion of the body closely underlying the hinge area, a notch is always developed. As examples, may be cited *Perna*, *Pecten*, *Avicula* and *Tridacna*. On the other hand, byssated Pelecypods in which the antero-posterior axis is more nearly parallel to the hinge axis, commonly there is only a slight byssal notch, or none at all. Such we find to be the case in *Mytilus*, *Modiola*, *Pinna* and most *Arcas*. In studying these genera it is evident that when the foot is close to the hinge axis a notch in the valves greatly aids in its easy protrusion; as if no notch existed the valves would have to open very widely to permit of its passage. Young *Pecten*, however, in virtue of the deep notch, protrudes its foot and crawls freely, while lying on the right side (see studies of *Pecten*), although the valves are almost closed. Genera in which the foot is far removed from the hinge line can protrude it, even if of considerable size, by a comparatively slight gaping of the valves, and a permanent byssal attachment seldom induces a considerable notch. Those in which the foot is far removed from the hinge line mostly crawl on the ventral border, with the valves raised perpendicularly, not as in *Pecten* and similar genera where crawling is effected by dragging the shell still lying on its right side, the foot being extended through a special notch in the right valve. From studies of *Pecten* I am led to believe that a notch is a feature caused by the extension of the foot quite as readily as by the existence of a byssus, although either organ would affect shell growth by its permanent existence, or activity.

The shell of *Perna* in the nepionic stage has not yet acquired adult characteristics.

Viewed from the left side, Pl. xxvii, fig. 1, it possesses a rounded wing anteriorly and posteriorly the wing is rounded but not produced beyond the borders of the valves. The hinge of this early period of growth, fig. 30, is markedly different from the adult. The cartilage pit is single, acutely triangular in outline, situated obliquely (as in *Mal-leus*, Pl. xxvi, fig. 19), and extends downward from the hinge area of the prodissoconch valve as in *Ostrea*, Pl. xxiv, fig. 19. As the shell grows, fig. 31, new cartilage pits originate on the hinge line each being triangular at first, but not as acutely so as is the first formed pit. Hinge teeth exist in young *Perna* (figs. 30–31), although wanting

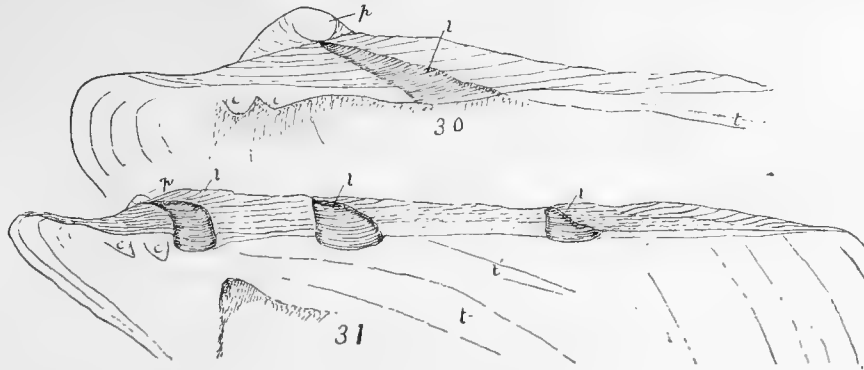


FIG. 30.—Young *Perna ehippium*, right valve; *p*, prodissoconch; *l*, single triangular cartilage pit; *c*, cardinal and *t*, lateral teeth. $\times 90$ diam.

FIG. 31.—*Perna ehippium*, older specimen than fig. 30, showing several triangular cartilage pits and two lateral teeth. Lettering as in fig. 30. $\times 24$ diam. (Drawn by the author.)

in the adult, Pl. xxvi, fig. 16. Two cardinal teeth in the right valve and one in the left are situated directly beneath the umbos. A slight posterior lateral tooth exists as well in either valve. The teeth correspond with similar teeth in a specimen of *Avicula sterna* with which they were compared and they are found in specimens of *Perna ehippium* up to a centimeter or more in height. These teeth are apparently directly inherited from *Avicula*, which is in all probability the immediate ancestor of *Perna*. During later growth new cartilage pits originate on the hinge line, and the triangular outline characteristic of the developing pits is lost, giving place to the perpendicular form of pits characteristic of the adult, Pl. xxvi, fig. 16. The hinge teeth also disappear during growth, and the form of shell characteristic of the species is rapidly built up.

The anatomy of adult *Perna* resembles that of *Ostrea* as already considered, section v, and the anatomy of the prodissoconch period of *Perna* is probably closely like that described in the oyster, p. 300, Pl. xxiv, figs. 1–2. At least one difference, however, exists, and that is the presence of a well-developed foot. The foot of *Perna* as indicated by the position of the notch in the succeeding dissoconch growth (Pl. xxvii, figs. 2–3) occupies an antero-ventral position in the prodissoconch shell, and a similar position was occupied by the foot in the young prodissoconch period of *Avicula*, fig. 33, p. 330, *Pecten*, Pl. xxvii, figs. 8–9, and *Anomia*, Pl. xxix, figs. 6–7. The position of the foot may be considered as affording evidence concerning the anatomy of the prodissoconch stage, as it doubtless closely underlies the anterior adductor muscle, its normal position in dimyarian Pelecypods, for *Perna* was unquestionably dimyarian at that stage. The foot of adult *Perna* is small compared with that found in Pelecypods where it is used actively in locomotion; it bears a deep longitudinal distal cleft as in *Pecten*, and from a second deeper proximal cleft, the byssus originates. The prodissoconch of *Perna* in shell features and implied anatomical parts is referable in origin to the Nuculoid radical, which

is also represented by the prodissoconch in *Ostrea*, *Avicula*, *Pecten*, etc. (see full discussion, section xv).

In studying fossil Pelecypods we find many species of Palæozoic Aviculoids which are directly comparable to the nepionic stage of *Perna*, Pl. xxvii, fig. 1. Some species of *Leioptera* and *Leptodesma*, as figured by Hall in the Palæontology of New York, Vol. v, part I, are very similar to young *Perna*. The most striking resemblance, however, is found in species of *Rhombopteria* (gen. nov. described in section xvi) from the Silurian, as figured by Barrande. *Rhombopteria glabra*, sp. Münster. (see Barrande, Pl. 228), is almost identical in form with young *Perna*. The form of shell found in the adult of species of *Rhombopteria* is shadowed in the stages of development of many genera of the Aviculidæ and their allies as *Avicula*, fig. 32, p. 330; *Pecten*, Pl. xxviii, fig. 9, etc. From these close comparisons, *Rhombopteria* is selected as the radical from which these genera are evolved as discussed in section xvi, and represented graphically in the table at the end of that section. The prodissoconch of *Perna* in common with that of *Ostrea*, *Avicula*, *Pecten*, etc., is the representative in the ontogeny of the individual of

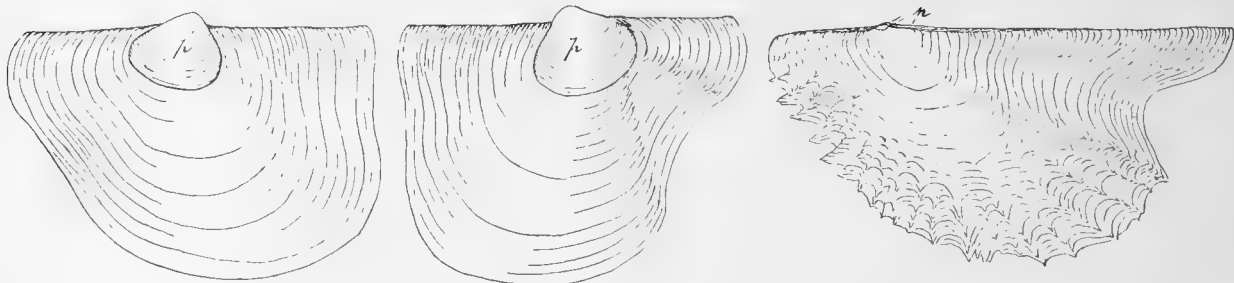


FIG. 32.

FIG. 33.

FIG. 34.

FIG. 32.—Young *Avicula sterna*, showing, *p*, the prodissoconch and succeeding nepionic stage, viewed from the left side.

FIG. 33.—Same specimen viewed from the right side, showing the byssal sinus. Figs. 32–33 are drawn from the umbonal tip of a young specimen by following the lines of growth. $\times 38$ diam.

FIG. 34.—Young *Avicula sterna*, showing a much later growth than figs. 32–34, $\times 6.3$ diam. (Drawn by the author.)

the Nuculoid radical from which the whole group evolved (section xvi), and the succeeding nepionic stages are referable in origin to species of *Rhombopteria* the next step up in the phylogeny of the group. The prodissoconch, also the teeth, single triangular cartilage pit and form of the shell in the nepionic stage of *Perna* show how closely stages in growth may be compared to ancestral kindred and how valuable such stages are in tracing the phylogenetic history of groups.

The developing shell of *Avicula* presents characters of interest in themselves and of great value in our phylogenetic studies. Through the kindness of Prof. A. E. Verrill,¹ I recently received some specimens of young *Avicula sterna*, Gould, from Panama. The specimens were growing thickly on the branches of Gorgonias, to which they were attached by a byssal fixation. A well defined prodissoconch exists at the umbos of the valves, figs. 32–33, and the right valve of the prodissoconch is somewhat larger than the left valve. The umbos of the prodissoconch are directed posteriorly; it is composed of homogeneous lime and shows fine concentric lines of growth. The prodissoconch of

¹I am indebted to Professor Verrill of Yale University, for other specimens besides the Aviculas mentioned, and I am also indebted to Dr. C. E. Beecher of the same in-

stitution for many valuable specimens of developing Pelecypods; some of which are described in this paper.

Avicula is closely comparable to the same stage of *Ostrea* and *Perna* as described, and the anatomical features of this stage of *Avicula* are doubtless similar to those of the genera mentioned.

The early dissoconch growth of *Avicula* is sharply defined from the prodissoconch by its changed form and histological structure. Whereas the prodissoconch is composed of homogeneous lime, the dissoconch externally is composed of prismatic cellular tissue, with an inner layer of nacreous tissue (compare with *Ostrea*, fig. 27, p. 314). The delicate spinose productions of the epidermis are made up of prismatic tissue like the rest of the superficial layer of the shell. In form the nepionic stage of the dissoconch is sub-rhomboidal, fig. 32; the hinge line is produced beyond the borders of the prodissoconch in a straight line and anteriorly is terminated by a slightly auriculated wing; posteriorly the wing is slightly rounded at the hinge line, and is not produced beyond the free borders of the valves as in later stages. In the right valve, fig. 33, the byssal sinus originates with the introduction of the nepionic stage and is progressively produced to the free border of the valves. At this stage, the developing shell of *Avicula* is closely like the developing shell of *Pecten* at the same stage, Pl. XXVIII, figs. 9-10 and *Perna*, Pl. XXVII, fig. 1. It also approaches near to the form of the young of many living and fossil allied genera, and in its left valve, fig. 32, bears a close resemblance to the adult of *Rhombopteria*, the primitive radical of the *Aviculidæ* (see section XVI). During the later growth of *Avicula sterna*, fig. 34, the posterior wing is gradually produced in an increasingly sharper posterior extension as indicated by the lines of growth in the figure, and soon the full characters of the adult are introduced. The stage represented in fig. 34, is compared in section XVI, with the ancient genus *Leptodesma*, which this stage probably represents in the ontogeny of *Avicula*. In the youngest specimen of *Avicula* observed, the hinge teeth are similar to those of the adult, and the cartilage pit is triangular, oblique and produced downwards from the hinge line of the prodissoconch as in *Perna*, fig. 30, p. 329. Similar characters to those found in *Avicula sterna* are shown in a specimen of *Avicula atlantica*, sp.? sent me by Dr. C. E. Beecher.

The prodissoconch of *Avicula* as in *Perna* and *Ostrea*, represents in development the Nuculoid radical of the whole group (discussion, section XV). The nepionic stage which is the next stage in the ontogeny of the individual corresponds closely with, and is the representative of *Rhombopteria*, which is the second step upward in the phylogeny of the group (see table, section XVI). The third stage in *Avicula* in which we find the posterior wing produced and the anterior wing auriculate, fig. 34, bears a close resemblance to typical species of the genus *Leptodesma* which is considered as the third step in the phylogeny of the group (serial steps and discussion, see section XVI). Thus *Avicula* in its development represents very fully the phylogeny of the genus, as also seen in *Perna* and very clearly in *Pecten*, section X.

A specimen of young *Meleagrina glabra*, Gould, from New Zealand, No. 584, Yale University Museum Collection, has a prodissoconch and succeeding nepionic dissoconch similar to that of *Avicula sterna*. One difference, however, exists, in that the young *Meleagrina* like the adult has no cardinal or lateral teeth as in *Avicula*.

Specimens of *Monotis tenuicostata*, from the Jurassic of the Black Hills of Dakota, were loaned me by Dr. Beecher for study. The prodissoconch is preserved in both valves. It has the umbos directed posteriorly, and resembles the prodissoconch of *Avicula*.

ula as far as can be ascertained in its partially eroded condition. The byssal sinus of the right valve originates in the initial stage of the dissoconch growth, as in *Avicula*.

In *Pseudomonotis echinata*, sp., Sow., I have been able to observe the condition of the young in specimens from the Cornbrash of Wilts, England, No. 10737, Museum of Comparative Zoölogy. A well-preserved prodissoconch like that of *Avicula*, exists at the umbo of either valve. The nepionic stage of the left valve, which seems to be the more normal, least modified valve in this species, is sub-rhomboidal in form and resembles the same stage of *Avicula*, fig. 32, p. 330. In the right, flattish valve, the byssal sinus originates with the introduction of the nepionic stage as in *Avicula*, etc.

In some well-preserved specimens of right valves of *Oxytoma inequivalvis*, sp. Sow., from the middle Lias, Pl. xxvii, fig. 7, I found a well-preserved prodissoconch. As in related genera the umbos of the prodissoconch are directed posteriorly, and the byssal sinus originates with the introduction of the nepionic stage on the ventral border of the prodissoconch as shown in the figure.

In specimens of *Cassianella* from the Triassic, a prodissoconch has been found similar to that of *Avicula*. It is worth noting that *Cassianella* is from the oldest geological

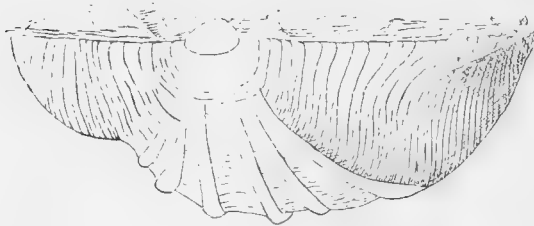


FIG. 35.—*Cassianella decussata*, tip of left valve, showing, *p*, prodissoconch, and early dissoconch growth. Original in Yale University Museum. $\times 30$ diam. (Drawn by the author.)

formation from which I have so far succeeded in finding a Pelecypod with the prodissoconch still intact. Dr. Beecher sent me recently specimens of *Cassianella decussata*, Münst, which show the feature mentioned, fig. 35. The prodissoconch is ovate with umbos directed posteriorly, and it is sharply defined from the succeeding dissoconch, as in *Avicula* and allied genera. The nepionic stage of *Cassianella* is similar to the same stage of

Avicula (compare tip of valve of fig. 35, with the whole valve of fig. 32, p. 330). The prodissoconch has also been observed in *Cassianella grypheata*, Münst, from the Triassic.

In specimens of *Vulsella rugosa*, Lam., kindly given me by Professor Verrill, I have found stages of interest. At the umbos of a young individual, fig. 36, a well-defined prodissoconch exists similar to that of *Avicula*. The prodissoconch is oval with umbos directed posteriorly. It is composed of homogeneous lime, and bears fine concentric lines of growth. The nepionic stage of the dissoconch, as in related genera, is sharply defined from the prodissoconch by its changed form and histological structure. The shell of the nepionic and later stages is composed on the outside of prismatic cellular tissue, with nacreous tissue in the deeper seated parts. The form of the nepionic stage is sub-rhomboidal, bearing a certain resemblance to the same stage of *Avicula*, fig. 32, p. 330; but the wings are almost lost sight of in *Vulsella*. During later growth the hinge line becomes twisted out of the straight line and commonly, for a brief extent at least, curves around the ligamental area as shown in fig. 36.

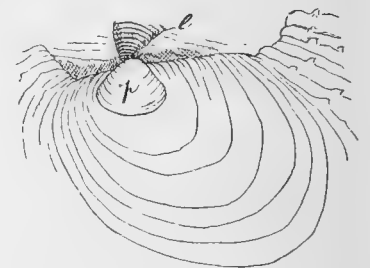


FIG. 36.—Tip of valve of young *Vulsella rugosa*, showing, *l*, cartilage pit; *p*, prodissoconch, succeeded by the early nepionic growth. $\times 38$ diam. (Drawn by the author.)

The genera *Malleus* and *Pinna* might be considered in this section, but I have not

succeeded in getting very young specimens of either genus. The observations which have been made on the development of these genera are given in section XVI.

IX. PECTEN. ANATOMY AND HABITS.

Material collected at Buzzards Bay, in 1888 afforded an opportunity to study *Pecten irradians*, Lam., fig. 37, which is common on the southern shores of Cape Cod. Through the kindness of Dr. Dall, I have also been able to study the young of several other species from the collections of the Smithsonian Institution at Washington. The consideration of the anatomy and life habits of *Pecten irradians* is taken up in this section and a study of the shell of that and the other species studied is described in section X.

On the fourth of August, in examining the glass plates in my drain-pipe traps (described in section II), a number of extremely young *Pecten*s were found. These specimens proved of great interest on account of the shell form and structure and also on account of anatomical features and the habits which I had the opportunity of observing, as they were kept alive for several days. No very young specimens were found on the sand-bar immediately around the drain pipes although diligently searched for, and the traps were a most invaluable assistance in catching extremely young molluscs which were easily seen on plates of glass by allowing the light to strike them obliquely.

The specimens found on the fourth of August varied slightly in size as shown in Pl. XXVIII, figs. 9-12. A few of the same age were found on the glass the next day; but later none of these youngest stages were seen. The habits of these were alike in all the individuals observed and the anatomical features were the same as far as traced.

The young *Pecten*s, Pl. XXVIII, figs. 1, 9, 12, were free, crawling on the glass. No byssus was observed until a considerably later stage and it is safe to say that this early period has not yet developed the habit of byssal fixation. It is a free period, preceding the byssal period. The young scallops were extremely active crawlers with a highly developed foot, which is capable of extreme prolongation, Pl. XXVIII, fig. 1, and is often produced beyond the edges of the valves to a length equal to the whole height of the shell. While lying on the right valve, the foot is extended through the notch close under the hinge line and is attached by a sucker-like action to the glass, shortening its length. It thus drags the shell along on its right side. The motion is very rapid and the little creature quickly passes over a considerable distance. Shells were frequently observed to clap as in the adult; but they did not swim by this means and it is quite possible that they were not capable of doing so, as special features of the mantle which serve the adult in swimming were not yet developed. The foot is so mobile and extensible that it may be twisted and turned in any direction at the will of the animal.

Older scallops and the adults lie on the right valve, and are rarely found lying on

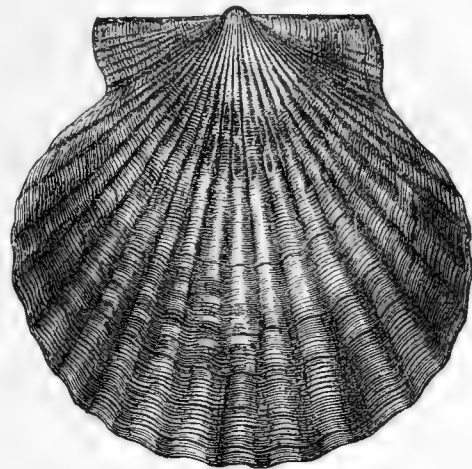


FIG. 37.—Adult *Pecten irradians*, Lam. Life size. (From Binney's Gould.)

the left side. This latter position, is due probably to an accidental overturning, which the scallop alters at an early opportunity. Professor Hyatt informs me in a letter that he has examined over three hundred specimens of *Pecten irradians*, all of which lie habitually on the right valve. The upper, left valve very commonly is more or less overgrown with algæ, but I have never observed them on the lower right valve. This habit of lying on the right valve is characteristic of many related genera as *Perna*, *Spondylus*, *Plicatula*, *Hinnites*, and *Anomia*. Patten (53) in his studies of *Pecten Jacobæus*, says that this species which has a deeply concave right valve and a flat left valve, lies habitually on the right side, and if turned on the left side in an aquarium, soon rights itself. The studies of young *Pecten irradians* were interesting on this point. I turned them several times on the left valve intentionally and in every case they almost immediately extended the foot with which they laid hold of the glass, and with a sudden jerk righted themselves, showing that they were uneasy in the reversed position. While actively crawling, the heart action is very rapid as may be seen through the translucent valves.

The foot of *Pecten* is marked by a deep groove in its distal portion and by means of this groove is capable of laying hold of objects of support by a distinctly sucker-like action. By this means they are capable of suspending themselves and I have inverted a glass slide on which a young *Pecten* was crawling and seen it hang perpendicularly suspended by the foot. This only applies to the very young, as older individuals have not the power in sufficient degree to support their weight. The crawling action may, however, be seen in older specimens more easily than in the very young, as they are large enough to be observed without the aid of the microscope.

The foot of a young *Pecten* has a well developed posterior retractor muscle, *pr*, Pl. XXVIII, fig. 1, on the left side. It takes origin in the proximal portion of the foot and is attached to the left valve on the dorsal border of the adductor muscle. A dissection of a *Pecten* of the same age as that of Pl. XXVIII, fig. 2, showed the posterior retractor inserted behind the adductor in its normal position. An anterior retractor was also observed attached to the shell in the umbonal region. It is an interesting fact that in *P. irradians* there is only one posterior retractor of the foot, and that one, the left retractor, whereas normally there are two posterior retractors in Pelecypods, one of which is inserted in either valve on the dorsal border of the posterior adductor muscle. This important peculiarity of the absence of a right retractor is apparently due to the fact that *Pecten* habitually lies on the right valve. When lying in this position it is obvious that the left retractor is in the direct line of traction, while crawling with the foot extended at an angle so as to reach the ground; whereas the right retractor, if it exists, would not be in the line of traction and has disappeared probably from relative disuse and atrophy.¹ In adult *Pecten magellanicus* both posterior retractor muscles are wanting, and it is stated as characteristic of the genus that the posterior retractors are absent or present only on the left side. Another feature due to this changed position in the mechanism of parts is the relative situation of the cleft in the foot. In Pelecypods which have a cleft in the foot and also crawl on the ventral border of the valves, the cleft is in the ventral border of

¹ A similar disappearance of the right retractor muscle exists in *Anomia*, Pl. XXIX, figs. 1-2. Lacaze-Duthiers has demonstrated it in adult *Anomia ephippium* and he there as-

cribes the loss of the right retractors to disuse and atrophy brought about by the peculiar position of the muscles and their relations to the byssal plug.

the foot as seen in *Mytilus*, *Modiola* and *Nucula*. On the other hand, in *Pecten*, Pl. XXVIII, fig. 1, *Anomia*, Pl. XXIX, fig. 2, and their allies which lie on the right valve, the cleft in the foot is in the right side, this being the side apposed to the ground in crawling. Whether the position of the cleft has changed, or the apparently changed position of the cleft is brought about by a twist in the foot, is not known.

Young *Pecten irradians* differs from the adult in many features of anatomy and habit. I will first consider the condition in the young and will call attention to the differences when discussing older stages. The mantle border of the young, Pl. XXVIII, fig. 1, is a simple thickening of the edge as shown more highly magnified in Pl. XXVIII, fig. 6. It has not yet acquired the complex structure of the mantle border of the adult. The eyes are arranged on the border, one in each plicated fold of the shell. As the plications in the two valves alternate, so the eyes alternate on the two mantle borders, each retaining a position in the furrow of its apposed valve. The tentacles at this stage alternate with the eyes, as shown in the figures; they are highly extensible, sensitive, prehensile, and are covered with papillose projections. When crawling, the young scallops use the tentacles actively and they constantly lay hold of the glass by their sensitive tips. Whether they assist in crawling by their prehensile activity is not known; but it is possible. They will wind the tips around a body put in their way, such as a needle or pencil point, and I have seen very young *Pectens* suspended from the glass sides of a beaker by the clinging power of extended tentacles, the animal being otherwise completely inactive.

At a little later date, a few *Pectens* were found considerably older than those thus far considered. The eyes of this stage, Pl. XXVIII, fig. 2, are still single in each plication of the shell, no more having yet appeared; the active tentacles, however, differ from the earlier stage, fig. 1, in that there are now two alternating with each eye. The mantle border has as yet no perpendicular wall or guard tentacles (described later) but presents one striking feature. When at rest the two borders are protruded beyond the edge of the shell in a short tubular form at the base of the dorsal¹ ear as shown in Pl. XXVIII, fig. 2. At this point excurrent action takes the direction indicated by the arrow and a rapid but intermittent outflow may be traced by means of the contained particles of effete matter. This extension of the mantle is at that time a pseudo-siphon; it is composed of delicate tissue and is retracted and extended exactly as may be observed in the anal siphon of young clams (*vide* section XIV), but it differs from a true siphon in that the walls are not joined by the concrecence of their apposed borders. No siphonal extension of the mantle was seen in *Pectens* younger or older than that here described, but in the adult it is important to notice that all excurrent action takes place at this same area of the shell. Dr. Dall informs me that he has seen a similar condition of siphonal extension of the mantle border in *Pectens* dredged from great depths.

It is an interesting fact in young *Ostrea* and *Pecten* that excurrent action takes

¹ In considering the relative position of the axes of the body to the shell it must be borne in mind that as in *Ostrea* (*vide* p. 309) the axes of *Pecten* are different from those of typical dimyrians (Pl. XXV, fig. 8). The position of the palps and foot in *Pecten* indicates the umbos as the anterior end of the shell, the free ends of the valves are posterior,

and the gills lie on the ventral border. The ear possessing the byssal notch through which the foot extends is therefore the ventral ear, not the anterior ear as commonly considered; and the ear on the opposite side is correlatively the dorsal not the posterior ear.

place at one definite area. These genera have mantle borders separate around the entire margin of the shell; yet the outflow is not in any direction as might be supposed, but is limited to one direction.

The gills of *Pecten* of the age of Pl. xxviii, fig. 2, consist of four sets of filaments all equally developed, but there is none of the irregularity of development of the separate gill lamellæ described in the oyster. The inner pair of gill filaments are reflected inwards and the outer pair are reflected outwards as in the adult, Pl. xxiv, fig. 12. The reflected borders are about half the total length of the direct borders whereas in the adult the reflected borders are proportionately longer. This condition in the young was doubtless preceded by a condition in which the filaments were simple, straight processes without reflected borders as described in young *Ostrea* and *Anomia*. The gills are ciliated but have not yet the ciliated interfilamental knobs or processes existing in the adult. There are no septa joining the direct and reflected portion of the filaments, characteristic of the adult, observed at this early stage.

When a *Pecten* of the age of Pl. xxviii, fig. 2, had been kept in confinement for a few days it became attached by a byssus and from my observations it is probable that, up to this period, the young lead a free, crawling existence without any fixation. With the introduction of the byssal period, as it may be called, the young *Pecten* undergoes a marked change in habits. Previously an active crawler, it now becomes most persistent in its byssal fixation, and leads a sedentary life. The animal lies on the right valve; the byssus is extended through the byssal notch as a number of delicate fasciated threads flattened into a disc at the point of contact with the object of fixation. The specimen if kept in a beaker of water frequently attached itself high up on the perpendicular sides of the glass to which position it had previously crawled. It occasionally broke loose voluntarily, or was intentionally detached and in a short time, commonly a few minutes, made a new attachment, showing that fixation is a feature of this condition. It was in the specimen of this early stage, when attached by a byssus, that the pseudosiphonal protrusion of the mantle was observed. When the animal is attached, the tentacles are more or less fully extended, the foot may be protruded or withdrawn, and feeding is active as indicated by faecal discharges in the excurrent water.

Pectens considerably older than those already discussed, measuring 1-3 cm. in height, are instructive. At this age the byssal habit of fixation still exists; in fact, specimens measuring slightly over 3 cm. have been found still attached, but I have never observed such a condition in adults. *Pectens* 1-3 cm. high, though retaining the byssal habit, are not as constantly attached and are more active, than the younger stage just considered. Two hundred or more individuals of this size were seen on the bar and perhaps half were attached. They were not observed in the act of crawling but they are capable of swimming actively as later described. On account of the size of the specimens it was easy to observe the process of formation of the byssal fixation. In observing it, the scallops should be confined in a dish as every movement is then clearly perceptible. Lying on the right valve, the foot is extended on the surface of the dish, the flattened distal portion taking a firm hold as if about to crawl. This position is maintained for a moment or two and then the foot is withdrawn within the body, by the motion of retrac-

tion it draws out, or spins, the byssal thread, which the creature had fixed to the surface of the dish while the foot was laid closely against it. Soon the foot is again extended, pressed flatly against the dish and another byssal thread is spun. The second byssal thread is always attached at a point a little removed from the point of fixation of the first thread; sometimes the two are separated by a distance of two or more millimeters. Additional threads may be spun; but three was a common number with specimens in confinement. Those on the bar, especially the larger individuals, frequently spun a large number of threads in the byssus. The byssal gland is situated in a proximal cleft-like depression in the foot separate from the more distal cleft-like depression which serves the animal in crawling, so that between the two there is a slight interspace without a cleft. Frequently when forming the byssus, the foot may be arched up in this interspace, Pl. XXVIII, fig. 7; the hold being maintained by the tip of the foot and at the same time the byssal cleft being pressed closely against the glass, so as to make the fixation of the byssal thread. While spinning the byssus the scallop is preoccupied and pays little attention to pricks or stimuli which at other times would meet with immediate response.

The attached scallop commonly remains fixed for a considerable time. If disturbed, however, or at will without apparent cause, it may break the byssal attachment by clapping its valves. It then commonly swims about, soon renewing, or not, the attachment as the impulse moves it. If one break the byssus loose it is torn out from the foot and left clinging to the sides of the dish. On examining separated threads we find that the proximal portions of the several threads are generally coalesced into one band, the distal portions being separately attached to the glass by expanded disc-like extremity. The threads may measure a centimeter or more in length but are more often shorter. In attempting to preserve specimens of *Pecten* in alcohol with the byssus intact it was found that they immediately detached themselves. Success was attained however, by first paralyzing them with cocaine, adding the solution gradually to a small volume of sea water.

The mantle of *Pectens* 2-3 cm. high has acquired adult characters. In young stages, as shown, the eyes are situated one in each plication of the shell and a single tentacle alternates with each eye, Pl. XXVIII, figs. 1 and 6. Later the position of the eyes being the same, two tentacles alternate with each eye, Pl. XXVIII, fig. 2. In the age under consideration, as in adults, the eyes are for the most part situated in the plications of the shell, but in addition to one eye in each plication, new eyes have arisen between those first formed. The new eyes, however, do not appear at regular intervals as did the first-formed eyes. In each mantle border may be counted (as noted by Verrill) about forty eyes, and between them are a large number of tentacles instead of only two as in the earlier stage. These marginal tentacles, like those in the young, Pl. XXVIII, figs. 1 and 6, are papillose, extensible and active, frequently winding about a small object in a prehensile manner.

Besides an increase in the number of eyes and tentacles, the mantle border of *Pectens*, of the age under consideration, has developed new features not seen in earlier stages. The border is produced perpendicularly in a thick marginal wall or curtain which has important functions. This wall is highly developed along the plicated borders of the valves but is reduced in thickness, and height as the base of the angle forming the ears,

fig. 37, p. 333, is reached. It is richly pigmented on its outer face and marked by perpendicular folds and ridges. Just below the free, inner margin of the mantle wall it is thickly set, with small equidistantly placed, arcuate tentacles, diagrammatically shown in Pl. xxviii, fig. 4, which may be called guard tentacles from their functional use. These tentacles are yellowish, not papillose, incapable of extension and move only in one plane. When the scallop is at rest the guard tentacles stand upright. In young individuals the tips of the tentacles of either mantle wall come in apposition, so that a grating or guard is formed between the separated mantle walls. In virtue of this grating no large body can pass into the gill chamber, while the animal is feeding with valves open, without striking the guard tentacles. Collision with these tentacles commonly causes the animal to shut its valves quickly. I say commonly, for irritation sometimes fails to produce the expected result. When swimming, the guard tentacles are turned outward and laid flatly against the outer border of the mantle wall. In adults the valves frequently are so widely separated that the tips of the guard tentacles are not in apposition, and the tentacles are less sensitive to stimuli than they are in young scallops of two or three centimeters in height. The guard tentacles are arranged equidistantly on the borders of the mantle walls from the base of the ventral to the base of the dorsal ear. The remaining portions of the mantle walls which are relatively slight and low, bear no guard tentacles. It is to be noticed, that the regions free from guard tentacles are the regions marked by the extension of the foot when young on one side and on the other marked by the excurrent flow of effete water, as well as by the flow of water when swimming.

The mantle borders of young and adults are separated for the greater part of their extent, being confluent on the hinge line and for a slight distance toward the byssal notch, on the ventral border. Dorsally they are confluent to the point marked as the inner angle of the ear, fig. 37, p. 333, being a somewhat greater distance than that of the ventral confluence. This relative confluence is correlated with the functional needs of the animal, as excurrent action takes place dorsally over such an area that it is not affected by the partial union of the mantle borders, whereas ventrally the foot actively swings up to the hinge line, requiring and maintaining a greater separation of the borders to that point. The mantle border is very broad and strong, and numerous, well-developed, radial muscles which bifurcate and anastomose freely serve to retract it. The muscles are more highly developed in *Pecten* than in any other Pelecypod studied, which fact is probably correlated with the active swimming habit.

It is stated that *Pecten* swims by clapping the valves, but how the motion is effected and the direction in which the animal moves has not been studied so far as I am aware and seems to be commonly misunderstood. The swimming habit of *Pecten* is one of the most striking features of this genus, and it is accomplished with such energy and rapidity that the creature attains great speed. In swimming, as when at rest, the left valve is always uppermost, and the plane of the edges of the valves is inclined to the surface of the water at an angle of about 45°.¹

It is best to study the swimming in young *Pecten*s some 3 cm. high, as at that age it is more easily seen than in adults, and does not differ from what may be observed in

¹The *Pecten*s in which the swimming habit was studied were confined in small aquaria, and it is possible that the

angle given and some other details might vary slightly if swimming freely in the open water.

them. Lying on the bottom with tentacles extended, the scallop suddenly folds the guard tentacles back so that they lie closely against the outer border of the perpendicular mantle wall. The valves are then closed by a quick action of the adductor muscle and water is forcibly expelled. The first water expelled is driven out posteriorly in the direction of the arrow *a*, Pl. XXVIII, fig. 8, and if this were the only or the main direction in which a current is expelled, the animal would by impact of water be impelled in the opposite direction or anteriorly; but the act of swimming is more complicated than this would indicate. When the valves have closed to a slight extent the borders of the two thick, perpendicular mantle walls come in contact and then no more water passes out as indicated by the arrow *a*, but instead, during further closure of the valves, it is forcibly ejected from the lower border of one ear, where the mantle wall is low and thin, as indicated by the arrow *b*, Pl. XXVIII, fig. 8. The water expelled at the point *b* is the most forcible current and probably of the greatest volume; by its means the creature is impelled in the direction of the arrow, *c*. The valves open quickly and clap again. The second time as before the first water is driven out posteriorly; but when the mantle walls come in contact, the direction of the excurrent water is again changed and is forced out from the lower border of one ear in the direction of the arrow *d*, Pl. XXVIII, fig. 8 *a*; being the strongest current, it impels the animal in the direction of the arrow *e*. This striking difference is noticeable, viz.: that at successive claps the water is driven out from alternate ears, first on one side and then on the other. The resultant action of the several currents and successive claps, illustrated in Pl. XXVIII, figs. 8-8 *a*, is therefore to drive the animal in the direction of the free borders of the valves or posteriorly. It is due to the alternate expulsion of the water first from one ear and then from the other as described, that the animal presents a succession of zigzag jerks in swimming. The direction of the current alternately to the two ears appears to be voluntary, as a scallop can scuttle over the bottom of a dish in a sidelong direction by successively expelling the water at each clap from one and the same ear. The action of the first current of water expelled posteriorly, before the mantle walls come in contact, gives the animal an upward jerk and it is in virtue of this jerk combined with the momentum in a posterior direction that it maintains its position on the surface of the water and also the high angle to the surface which it presents in swimming. The current driven out posteriorly in the initial closure of the valves is so powerful that water may be squirted by adults to the height of five inches or more from the surface by this action.

In studying the shell we find a feature correlated with the swimming habit in the incomplete closure of the valves on the eared areas; so that when the free borders of the valves are in immediate contact there is still sufficient space for excurrent action at these areas, and the valves close completely at each clap, for there is in swimming a sharp clicking noise which could be caused only by the striking together of the valves. Scallops are said to migrate in bands, being seen swimming in large numbers at some seasons of the year. They are among the most active of all Pelecypods and a careful study of their habits would doubtless prove fruitful and highly interesting.

As stated, in young scallops, the outflowing water which has served the function of aeration is passed out from the shell at a definite point on the dorsal border as indicated by the arrow in Pl. XXVIII, fig. 2. This is equally marked in character and more notice-

able in the adult. In such the water is driven out so forcibly by the rapid ciliated action of the gills that a rapid gyrating current was imparted to the whole mass of water in a large dish or preserve jar in which the animal was. Further, several times on turning a scallop over; so that the excurrent action took place in the opposite direction, almost instantly the whole mass of water responded and moved in the reversed course impelled by the changed direction of the current. The faeces of *Pecten* may be seen escaping in pellets, the form of which in section is that of a clover-leaf, and they are produced in more or less drawn-out ropy masses, Pl. xxviii, fig. 5; in one instance observed, measuring 14 cm. in length. Ryder (60) observed that the faeces of the oyster have a distinct almost horse-shoe form, due to the shape of the intestinal tract and in insects the form of the faeces is often a specific characteristic. It is possible that a study of this feature in molluscs might show similar results.

The adult of *Pecten irradians* is a free swimmer. No indications of a byssal fixation were seen at this age, and the foot is a highly atrophied organ. I have never seen the foot extended beyond the margin of the valves in the adult, although it is so active in the young, and it may then fairly be considered a retrograde and probably functionless organ. There is, therefore, a series of periods of habits in the life of *Pecten*. In the prodissoconch stage of *Pecten* (discussion later, section x), it is either a veliger swimmer, or crawls on the ventral border of the valves; in the early nepionic stage (Pl. xxviii, figs. 1, 9, 10) it is an active crawler, lying on the right valve; in late nepionic and nealagic stages, it is attached by a byssus more or less constantly, but also has the power of using the foot; in the adult, it is a free swimmer and the habits of crawling and byssal fixation seen in the young are lost. Some species, as *Chlamys* (*Pecten*) *varius*, are said to retain the byssal habit of fixation throughout life.

Frequently *Pecten*s show an extensive loss or injury of the mantle. One adult specimen observed had the left lobe on the ventral side entirely wanting, and the corresponding lobe on the right side was destitute of the eyes, tentacles and pigment. The damaged lobe was bereft of sensation, the creature showing no response when it was pinched or shadowed; but the animal was apparently uninjured otherwise. Such injury is probably due to the attacks of predatory animals, as when lying with its valves wide open it is an easy prey. Some indications pointed toward disease, and the loss of the mantle may be due to that cause. That scallops suffer a severe loss or injury to the mantle and recover, is amply proven by frequent specimens of mended shells. The margin of the shell is not injured by the predatory attacks (if such they are), but further shell growth is prevented at the injured point by the loss of the mantle. When one mantle border is injured, the other repairs the damage which would be caused by local want of shell growth, by curving the shell deposition of the uninjured side rapidly inwards, thus obviating the deficiency of the injured area. This ingrowth is probably induced by the lack of resisting support on the part of the damaged border. Adults which have been thus damaged in youth show that in time the injured mantle border is renewed, and normal shell deposition takes place, the early-damaged period being indicated by hollow-like, uneven depressions in the shell surface. In the oyster I have never seen injuries to the mantle in living animals, and no evidence of serious injuries, later repaired, are noticeable in a study of shell growth. The oyster is more sensitive to touch than the

scallop, the valves are less widely separable, when open, and at time of danger stay shut, instead of opening almost immediately after closure, as with scallop shells; therefore, the oyster is less liable to attack, at least from certain classes of enemies, than is the scallop. A surprising want of sensibility is noticeable in adult *Pecten*s. It is often possible to insert a quite large body into the shell before it closes; but the young are more sensitive. Frequently pricking the mantle border with a needle produces little effect in adults. Both adults and young are sensitive to light, so that passing the hand or even a pencil in *front* of the valves they will quickly close, as described in *Pecten jacobæus* by Patten. They open almost immediately, however, and frequently repeated stimuli soon lose their effect.

Pecten irradians is hermaphroditic, the reproductive organ is of large size, and the two sexual functions are distributed regionally. The gland as a whole is roundly triangular, extending between the gills on the ventral border of the adductor muscle, while anteriorly it passes into and is lost in the liver mass. The gland is composed of two distinctly marked portions or areas. The ventral area is pinkish white and consists wholly of the male or sperm-bearing portion; the dorsal area is brownish-yellow in color and consists of the female or egg-bearing portion of the gland. The divisions of the organ lie parallel, but anteriorly the whole mass is male, while the female portion occupies the larger part of the posterior portion of the organ. The whole gland is more or less pigmented with black, especially on its ventral keel. Abundant active spermatozoa were found in the pinkish or male portion, with well developed heads and vibratile tails; but no eggs, it being solely spermiatic. In the yellowish-brown dorsal portion were found developing and ripe eggs. The eggs are rounded or pear-shaped, granular, show nuclei and resemble the egg of an oyster, in size and appearance. A few spermatozoa were found in the female portion, but their presence was probably due to accidental introduction while examining the contents of the gland, as it is almost impossible to avoid introducing a few under such circumstances, and we may fairly suppose that the female portion also produces but one element. The sexual gland of *Pecten irradians*, it will be seen, is very similar to that of *P. glaber*, as described by Lacaze-Duthiers (40).

The gills of adult *Pecten irradians* are equal in length and differ much from the gills of the oyster. The filaments of the gills are reflected on themselves to such a length that the reflected portion equals about two-thirds the length of the direct portion as shown diagrammatically in Pl. XXIV, fig. 12. The reflected borders are free, not joined by concrescence with the reflected borders of opposing gill filaments, or with the mantle lobes, as in *Ostrea*. The filaments are joined to one another by the interlocking of tuft-like, ciliated nodes, situated at intervals. About 25-30 nodes are borne on each filament, and the nodes of contiguous filaments are in apposition. A similar structure exists in *Mytilus*, and is described by Peck. This connection does not exert a very strong binding influence, so that when alive the filaments of *Pecten* are often separated, and in alcoholic specimens are notably disconnected. The ciliated nodes serve to keep the filaments together, but quite as much to keep them separated, by an interspace to allow of the free passage of water. In the adult *Pecten*, at intervals of every 11-15 filaments, a delicate connecting septum or wall is developed between the direct and reflected border of the filaments, Pl. XXVIII, fig. 3. These walls strengthen the reflected borders and also

apparently direct currents of water in channels as it flows through the grate-like gill. When the reflected border of the filament ceases to cover the direct border, this wall is built into a peculiar plicated ridge or blade, *bl* (fig. cited), from the direct border of the filament, and continues in this blade-like fashion to the point of origin of the filament. The gills are suspended by fasciated membranes which connect the bases of the two pairs with the adductor muscle, with the visceral mass anteriorly, and with the mantle lobes posteriorly. Similar fasciated membranes also exist in *Anomia glabra*, Pl. xxix, figs. 1-2.

X. PECTEN. THE SHELL.

Characters are found in the young developing shell of *Pecten irradians* and other species which are widely different from those peculiar to the adults and a consideration of these features will now be taken up.

The first specimens of young *Pecten irradians* obtained were found in the drain-pipe traps at Buzzards Bay on the fourth of August. The youngest of these specimens is shown in Pl. xxviii, fig. 9, viewed from the left upper side, while fig. 10 is the same individual viewed from the right side on which the animal habitually lies. Pl. xxvii, fig. 9, is a similar specimen viewed from the umbonal area of the right side, more enlarged. The prodissoconch, *p*, in the several figures is as sharply marked off from the succeeding dissoconch as in *Ostrea*, *Perna* and *Avicula*, Pls. xxiv, xxv and xxvii. It is separated from the dissoconch as in the genera mentioned, by its form, histological structure and inferred anatomical features. The umbos of the prodissoconch of *Pecten* are directed posteriorly; but they are not as pronounced and arcuate as in *Ostrea* and *Perna*. The structure of the prodissoconch is homogeneous and laminar, showing fine concentric lines of growth. There is not the slightest indication of the byssal notch in the prodissoconch valves; but it originates in the initial stages of growth of the succeeding dissoconch, Pl. xxvii, fig. 9 and Pl. xxviii, figs. 10 and 13. As was argued when discussing *Perna* and *Avicula* (p. 329), the position of the byssal sinus in its relation to the prodissoconch shell indicates that the foot of that period of development occupied a position on the free ventral borders of the valves, its normal position in dimyarian Pelecypods. The prodissoconch stage of *Pecten* was doubtless dimyarian, a supposition confirmed by the shape of the shell, the position of the foot and the affinities of *Pecten* to *Avicula* and *Ostrea*, in which last genus two adductor muscles are shown to exist at that stage, Pl. xxiv, figs. 1-2.

The habits of the prodissoconch stage of *Pecten*, we know only from analogy and the structure indicated by the hard parts; but as it differs from the *Ostrean* prodissoconch in possessing a foot, it may be at this period, a veliger swimmer as is *Ostrea* or a purely crawling form. If the latter, it doubtless crawls on the ventral border of the valves as is the habit in Pelecypods in which the foot is extended from between the ventral border of the valves opposite the hinge line. Only very young *Pecten*s show the prodissoconch still intact, as it is not retained in this genus as long as in the sedentary oysters, *Aviculas* and *Pernas*. The prodissoconch of *Pecten* as in *Ostrea*, *Perna*, *Avicula*, etc., is traceable in origin to the Nuculoid radical, from which the *Aviculidæ* and their allies were derived (discussion, section xv, and table, section xvi).

The succeeding dissoconch growth in *Pecten* is clearly and sharply separated off by its changed form and histological structure. Whereas the prodissoconch shell is homogeneous and laminar in structure, the succeeding dissoconch of *Pecten irradians*, in its early stages, Pl. XXVIII, figs. 9-12, has a thin layer of prismatic cellular tissue in the right valve, the same feature having been observed in *Ostrea*, fig. 27, p. 314; also in *Anomia*, as shown in later studies. The early stages of the dissoconch growth of *Chlamys* (*Pecten*) *islandicus*, Chemn., *Pecten dislocatus*, Say, *P. magellanicus*, Gmelin and *P. monotimeris*, Con., also show marked prismatic cellular structure in the right valve. The prismatic structure of these several species does not occur in patches here and there, but extends over the whole early dissoconch shell in a thin but clearly marked layer. This is a most interesting fact as adult *Pecten irradians* does not exhibit any evidence of prismatic structure, though it is well developed in the young. Professor Carpenter in his first paper on shell structure, in 1844, says that he has seen traces of cellular structure in the Pectinidæ; but believes that it is not to be considered as constant or peculiarly characteristic of the group. In his later paper in 1848, he states that he has since found prismatic cellular structure, thin, but beautifully preserved in *Pecten nobilis*, which he figures. This is the only case I find mentioned in which prismatic structure is known in *Pecten*. Dr. Dall (16), however, in recent studies of deep-sea molluscs has observed prismatic cellular structure in many species of *Amusium*, and in the allied genera *Pseudamusium* and *Propreamusium*. In these cases the prismatic structure, though often limited in extent, was not confined to the right valve, as in my observations of young Pectens. Dall notes that this structure is especially characteristic of abyssal species of this group, in which also the shell is extremely thin and fragile. My observation of prismatic structure in the young of five species studied, proves that this feature which is not a characteristic of the group may yet be found in the young. The Aviculidæ, in which prismatic structure is highly characteristic, are in the line of ancestry of the Pectinidæ. The occurrence of prismatic structure in young Pectens is therefore a good example of the principle of acceleration of development which is that ancestral characters may be found in the young which are wanting in adult individuals.

Although prismatic structure is characteristic of the right valve in young *Pecten irradians*, the left valve in this and the other species studied has no prismatic layer. In *P. irradians*, the left valve in its early nepionic stage is marked by a peculiar pitted structure. The degree of pitting varies in different individuals, but in none was it as marked a feature as in young *P. dislocatus*, where it is highly accentuated.

In *Pecten* the shell of the first true dissoconch or nepionic period, Pl. XXVIII, figs. 9-10, is markedly different from succeeding stages, as well as from the early completed prodissoconch stage. The hinge is produced as a straight line and the borders of the valves descend in a curve from the extreme limits of the hinge line without possessing the ears which are characteristic of the adult in all species of the genus. The ventral border of the left valve, fig. 9, has no byssal notch but near the hinge area is produced in a lobe-like curve, the lobe projecting beyond the border of the byssal sinus of the right valve as shown in fig. 10. There are no plications of the shell at this stage although these originate early and are characteristic of the adult. The features of the ventral lobe, and the absence of ears and plications, give the shell as shown in the figures cited

a totally different aspect from that of later stages and also different from any form known in other species of the genus.

The right valve of young *Pecten irradians*, on which it rests, Pl. xxviii, fig. 10, is marked by a deep byssal notch, originating as stated in the initial stages of the dissoconch shell as indicated by the lines of growth shown in the enlarged figure of the hinge area in Pl. xxvii, fig. 9. The border of the notch on its lower side is marked by a well defined tooth-like process, Pl. xxviii, fig. 10. In later growth, Pl. xxviii, fig. 13, more tooth-like processes develop and they are characteristic of young specimens up to four or five centimeters in height but none exist in the adult shell. The left upper valve overhangs the right lower valve by a slight extent along the free margins, fig. 10, as in young *Ostrea* and *Anomia*. The color of the young shell in both valves is of a light yellowish-brown.

In the consideration of *Perna* (p. 328) it is shown that when the foot lies close up to the hinge area in Pelecypods a special notch exists for its extrusion. The notch is required because if not existent the valves would have to open very widely to allow of the passage of the foot at a position so close to the point of union of the valves. Perhaps an equal reason for the need of the notch is the fact that such forms lie on one valve and drag the shell in crawling by extending the foot over the edge of the lower valve. They do not creep on the free borders of the valves as do ordinary dimyarians in which the foot is extended from a point far removed from the hinge line by a slight gaping of the valves, without the aid of any special sinus. As shown on p. 333, *Pecten irradians*, when very young; Pl. xxviii, fig. 1, has no byssal fixation, the animal leading an active crawling existence. The notch may therefore be considered as a foot notch rather than a byssal notch at this period. The existence of a byssus or the constant extension of an active foot would equally affect shell growth by exerting pressure on the mantle border, thus causing its local retraction and retarding shell deposition at the point of extrusion, so that it is not necessary to imply the existence of a byssus because a notch exists at an area where the byssus would be produced if it existed.¹ This has important bearing on fossil forms which are considered as byssated or attached, if a notch exists in this region; whereas they may with equal reason be considered, as far as the notch is concerned, as free forms which crawled while lying on one side with the foot extended through a special notch produced by the existence of such a habit. This mechanical explanation of the formation of the notch in *Pecten* shows what close relations may be traced between the form of hard parts and the anatomy and habits of the animal.

A view of the hinge area and byssal notch of a *Pecten* of the same age as the above considered specimen viewed from the right side is shown in Pl. xxvii, fig. 9. The relation of the prodissoconch to the dissoconch and byssal notch is clearly indicated and it is noticeable that the left umbo protrudes beyond the right. This is due to the greater convexity of the left valve, as is also noticeable in *Chlamys islandica*, Pl. xxvii, fig. 8.

The early nepionic stages of *Pecten magellanicus*, *P. dislocatus* (traced by following

¹In this connection a comparison may be made of the early nepionic shell of *Pecten*, Pl. xxviii, fig. 10, viewed from the right side with a similar view of young *Anomia*,

Pl. xxix, fig. 6. The early condition of *Pecten* does much to elucidate the somewhat similar form of shell growth of young *Anomia*.

the lines of growth) *P. testæ* and *Chlamys islandica*, Pl. XXVIII, fig. 14, agree with the same stage of *P. irradians*, Pl. XXVIII, figs. 9-10, in the form of valves. This form may therefore be considered as typical of the first stage of growth of the dissoconch shell of the group. In studying genera of the palæozoic Aviculidæ, we find genera that agree closely in appearance with the young shell of *Pecten*; especially when it is viewed from the left side as in Pl. XXVIII, fig. 9. The genera *Actinoptera*, *Leiopteria* and *Leptodosma*, as figured in Hall's Palæontology of New York, are very comparable to this early stage of *Pecten*. A still nearer comparison may be made in species of the Silurian genus *Rhombopteria* (gen. nov.) fig. 51, section XVI, which are closely comparable to young *Pecten* in all the species observed. *Rhombopteria* is selected as the primitive radical of the Aviculidæ and their allies (see discussion and table, section XVI), and it is one of the best proofs of the correctness of that view that the nepionic stage of *Pecten* so closely corresponds with that early type. In the studies of *Avicula* and *Perna*, the young of those genera, fig. 32, p. 330, and Pl. XXVII, fig. 1, is compared closely to the same ancient genera to which I have just compared young *Pecten*. A comparison of young *Pecten*, Pl. XXVIII, fig. 9, with the similar period of growth of young *Avicula* and *Perna*, in the figures cited, shows that at this early age the three genera are closely similar. Differences in the angles of contour exist, especially in the hinge line; but they are slight in degree, and the important phylogenetic conclusion may be made that these genera in the nepionic stage are so alike that they are referable in their inherited form to the same ancestral types. Thus we see that the form as well as the prismatic structure of the shell of young developing *Pectens* may be traced to ancestral types from which the genus was evolved.

A stage of shell growth in *Pecten irradians*, Pl. XXVIII, figs. 12-13, later than that just considered, shows the beginning of features characteristic of the family and species to which the young scallop belongs. Plications similar to those of the adult begin to be marked in either valve and ears to be developed, as shown in fig. 12, viewed from the left side, and fig. 13, viewed from the right side. The byssal notch is strongly marked, as in the earlier stage, and it is to be observed that the notch is much deeper relatively in this early, active, creeping stage than in the adult, where the use of the foot as a creeping organ is lost. The base of the byssal notch, fig. 13, shows four marked, tooth-like processes, of which one only was present in Pl. XXVIII, fig. 10. These teeth may prove of value in tracing relationships; but their function, if any exist, is not understood. The plications of the shell are clearly defined and originate suddenly, indicating a stage by their introduction. The plications are like those of the adult, fig. 37, p. 333, and they are the same which are retained throughout life, no new plications, originating by bifurcation or interposition, in this species. The left upper valve does not extend beyond the right valve on its free margin as in the earlier stage, fig. 10.

A later period of growth in *Pecten irradians* is shown in Pl. XXVIII, fig. 2. The ears are more accentuated than in the previous figures, though they do not bear to the whole shell the same relative size and shape, as in the adult, fig. 37, p. 333. The hinge line of this stage, fig. 2, is much shorter than in the earlier stage, Pl. XXVIII, figs. 12-13, but much longer relatively to the breadth of the valves than in the adult. In other features, excepting the depth of the byssal notch, this age does not differ essentially from the adult

in the form of the shell. Differences in the anatomy and habits, however, exist, as discussed in previous pages.

I have shown that the early, nepionic shell growth of *Pecten*, Pl. xxviii, figs. 9–10, has a form referable in origin to the adults of ancient members of the Aviculidæ, and I believe that the form of the later shell growth is also of phylogenetic significance. The hinge line of *Pecten irradians*, in Pl. xxviii, figs. 12–13, is relatively long as compared with the condition found in the adult of this or other species of *Pecten*s, and correlative-ly the ears are very slightly developed as compared with the adult. The same condition of relative great length of hinge line and want of development of the ears is seen in similar stages of development of *Chlamys (Pecten) islandica*, Pl. xxviii, fig. 14, *Pecten magellanicus* and *P. dislocatus*; therefore it may be considered as typical of developing *Pecten*s. In Hall's Palæontology, Vol. v, Part 1, we find forms of Devonian Pectinidæ under the genus *Pterinopecten* which agree closely with the form of shells here figured in developing modern *Pecten*s. The agreement is in the relatively great length of the hinge line and slight production of ears, which features characterize *Pterinopecten* and separate it from the nearly allied genus *Aviculopecten*. *Pterinopecten* is the least removed from the Aviculidæ, and is the simplest known form of the Pectinidæ. The young of *Pterinopecten* resembles the adult of *Rhombopteria* and the adult resembles the young of *Aviculopecten* and *Pecten* (see section xvi). It forms, therefore, a strong link in our phylogenetic series, and is placed as the first departure from the Aviculidæ in the *Pecten* line of variation (see discussion and genealogical table, section xvi).

The palæozoic genus *Aviculopecten*, as amended by Hall, differs from *Pterinopecten* in a greater production of the ears and in a relatively shorter hinge line. Turning to the developing shell of *Pecten irradians*, we find that the later growth, Pl. xxviii, fig. 2, differs from the earlier growth, Pl. *id.*, figs. 12–13, as *Aviculopecten* differs from *Pterinopecten*. The same stage also differs from the adult fig. 37, p. 333, as *Aviculopecten* differs from *Pecten*. This later stage is therefore traceable to *Aviculopecten* as its ancestral representative, and also the position of *Aviculopecten* is clearly indicated in its relation to other genera (see discussion and table, section xvi).

The prodissoconch of *Pecten* as stated (p. 342) is referable in origin to the Nuculoid radical, represented in the development of the Aviculidæ and their allies as illustrated by typical genera. It is further shown that in the development of a modern *Pecten* we find in the first stages of dissoconch growth a form of shell, Pl. xxviii, fig. 9, presenting characters which make it referable in ancestral origin to *Rhombopteria* a member of the true Aviculidæ, later succeeded by a growth, Pl. *id.*, fig. 12, bearing marked features referable in origin to an ancestral genus *Pterinopecten*, which is transitional between the Aviculidæ and the Pectinidæ. Still later a stage exists Pl. *id.*, fig. 2, which is referable in its inherited form to *Aviculopecten*, and finally, the true *Pecten* features characteristic of the adult, fig. 37, p. 333, are established. The geological sequence of these several groups is in the order indicated by the development of *Pecten*. We have, therefore, a clear case of the ontogeny of an individual illustrating the phylogeny of a group (see table, section xvi).

As further substantiation of my position that the Pectinidæ were evolved from the Aviculidæ, it may be noted that in the Challenger report, Vol. xiii, part xxv, Professor

Smith figures a deep-sea species, which he calls *Pecten aviculoides*, on account of the close resemblance which it bears to *Avicula*, although he considers it a *Pecten*. Again, a fossil from the Lias shales, as Professor Carpenter notes, was by one author named *Avicula* and by another *Pecten*, the mixture of characters being such as to sanction its being placed in either genus, according to the value attributed to different features. Carpenter affirms that it is a true *Pecten* because of a coarse shell structure like *Pecten* and an absence of prisms found in *Avicula*. Both these forms may properly be considered as representing in the adult a combination of types which I have shown is traceable in early stages of the developing young.

Whereas very young specimens of *Pecten irradians* are yellowish-brown, older young and adults are commonly bluish-gray, the coloration often being less or wanting in the furrows of the upper, left valve. The lower valve may be of the same color as the upper, but is generally less pigmented, especially in young individuals, and specimens are frequent in which the upper valve being dark blue-gray, the lower is nearly or quite white. This difference bears a direct relation to the amount of light to which the two valves are exposed, the paler being the lower valve, which is constantly turned away from the light. In studying other species of *Pecten*, many of which are highly colored, we find that the same condition exists, the lower right valve being white, or of a paler color than the left upper valve, which may be brilliantly colored: red, brown or yellow. An example of a striking contrast is *Amusium (Pecten) japonicum*, in which the upper valve is rich red, the lower, pure white. In the Spondyli, which are attached by the right valve, the lower valve also is white, or paler than the upper left valve, which is turned toward the light and is often highly colored. Fischer notes the difference in color of the valves in Spondyli, and states that an abyssal species of *Spondylus* has both valves blanched. This relation of the coloration to the amount of light received by the two valves in bivalves is more or less noticeable in the lower and upper side of univalves and is briefly considered by Tryon. Dr. Dall (16) considers the allied subject of the coloration, surface marking and thinness of the shells of abyssal species, in his interesting conclusions published in the Report of the Blake Mollusca.

Pecten magellanicus Gmelin (*P. tenuicostatus*, Mighels). A number of young specimens of this large species measuring from 2-6 mm. in height were dredged at several stations by the U. S. Fish Commission Steamer Albatross. They are entered as No. 62307 in the Smithsonian Institution Catalogue. Sharply-defined but quite small prodissoconchs, like those figured in *Pecten irradians*, mark the umbos of all well-preserved specimens. Fig. 38, p. 348 represents one of the smaller specimens. The early dissoconch as indicated by the lines of growth is similar in form to *Pecten irradians*, Pl. xxviii, figs. 9-10, no ears having developed and there is a deep byssal notch in the right valve although it is slightly indicated in the adult. The byssal notch of the right valve, however, bears no teeth as in the other species described. The hinge line equals nearly the whole width of the shell as in *Pecten irradians*, Pl. xxviii, fig. 12; but, as in that species, differs in this character from the adult. The hinge area on either side of the cartilage pit bears a wide hinge plate, sinuous in outline and marked by numerous flutings. The flutings are nearly perpendicular to the hinge line, but are slightly inclined toward the umbos. Although characteristic of the young, this hinge plate is wanting in the adult.

A similar hinge plate exists in *Pecten monotimeris*, Con., and it is described by Dall (16) in the young or adult of several species of *Pecten*, and in *Pseudamusium* and *Dimya*. This fluted plate, Dall considers as a form of dentition augmenting the strength of the hinge line (on the hinge of Pelecypods, etc., Am. Jour. Sc. Dec. 1889).

The right valve of *Pecten magellanicus* has a thin layer of well defined prismatic structure, fig. 39, and the prisms are larger than those observed in other species of *Pecten*. They are peculiar in being for the most part almost quadrangular, and are arranged with extreme regularity parallel to the lines of growth; but where slight fractures have induced irregular shell growth, they are polygonal as in other species of *Pecten*. The right valve in the young specimens studied seldom shows radiating striæ but they sometimes exist slightly emphasized in the last-formed portion of the shell, as series of dis-

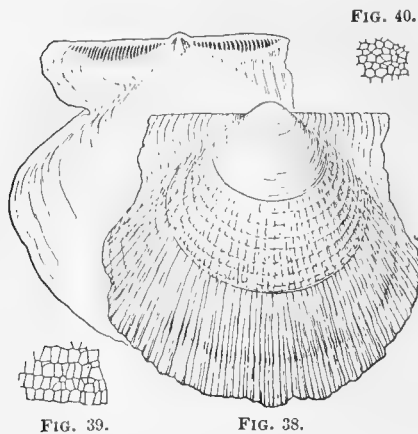


FIG. 38.—Left and right valve of young *Pecten magellanicus*, showing fluted hinge plate byssal sinus, and marking of the left valve characteristic of the period of development. $\times 18$ diam.

FIG. 39.—*Pecten magellanicus*, prismatic structure of right valve. $\times 90$ diam.

FIG. 40.—*Pecten dislocatus*, prismatic structure of right valve. $\times 90$ diam.

Original specimens in Smithsonian Institution, Washington (drawn by J. H. Emerton).

connected knobs. The ventral ear of the right valve, on the contrary, bears coarse costæ crossed by imbricating lines of growth. In the adult, the radiating ridges of the right valve are much flatter and less accentuated than in the left upper valve. The left valve, fig. 38, after the earliest nepionic stages, which are smooth, is marked by a stage of concentric and radiating ridges both sharply defined and dividing the shell surface into sunken squares. Knobs or bosses ornament the intersection of the ridges. The structure seen here is a common form of surface ornamentation among fossil Aviculidæ. This peculiar marking of the early stage is very characteristic although limited in extent and ceases suddenly being succeeded by fine somewhat sinuous radiating ridges which are retained thereafter, and are characteristic of the adult.

Some adult specimens of *Pecten magellanicus*, from the Georges' Banks, are interesting for a comparison with the observations on anatomical features of *P. irradians*. The species is well fitted for study on account of the size, adult specimens measuring 15 cm. or more in height. The adductor muscle is double and the two portions are strongly accentuated. The borders of the two portions of the muscle are free on their limits and at the point of insertion in the shell produce two well-marked impressions instead of a single slight one as in *Pecten irradians*. There is no posterior retractor muscle of the foot in this species; but it quite likely exists in the young, as that bears evidence in its shell, fig. 38, of being an active crawler. The foot is marked by two clefts, the distal one for crawling, the proximal one the seat of the byssal gland as in *Pecten irradians*. The mantle as in that species, has a thick marginal perpendicular wall, decreasing at the eared areas and thickly set with guard tentacles, extensible tentacles and eyes, indicating similar habits to those described in *Pecten irradians*. The gills, intestine, and reproductive body are also the same as may be observed in *Pecten irradians*.

Chlamys (Pecten) islandica, Chemn. sp., specimen No. 27294, Smithsonian Institution

catalogue, is a young individual 3 mm. in height. This specimen is figured in Pl. xxviii, fig. 14, as viewed from the left side and Pl. xxvii, fig. 8, is the umbonal area more magnified, viewed from the right side. The prodissoconch is sharply defined and the umbos are directed slightly posteriorly. It bears concentric lines of growth, no indication of a byssal sinus and is homogeneous in structure. The succeeding dissoconch is yellowish-brown and in its early stages has a well-defined, prismatic layer in the right valve. In the oldest period of this young specimen no prismatic layer exists, the structure being lost thus early in shell growth. The left valve has a punctate structure as mentioned in some other species. The early nepionic stage as discerned by following the lines of growth is seen to be similar in form to the nepionic stage of *Pecten irradians*, Pl. xxviii, fig. 9. The left valve is marked by a deep byssal notch, Pl. xxvii, fig. 8, the lower border of which bears teeth similar to those of *Pecten irradians* and these teeth exist also in the adult of *Chlamys islandica*. At the close of the smooth, early nepionic stage of *C. islandica*, we find radiating plications similar to those of the adult originating at a definitely marked area, Pl. xxviii, fig. 14. New plications develop in succeeding growth between those first formed, instead of the first formed being the only ones built as in *Pecten irradians*. The hinge line is very long proportionately to the width of the shell as compared with the adult condition; the same feature being characteristic of the young of all the species described. The ears in this early stage are nearly equal, whereas in the adult the ventral (anterior) ear is characteristically much larger than the opposite or dorsal ear.

Pecten dislocatus, Say. A number of young specimens of this species are in the collections of the Smithsonian Institution, under the catalogue number 62278. They were dredged off the coast of the Carolinas at several stations. The specimens vary from 3 to 13 mm. in height. All the youngest show a prodissoconch like that of *Pecten irradians*, Pl. xxviii, figs. 9-10. The prodissoconch bears fine concentric lines of growth, has no indication of a byssal notch and is not prismatic; also the umbos are directed posteriorly as in all this group. The right valve has in early nepionic stages a well-defined prismatic layer, fig. 40, p. 348, the prisms being of about the same size as those in *P. irradians* and *Chlamys islandica*, but smaller than those in *Pecten magellanicus*. Conversely, the left valve has no prismatic layer; but it has a very characteristic pitted structure in its early stages. The pits are not deep, but numerous and very closely related to one another. They disappear with the close of the smooth nepionic stage. A similar structure is described in some other species; but in none, unless *P. testæ*, is it as noticeable and clearly marked as in this species.

The early nepionic stage of *Pecten dislocatus*, as ascertained by following the lines of growth, which are particularly well defined in this species, is seen to be of the same form as that of *Pecten irradians*, Pl. xxviii, figs. 9-10. No ears exist at this period and the hinge line in length equals the entire width of the shell. A deep byssal notch exists in the right valve originating with the close of the prodissoconch stage. In later growth plications in the shell originate suddenly as in *Pecten irradians*, Pl. xxviii, fig. 12, causing by their introduction a marked stage as in that species. Ears also develop with succeeding growth and the hinge line gradually loses its great length proportionately to the

width of the shell. The base of the byssal notch bears a number of teeth like those of *Pecten irradians* and *Chlamys islandica*, but they are wanting in the adult.

Pecten testæ. In the Jeffreys collection, now in the Smithsonian Institution, there are two very young specimens of this species, catalogued as No. 62607. I saw them in Washington, but did not borrow them as I did specimens of the above described species. From a drawing made at the time (previous to my studies of other young Pectens) the upper left valve exactly agrees in form and is of about the same size as *Pecten irradians*, Pl. xxviii, fig. 9. A prodissoconch like that of *P. irradians* and other species exists in my drawing of the specimen. The early dissoconch shell has no ears and is comparable to ancient forms of the Aviculidæ as discussed in considering the same period of development of *Pecten irradians*, with which it agrees in form as far as my drawing indicates. Minute, punctate structure of the dissoconch was observed in this species similar to that noted in *Pecten dislocatus*; but I cannot say whether prismatic structure exists although in all probability it does.

Specimens of *Pecten monotimeris*, Con., recently received from California, have a similar prodissoconch and nepionic stages to those described in *P. irradians*, as ascertained by following the lines of growth. In the nepionic stage, the right valve has prismatic cellular structure and the left valve punctate structure as in *P. irradians*, but as in that species these features are early lost.

XI. GENERA ALLIED TO PECTEN.

Of the genera here considered I have had only limited opportunities to study the young; for, as conchologists commonly pay little attention to the young of molluscs, it is a difficult matter to obtain early stages of genera not living in our own waters.

Hinnites, Pl. xxvi, figs. 3-4, is a genus closely related to Pecten, but as it has been described in section VII, I will give only brief supplementary notes at this point. It is shown, p. 324, that *Hinnites cortesi* is pecteniform and regular when young; later it solders one valve to a foreign body and with this change in habit assumes an irregularity of growth rendering its valves, especially the attached one, comparable to *Ostrea* in form. The form of the valves is ascribed to the condition of cemented fixation. The relation of Hinnites to Pecten I believe is directly comparable to the relation of *Ostrea* to *Perna*; the difference being that Hinnites in the nepionic and nealagic stages is free or byssated and then retains the ancestral Pecten features. It does not become attached and assume the ostrean irregular growth (wiping out early characters) until a comparatively late stage of development, Pl. xxvi, fig. 3. On the other hand, *Ostrea* is attached at the close of the prodissoconch period and at once assumes the ostrean form, by this means eradicating features which might otherwise render the early dissoconch growth comparable to the ancestral *Perna* or *Perna*-like form. The age at which fixation takes place varies somewhat in individuals, as may be seen in series of specimens of *Hinnites giganteus*. That species is instructive as showing how, in the development of the individual, the imbrications of the lines of growth in the nealagic pecteniform stage gradually become more and more produced, until in the adult they form spinous productions of the

valves. The spines of the left (free) valve are comparatively sharp and acicular, while those of the right (attached) valve are flatter and spathulate; though both forms of spines may be serially traced to the imbrications of the young, where they are alike in both valves.

Spondylus as a genus of attached Pelecypoda naturally draws attention in these studies. It is cemented by one valve and its irregular, inequivalvular shell, Pl. xxvi, fig. 1, has been ascribed to the conditions of cemented fixation (*vide* pp. 318 and 323). The cambered structure of *Spondylus* has been also considered and I wish here only to describe the young.

In the collections of the Boston Society of Natural History are specimens of *Spondylus asperrimus*, Sby., from the Pacific Islands, bearing the catalogue number 8494. The upper left valves of the specimens are produced on the hinge line as slightly developed ears and have a decidedly pecteniform aspect, as is characteristic of this valve in living and fossil Spondyli. The lower right valves which are or have been attached, are composed of highly irregular, concentrically rugose and spinous shell growth, as is also characteristic of species of this genus. One of the specimens of a right valve, however, is very well preserved up to the initial stages of growth. At the umbo of this well-preserved specimen of *Spondylus asperrimus*, Pl. xxvii, fig. 4, is a prodissoconch similar to that described in species of *Pecten*. The prodissoconch is rounded or oval in outline and is clearly marked off from the succeeding shell growth.¹ It is not sufficiently well-preserved to show lines of growth; but it has no byssal notch which exists, however, in the first stages of the succeeding dissoconch growth, as in *Pecten*, Pl. xxvii, fig. 9. The first nepionic stage of shell growth in *Spondylus*, as shown in the figure, is pecteniform. It has a long hinge line relatively to the width of the shell at that age, and a deep byssal sinus. As in the prodissoconch most of the lines of growth of this early stage have been worn off. At the close of the pecteniform stage the animal became soldered to a foreign body and the succeeding shell deposition, affected by the new condition of cemented fixation, has assumed the irregular and rugosely distorted growth characteristic of young Spondyli. In the first stages of the irregular growth, the byssal notch is soldered over, and eradicated in a similar fashion to that shown in *Hinnites*, Pl. xxvi, fig. 3. A prodissoconch and nepionic stage similar to that described in *Spondylus asperrimus*, has been observed also in specimens of *S. croceus*, Chemn. and *S. variegatus*, Chemn. sp.?, at the New York State museum; and in *S. ducalis*, Chemn. and *S. varians*, Sow., at the Peabody Academy of Science, in Salem.

The above description of the development of the shell of *Spondylus* is directly comparable to what has been described in the shell of *Hinnites*. Both valves before fixation are pecteniform in these genera; as soon as attached the lower valve loses this early existent, ancestral feature and assumes the irregularity characteristic of attached Pelecypoda with of course the peculiar order of irregularity normal to *Spondylus* or to *Hinnites*. As the lower valve becomes irregular and distorted, the upper valve in both genera, acting in sympathy, becomes irregular also; but, as previously claimed, the dis-

¹A specimen of a left valve of a young *Spondylus*, in the Smithsonian Institution collections, catalogue No. 62242, shows a prodissoconch like that described above in a right

valve. It is rounded, with slightly developed umbos. Its limits are marked off from the succeeding dissoconch as in Pl. xxvii, fig. 4, of a right valve of *S. asperrimus*.

tortion of the upper free valve is seldom as great as the distortion of the lower cemented valve. Specimens of *Spondylus imperialis*, Chemn., in the Society's collections, show the remarkable condition of being perfectly equivalvular. Both valves have ears on the hinge line and though spinous, both are equally so. The right valve has no triangular hinge area or talon and the umbos of the two valves are closely related. Studying these shells, I found no evidence that they had been attached during any period of their growth. With this freedom from fixation we have, therefore, an equivalvular shell which is a wide departure from the typical condition of the genus.

The conclusion arrived at that the free valve of attached, cemented Pelecypods is least modified and therefore retains more of the ancestral characteristics, which are nearly or quite eradicated from the cemented valve (section VII), thus finds strong support in *Spondylus*. In many figures of fossil *Spondylus*, published by MM. d'Orbigny and Pictet, (also see Pl. xxvi, fig. 1), we find striking dissimilarity in the two valves, the attached one being always the most modified. The free valve which is least modified retains in a marked degree, especially in the young, characters which are traceable to the Pectinidæ, from which the Spondyli have doubtless evolved. I have not dissected a *Spondylus*; but from published notes gather that this genus is closely connected with *Pecten* by anatomical features.

Plicatula is a genus placed next in kinship to *Spondylus*, the anatomy being similar according to authors. Some very young shells of *Plicatula marginata*, Say, Pl. xxvii, fig. 5, from the Miocene Tertiaries of North Carolina present features of interest. A distinct prodissoconch, similar in form to that of *Pecten* and *Spondylus*, exists. It is rounded with slightly developed umbos which are directed posteriorly. The specimens, as shown in the figure, bear a considerable resemblance to young oysters of a similar age; and as it may be thought that a mistake has been made in the identification, I may say that they show the typical teeth of *Plicatula*, also series of specimens have been traced from the very young to the mature condition. The prodissoconch umbos in specimens of *Plicatula*, when attached to the object of fixation, Pl. xxvii, fig. 5, point to the right of the observer viewing them from above, whereas in *Ostrea*, Pl. xxv, figs. 1-5, they point to the left, which is due to the fact that *Plicatula* is attached by the right valve, whereas *Ostrea* is attached by the left. In both genera, the prodissoconch umbos are directed posteriorly relatively to the anatomy which is known directly or by analogy to have existed at the close of the prodissoconch period.

The early nepionic stage of *Plicatula*, Pl. xxvii, fig. 5, is very similar in appearance to a young oyster, as stated. The lower right valve is flat and closely related to the object of fixation, while the upper left valve is convex.¹ No byssal notch is discoverable in the earliest stages of dissoconch growth, and this feature, together with the form of the valves, indicates that *Plicatula* became permanently attached at the close of

¹ It has been observed by authors, that the upper valve of fixed Pelecypods, such as *Ostrea* and *Anomia*, also univalves, as *Crepidula*, frequently simulates the outlines of the object of support, ridges, knobs, etc., on the foreign body, being perfectly reproduced in the free valve. The most striking case of this, I have seen, is in a finely pre-

served specimen of *Plicatula marginata*, from the Tertiaries, in which the free valve reproduces with beautiful exactness the structure of a Bryozoön over which the attached valve was growing. Not only a general copy is made, but each cell is outlined in the upper valve of the *Plicatula*.

the prodissoconch stage, as is conclusively shown to be the case with oysters. Adult *Plicatula marginata*, is deeply plicated; but the plications, as in plicated oysters, do not originate until the shell growth extends beyond the limits of the object of fixation.

Plicatula, taken in connection with the preceding genera, is a valuable proof of the correctness of the conclusion that cementation destroys indications in the shells of Pelecypoda of their ancestral relationship. Pecten, Hinnites, Spondylus and Plicatula may be serially connected in the order indicated by a study of the shell, and from what I can gather, the anatomical features would present a similar series. Using some license so as to express it graphically, one may say: solder a Pecten when partly grown and the succeeding growth is irregular, forming the genus Hinnites, Pl. XXVI, figs. 3-4; solder a Pecten at a much younger period and the succeeding growth is irregular, forming the genus Spondylus, Pl. XXVII, fig. 4; solder a Pecten at the close of the prodissoconch stage, before any dissoconch growth has taken place, and the succeeding growth is irregular, forming the genus Plicatula, Pl. XXVII, fig. 5. In all, the irregularity of growth commences with the introduction of the cemented period. Spondylus is probably a branch from Pecten through the intermediation of Hinnites, which unquestionably is closely akin to Pecten. So near are Spondylus and Hinnites, that Stoliczka says some fossil forms, first considered as Spondyli, have since been transferred to Hinnites.

Brief studies of Lima have been made. Lima has a perpendicular mantle wall like that of Pecten which is shown to be so actively functional in swimming, and it probably subserves the same purpose in Lima, as the swimming of that genus, described by Dr. Jeffreys (see Tryon), is performed similarly to that of Pecten. This difference exists, however; Lima swims with the plane of the edges of valves perpendicular, whereas in Pecten they are horizontal while swimming. From the shape of the mantle walls and shell, also from the description of the swimming movement, it appears that in Lima the excurrent flow of water which propels the animal all takes place through one eared area, the ventral, instead of alternately from either ear as in Pecten. In the species of Lima examined, there were no guard tentacles on the free borders of the mantle walls as in Pecten, Pl. XXVIII, fig. 4, but Jeffreys' description of Lima includes such organs. The marginal tentacles at the base of the perpendicular wall are thick and numerous. Dr. Jeffreys describes them as twining actively and presenting a tenacious prehensibility, grasping the fingers when approached toward them. This prehensibility I have described in Pecten though it is there less marked in degree. The gills of Lima have the reflected portion of the filaments equal in length to the direct portion, and the tip of the reflected portion of each lamina is again reflected, presenting an abbreviated additional lamina.¹ The gills of Lima differ from those of Pecten in that the separate filaments are joined by bars which form a direct concrescence of the several filaments instead of by the interlocking of ciliated processes, as in Pecten; and in this character Lima agrees with Ostrea.

A young *Lima elliptica*, in the Jeffreys' collection at the Smithsonian Institution, shows a well-marked prodissoconch. In a drawing which I made at that museum, Pl. XXVII, fig. 6, the prodissoconch is sharply marked off from the succeeding dissoconch, and it

¹ In *Pecten irradians*, the tip of the reflected filaments is bent back on itself slightly, Pl. XXIV, fig. 12, indicating the initial stages of such an abbreviated additional lamina.

Lacaze-Duthiers also observed such a brief reflection in the outer filaments of *Anomia*.

has well-developed umbos. The succeeding dissoconch is limaform, but no prismatic structure was observed as in young *Pecten*; it may, however, exist in well-preserved specimens.

XII. ANOMIA. ANATOMY AND HABITS.

Anomia freely attached themselves to the glass slides in my drain-pipe traps and therefore I had an opportunity to study the young under this favorable condition with transmitted light. The species is *Anomia glabra*, Verrill, figs. 41-42, which is abundant in the shoal waters of Buzzards Bay, often covering shells and stones as thickly as do oysters.

Anomia have not in the same degree as oysters the power of resisting drying which is so characteristic of that mollusc, and rarely set at points which are long exposed at

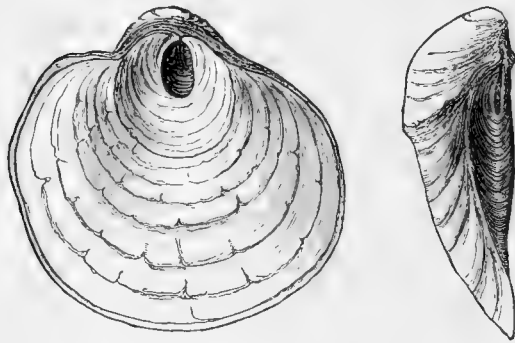


FIG. 41.

FIG. 42.

FIG. 41. Adult *Anomia glabra* viewed from the right, lower side; natural size.

FIG. 42. The same in profile view. (From Binney's Gould.)

low tide. They grow rapidly and some specimens attached to glass slides measure 25 mm. in height, the result of the summer's growth. These almost equal the adult in size as the latter rarely exceed 40 mm. Examining *Anomia* where a number are attached to a single rock or shell, it will be found that the longer axes of the specimens in most cases are nearly parallel, the reverse of the condition of oyster spats, where the axes point at every angle in the plane of the surface of attachment. This parallel arrangement in *Anomia* seems to bear a relation to the direction of strongest currents, the animals arranging themselves during their early locomotive stage in the plane

of least resistance and afterwards becoming permanently fixed in this position. On the other hand, oysters which have no crawling locomotive stage, pay no attention to prevailing currents in their position of fixation. A marked case of animals arranging themselves with regard to currents was observed in *Crepidula fornicata*, Pl. XXIII, fig. 22. Large numbers of colonies were found at Buzzards Bay like the figure in which all the individuals were headed one way. This arrangement in one plane does not always hold in *Crepidulas* as they may be arranged at different angles; in such cases we may reasonably suppose that no strong prevailing current existed in the location where the animals grew.

Anomia was formerly considered as related to Brachiopods, but such a connection has long been disproven. Forbes and Hanley and Lacaze-Duthiers compared *Anomia* to *Pecten*; but notwithstanding this, a close relationship of the genus to *Ostrea* has been as a probability quite generally entertained. This assumption appears founded on a certain similarity of the shell of *Anomia* to an oyster, especially a young oyster. *Anomia* belongs to the same broad group as the oysters, as proven by features of anatomical and shell structure; but it is more nearly related to *Pecten* than to *Ostrea*. Previous studies have shown that the form of the shell in Pelecypods is often highly modified by

special conditions, as the cementation of a valve, or by anatomical features and habits of the individual. I think therefore that the peculiarity of the shell in *Anomia* may be considered as an adaptation to its environment¹ and not due to any genetic connection of the group. On this question we have the support of the conclusions of Professor Lacaze-Duthiers, who in his well-known paper on *Anomia ephippium*, L., says: ". . . l'ossicule de l'Anomie est un byssus, et toutes les anomalies sont la conséquence de la position de l'animal sur la côté droit, et de la soudure du byssus aux corps étrangers." His studies were anatomical, based on the ambiguous adult and it is my pleasure as a result of studies of the young, to be able to show conclusively the correctness of some of the deductions of the eminent French investigator.

The youngest specimens found alive on glass slides were about the size of Pl. XXIX, figs. 5-6. At this age and up to a considerably later period of growth, the young are freely locomotive, crawling actively at intervals by prolongation of the highly developed foot. The lines of growth in fig. 6 indicate that, when very young, the byssus was on the extreme margin of the valves; but in this figure the byssal sinus has already become sub-central in position and partially enclosed by the growth of the right valve. At this age the byssal fixation is only maintained a part of the time, or perhaps more correctly speaking the byssal attachment may be said to be voluntarily and frequently abandoned. The byssus of this early period is composed of a series of bundles of threads which flatten against the surface of the glass as seen from the right side through the glass to which it is attached. The byssal hold at this age is an act of volition on the part of the animal, as if paralyzed with cocaine they may be easily washed off a glass slide by a stream from a pipette, whereas in the normal condition they cannot be dislodged by any force short of scraping. The cocaine treatment is a good method to employ in collecting very young *Anomia* attached to shells, rocks, etc., because if scraped off, the lower valve, which, in this species, is of extreme tenuity, is almost certain to be destroyed. When older the byssal attachment becomes permanent by the calcification of its tip.

A young *Anomia* viewed from the left side is shown in Pl. XXIX, fig. 1, and the reverse or right side of the same individual seen through the glass to which attached is shown in fig. 2. The relations of these views to one other and to the adult described by Lacaze-Duthiers are of much interest. The single adductor muscle of the valves, *ad*, figs. 1-2 (also in the diagram Pl. XXIX, fig. 3), is situated a short distance below the heart, *h*. It is very small relatively to the size normally found in Pelecypods, a fact having important bearings. This is the only muscle indicated in the left valve which passes to the right valve or which finds its counterpart in that valve and the same condition exists in the adult. A large byssal muscle, *bm*, fig. 1, inserted in the left valve passes to the foot and byssus, the calcified attachment of which is shown at *bs*, fig. 2. The byssal muscle at its insertion in the left valve has a peculiar sinuosity in its posterior face which is not understood. A posterior retractor of the foot, *pr*, figs. 1 and 3, is attached to the left valve a short distance from the byssal muscle and close to, but separated from, the adductor. It is somewhat remarkable that the posterior retractor lies on the ventral border of the adductor, as the typical position of the posterior retractor in Pelecypods

¹In *Anomia*, the shell itself is not cemented to foreign bodies as in the ostrean forms considered; the attachment

is by means of the calcification of the byssal tip, and is not to be confounded with the cementation of one valve.

is on the dorsal border of the adductor, as in *Mya* and *Modiola*, Pl. xxv, figs. 9–10. The fibres of the posterior retractor pass forward to their insertion in the foot and merge with the byssal muscle as distinctly seen from the left side. An anterior retractor of the foot, *ar*, figs. 1–3, is inserted in the left valve near the umbonal region. Whereas in the young the adductor, posterior retractor of the foot and byssal muscles are distinct and separate, in the adult they are rendered ambiguous by being in close contact with one another, although making three separate scars in the left valve of the shell. The true nature of the muscles of the adult, as described by Lacaze-Duthiers, is therefore seen to be clearly apparent in the young.

In young *Anomia* attached to glass slides where the action of parts may be observed through the very translucent valves, it is noticeable what an active part the byssal and retractor muscles of the foot take in pulling down or closing the upper, left valve, on account of being attached distally by means of a calcareous union to the object of support. This is rendered clear by comparing Pl. xxix, figs. 1–2 with the diagram fig. 3. By the action of these muscles the upper left valve is brought in close contact with the object of support, so that it conforms to the surface as does the shell of a *Crepidula*, or limpet, under somewhat comparable conditions of fixation. In correlation with this changed function of the retractor muscles of the foot, and byssal muscle in *Anomia glabra*, it is important to notice that the adductor muscle is very small and the lower right valve extremely thin, a mere veil of tissue in the young, so that it would be almost functionless for protection, if the young could be exposed to attack from this side, which however is not the case. It is thus evident that the byssal muscle and the anterior and posterior retractors of the foot in the young are together pseudo-functionally an adductor in their action and as a correlation a reduction of the actual adductor and lower valve has taken place. This condition of affairs is evidently brought about by the position of the parts relatively to the surroundings and is ascribed to them. Lacaze-Duthiers ascribes the absence of retractor muscles of the byssus and foot on the right side to atrophy and loss from disuse. The great size and amalgamation of the byssal muscle and posterior retractor he ascribes to the changed directions of the fibres and the functional activity in the changed position, perpendicular to the object of leverage. He may have intended the comparison of the muscles to an adductor which I make, but it is not so understood from his text.

The young *Anomia* opens its shell by the lifting of the upper valve alone and it has considerable forward and backward as well as lateral motion due to its peculiar method of attachment. When quietly feeding, the anterior retractor of the foot, *ar*, Pl. xxix, figs. 1 and 3, may shorten and this muscle being inserted at the byssal region of calcareous fixation the animal responds by moving backwards; conversely, if the posterior retractor, *pr*, figs. 1 and 3, shortens, the shell is moved forwards, as will be understood by considering the diagram, fig. 3. In the adult there is little or none of this forward and backward motion, as the byssal plug is closely surrounded by shell growth and also the position of the posterior retractor is changed so that it could hardly bring about such a movement.

The foot in adult *Anomia glabra* is a small reduced organ; but in the young it is very large and active, Pl. xxix, figs. 1, 2 and 5. The base of the foot is marked by a deep

cleft up to its extreme distal portion and the very young, fig. 5, in crawling extends and flattens it against the object of support in a prehensile disc-like fashion, as described in *Pecten irradians*. After the animal becomes permanently fixed, figs. 1 and 2, the foot was not observed to extend beyond the margins of the valves; but it was constantly moved within the mantle walls in a sinuous manner. The foot is of large volume embracing the byssus at its point of attachment to the glass slide, fig. 2, and the open cleft of the foot makes a V-shaped space immediately in front of the byssus; but soon the walls of the cleft are in contact. The byssus is thus seen to originate from a cleft in the base of the foot as in ordinary byssated Pelecypods.

The upper proximal face of the calcareous plug of adult *Anomia* is marked by lines parallel to the longer axis of the shell and similar lines are noticeable in the basal portion of the plug, *bs*, where attached to the glass, Pl. XXIX, fig. 2. The lines are made up of parallel series of amalgamated, calcareous, discoid points seen in the fore part of the byssal attachment in the figure. The discoid points are directly comparable to the discoid points of fixation of separate byssal threads observable in *Pecten*, *Mytilus*, etc., the difference being that in *Anomia* the several points are calcified. In the young we have therefore the fullest substantiation of Lacaze-Duthiers' homology of the plug of *Anomia* with the byssus of other Pelecypoda; for we can actually see the byssus coming from the cleft in the foot and the separate byssal threads amalgamating to form the calcareous plug.

The palps of *Anomia*, Pl. XXIX, figs. 1-2, originating close to the umbos pass to the right of the anterior retractor muscle and to the left of the foot and terminate in close relation to the anterior limits of the gills. They are marked by plicated ridges on their posterior borders. The coils of the intestine were not followed, being hidden in the dark brown liver follicles which cover the greater part of the body mass. The liver presents two regions of densest portion separated by a lighter portion in which there are few follicles as shown in the figures. The rectum passes over the dorsal border of the adductor muscle and is produced to a considerable extent into the cloacal chamber, the anus, *a*, being free, figs. 1-2, and in the adult a similar condition exists. A highly developed cæcum, *c*, fig. 2, as in the adult, is prolonged in a curved line from the body mass past the ventral border of the adductor and to the right of the gills ending blindly in the cloacal chamber. It is clear in the young as it is not complicated by the existence of the reproductive gland found in the adult.

The heart, *h*, consists of a ventricle and probably two auricles as in the adult,¹ but the heart in the young is surrounded by a pericardium, whereas in the adult Lacaze-Duthiers says that this is wanting. He expresses the belief that the pericardial walls may have become united with the walls of the heart proper and in view of its early existence this is a reasonable explanation of its disappearance. On the left side a large vessel, *v*, fig. 1, passes from the heart in front of the byssal muscle and to the gills of the left side; another vessel, *v*, passes between the adductor muscle and retractor of the foot. These are similar to those of the adult after Lacaze-Duthiers. Other vessels ramify in the mantle as described in young oysters. The pulsations of the heart are variable. In fig. 1 were counted eighty

¹I express this with a degree of caution, as I did not actually observe in the young the second auricle described in the left side of the adult by Lacaze-Duthiers; but other

parts being so coincident with his figures and description, its presence is assumed; as he says it is with difficulty seen in the adult.

to eighty-four heart-beats per minute in several counts. At other times in the same specimen forty-four, forty-two and twenty-one beats were counted; but these were much below the normal. In a younger specimen sixty beats were recorded at several counts. Watching the heart it may be seen to stop for a considerable time and then begin again first beating slowly; but soon getting up to its normal rapidity. The cessation of pulsations may be induced by disturbing the animal and the pulsations are most regular and active while the *Anomia* is quietly feeding with the mantle extended.

The gills in very young *Anomias* the age of Pl. XXIX, fig. 5, are simple, straight filaments not joined to one another in any way and the tips not yet recurved upon themselves. (Compare with young oyster gills, Pl. XXIV, fig. 6.) Dissecting specimens of the age of Pl. XXIX, fig. 1, it was found that the inner pair of gill plates had their filaments reflected dorsally and the filaments of the opposed lamellæ were joined to one another by the concrescence of their dorsal borders. The two outer gills, on the other hand, had their filaments reflected upon themselves; but the recurved part equalled only about half the length of the direct part. The same relation of filaments exists in the adult gill diagrammatically shown in Pl. XXIV, fig. 11. The individual gill filaments in specimens of the age of fig. 1, as also in the adult, are joined to one another by concrescence at the tips of the dorsally reflected borders; but they are not joined to one another at other points. Further the filaments have not the nodular ciliated processes characteristic of the gills of *Pecten*. Therefore, the gills of *Anomia* have filaments which are individually free to a somewhat remarkable extent. This is interesting as showing an almost primitive condition in one organ when other organs are so modified as to render *Anomia* one of the most highly specialized of the Pelecypoda. The gills are connected with the body by two membranes, s, Pl. XXIX, figs. 1-2, which have been described (Tryon) as falciform. These membranes are attached to the adductor muscle, to the body anteriorly from that point and to the mantle wall posteriorly to the adductor. The posterior attachment is not shown in Lacaze-Duthiers' figures; but it is a marked feature in the young of *Anomia glabra*. A large foramen exists in each of these membranes. The foramen of the left membrane, fig. 1, is the larger and my attention was attracted to it by seeing the extensible and restless foot prolonged across the body and thrust through this hole. In fact it was a favorite act with this individual at least, for after noticing it I frequently found the foot thrust through the foramen. The foramen in the right gill membrane, fig. 2, is smaller than that in the left. The membranes extend in a free curving line to the posterior extremity of the gills. The gills are capable of considerable motion and frequently in the young may be seen protruded beyond the margins of the valves and even beyond the borders of the extended mantle lobes as well. The length and width of the several gills is different as pointed out by Lacaze-Duthiers. In comparing Pl. XXIX, figs. 1-2, it is seen that the gills on the left side are much longer and broader than on the right side on which the animal rests, a feature which, as Lacaze-Duthiers said, is doubtless connected with the conditions of fixation.

The mantle of *Anomia* presents peculiarities which are necessitated by the abnormal position of the byssus. The mantle lobes are free except for a short distance on the ligamental area (observed in an adult) where the lobes of the two sides are confluent. The right lobe has a deep re-entrant fold where it surrounds the byssus, shown in Lacaze-Duthiers' figures and slightly indicated in Pl. XXIX, fig. 2. The margins are fringed

with active extensible tentacles which are in constant motion. The tentacles of the young are pigmented with black in scattered spots and bands of color which are arranged at right angles to the longer axis of the tentacles. I did not observe radial muscles in the mantle of *Anomia* similar to those described in *Ostrea* and *Pecten*, and if they exist as they probably do, they are inconspicuous.

XIII. ANOMIA. THE SHELL.

Professor Morse published a brief account of some extremely young shells of *Anomia* in which he showed that an early, probably "dimyarian" shell precedes the characteristic Anomian form of shell. He also showed the initial stages of the byssal notch. The specimens studied, judging from his description and a comparison with my own observations, were the young of *Anomia aculeata*, Gmelin.

In *Anomia glabra* an ovally rounded, nearly equivalvular prodissoconch exists at the umbos of perfectly preserved young specimens, Pl. xxix, figs. 4-6. The prodissoconch in this species is opaque, of homogeneous structure, bearing fine concentric lines of growth, and the umbos which are nearly central are directed slightly toward the posterior end of the shell.¹ In this position of the umbos my observations differ from those of Professor Morse as he says the umbos are nearer the anterior margin of the shell. The left prodissoconch valve of *Anomia glabra* has no indication of a byssal notch but the right valve has a notch on its ventral border as shown by the lines of growth in Pl. xxix, fig. 6. It is therefore seen that at this extremely early period *Anomia* is already capable of forming a byssal attachment, and crawled on the right side with the foot extended at this area. The shell evidently lay on one side as observed by Morse. A byssal notch in the prodissoconch is a point in which *Anomia* differs from the byssated Pelecypods which have been so far discussed. In *Perna*, *Avicula*, *Pecten* and *Spondylus*, Pl. xxvii and xxviii, a byssal notch is indicated in the first stages of the dissoconch growth; but no trace of a notch exists in the prodissoconch.

The dissoconch growth of the left valve of *Anomia glabra* in its early stages, Pl. xxix, fig. 4, is at first nearly round, but slightly larger on the ventral side. It is thin, translucent, has a highly polished surface and bears numerous, delicate lines of growth, but shows no prismatic structure. An older specimen of a left valve, Pl. xxix, fig. 5, is less rounded, its faster ventral growth having produced a bulging in this direction which seems to be characteristic of specimens of this age. Whereas in fig. 4, the prodissoconch is on the anterior border of the valve and projects slightly beyond it, in fig. 5, shell growth is taking place in front of the prodissoconch, which is the primitive umbo of the valve, and in succeeding growth this feature is carried still farther as seen in fig. 8, so that in the adult the initial umbo is pushed in quite far from its original position on the anterior border of the valves. As growth continues from the stage fig. 5, the shell becomes more and more rounded, rapidly assuming the form characteristic of the adult. The young is so highly polished that the shell well deserves the popular name silver-shell which it bears.

The right valve at a very early period, Pl. xxix, fig. 6, differs much from the adult

¹The umbos are directed posteriorly so slightly in *Anomia* that it is not a marked feature as in *Ostrea*, *Perna*,

Pecten, etc., in which the umbos of the prodissoconch are more inclined toward the posterior region of the shell.

and is less highly modified. The initial stages of dissoconch growth commence on the free border of the prodissoconch valve; but succeeding shell deposition is extended posteriorly and then ventrally more and more, as may be seen by following the lines of growth, figs. 6-7, until finally a deep almost enclosed sinus is formed around the byssus, as shown in the figure. At this stage it is desirable to compare the right valve of *Anomia*, fig. 6, with my figure of the first stages of dissoconch growth of *Pecten*, Pl. xxviii, fig. 10. In both, a deep and somewhat comparable notch is formed by the existence in one case of a byssus and in the other of a highly active foot; both organs affecting the form of the valve by causing a local retraction of the mantle and thus putting an obstacle in the way of shell deposition at that area. We see in the comparisons of these figures the verification of the statement made by Forbes and Hanley nearly fifty years ago that "the perforation in one of the valves of *Anomia* is chiefly a greater extension of the auricular sinus in *Pecten*." In later growth the ventral border of the valve surrounds the byssal notch in an increasing degree until soon it is completely enclosed. The lower valve is peculiar in that the mantle border of the umbonal region deposits shell around the prodissoconch, enclosing it by degrees and partially covering its umbonal portion as shown in Pl. xxix, figs. 6-7. This is due to the fact that the primitive umbos recede from the shell border, being pushed back by the peripheral growth of the valve as seen viewed from the left side in Pl. xxix, figs. 4, 5 and 8. When the byssus in young *Anomia* is nearly or quite surrounded by the growth of the right valve as in Pl. xxix, fig. 2, the foramen is very small. In the adult, fig. 41, p. 354, on the other hand, the foramen of the right valve is many times larger and to accomplish this increased size of the hole an extensive resorption of the shell has taken place. During this resorption, lines of growth which were continuous when young become separated and may be traced on either side of the foramen, as in the figure cited.

The lower right valve in the young does not equal the size of left upper valve which overhangs its border by a considerable amount, Pl. xxix, figs. 6 and 2; it is also of excessive thinness and so delicate that great care is required in handling not to injure it. The right valve shows the most beautiful, prismatic structure of which it is entirely composed in early stages, and it is so transparent that the organs can be seen as through a glass film. The extreme reduction of the lower valve in young *Anomia glabra* is evidently correlated with its conditions of environment. The byssal and retractor muscles are functionally active in drawing down the upper valve, and when that valve is closed the lower valve is completely protected. The reduction of the true adductor muscle as described and the thinness of the right valve are doubtless correlated; for, on account of its delicacy, the strong action of a normal-sized adductor would certainly break the valve. At this early period the right valve truly seems like a disappearing organ. In later growth the right valve increases in thickness and frequently extends beyond the object of support, but it does not acquire the thickness and solidity of the left valve.

I have stated that the right valve in young *Anomia glabra* is wholly composed of prismatic cellular tissue. This structure predominates throughout life in this valve, and in the adult the right valve entirely consists of prismatic cellular tissue with the exception of a thin layer of whiter porcellaneous tissue which surrounds the byssal foramen and point of insertion of the adductor muscle. The left valve, on the other hand, does

not have a prismatic layer at any period in the life of the individual; but is sub-nacreous excepting for a small area around the point of insertion of the muscles, where as in the right valve there is a deposition of porcellaneous tissue. This difference in the structure of the two valves is a remarkable feature and occurs in related genera, for I have shown that a thin prismatic layer exists in the right valve of young *Pecten* and in the right valve of young *Ostrea* but not in the left valve of either genus in early stages.

I have not found any published observations of prismatic structure in *Anomia glabra*, but Carpenter, in his second paper (1848), on shell structure, stated that a thin external prismatic layer exists in *Anomia ephippium*; but is early worn off. In this connection, an interesting point is recorded in one of Dr. C. A. White's papers,¹ that among Tertiary fossils it is rare to find a right valve of *Anomia* although left valves are abundant. He ascribes the loss of right valves to their fragility owing to their prismatic composition. On the other hand, a number of species of European Tertiary *Anomias* in the collections

of the Museum of Comparative Zoölogy have both valves equally preserved. A very thin layer of prismatic tissue exists in the right valve of *Anomia ephippium*, as observed in specimens kindly sent me by Dr. Dall; but it does not exist in the left valve of that species, both valves being composed wholly or for the most part of sub-nacreous tissue, with the addition of porcellaneous tissue around the muscular insertions as in *Anomia glabra*. The difference in the structure of the right valve of *Anomia glabra* makes a good specific distinction, which separates that species clearly from *A. ephippium*, which it approaches very nearly in external form.

Young specimens of *Anomia aculeata*, Gmelin, fig. 43, were collected at Cohasset and Beverly, Mass. A yellowish prodissoconch exists at the umbos. The left valve of the prodissoconch has a slight sinuosity which corresponds with the comparatively deeper byssal notch in the right valve, whereas no sinuosity of the left valve and a shallower notch in the right exists in the prodissoconch of *Anomia glabra*, Pl. XXIX, figs. 4-8. This feature is shown in fig. 43, but is more marked in degree in younger specimens. The prodissoconch of *A. aculeata* is ovally rounded in outline with fine concentric lines of growth and umbos which are nearly central but directed slightly posteriorly as in *A. glabra*. The succeeding dissoconch growth of *Anomia aculeata* is chalky white, of somewhat irregular growth; and not polished or as translucent as is *A. glabra*. The left valve of the dissoconch does not perpetuate the sinuosity of the prodissoconch valve. This valve is smooth for a brief period and then the plications and spines characteristic of the species are commonly introduced. I say commonly, for associated specimens are frequently wanting in the spinous character, although unquestionably belonging to the same species. The right valve of the dis-

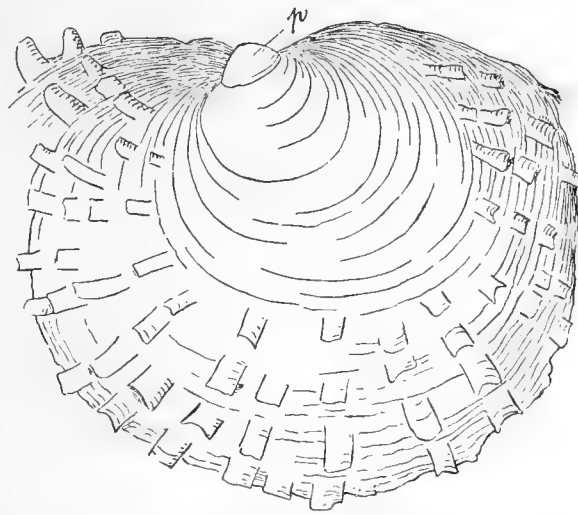


FIG. 43. Young *Anomia aculeata*, tip of left valve, p, prodissoconch, succeeded by early smooth and later spinous dissoconch growth. Cohasset. $\times 60$ diam. (Drawn by the author.)

¹ Non-marine Fossil Mollusca of North America, Washington, 1883, p. 16.

soconch of *A. aculeata* has a growth similar to that described in *A. glabra*; but is chalky white and much thicker than in that species. The right valve is wholly or for the most part composed of prismatic cellular structure whereas that tissue is wanting in the left valve as in *A. glabra*. My observations of the young and adult lead me fully to concur with Professor Verrill who says that he believes this species is perfectly distinct from *Anomia glabra*.

In regard to the affinities of *Anomia*, it is closely related to *Placuna* and many intermediate forms may be traced as noted by authors. The anatomy of *Placuna* is essentially like that of *Anomia*; but the mantle border has a curtain like *Pecten* (Tryon). The shell of *Placuna* is composed of fine nacreous layers, but in the young I have found traces of prismatic cellular tissue in the right valve. This tissue was very thin and limited in extent on account of being worn away, but existed in patches. Woodward (79) mentions that, when young, *Placuna* has a byssal sinus in the right valve and I have found young specimens which show an enclosed byssal plug like that of *Anomia*, as described in section XVI. *Anomia*, anatomically and in shell structure, is much more nearly allied to *Pecten* than to *Ostrea*. It is probable that *Anomia* was derived from the *Pectinidæ* from the *Amusium* or *Hemipecten* group, for the latter resemble *Anomia* in having thin nacreous shells. In considering *Hemipecten*, Zittel remarks that Jurassic species of *Placunopsis* are probably confounded with *Hemipecten*, thus inferring a close similarity in the two genera. *Placuna* was probably derived from the early *Anomiadæ* as all evidence points toward an ancestry in that group. The geological appearance of these groups accord with their inferred zoological affinities as I have described them. That such a highly modified form of shell as *Anomia* could have been derived from the *Pectens* is more easily believed when we see how highly modified are *Pedum*, *Hinnites* and *Spondylus* which are more direct derivatives of *Pecten*.

XIV. STUDIES OF A FEW OTHER GENERA.

The genera so far studied are all linked in one great group of the *Aviculidæ* and their allies (see table, section XVI), by characters of anatomy and shell structure which connect the several members. The genera thus referred to are *Ostrea*, *Gryphæa*, *Exogyra*, *Perna*, *Avicula*, *Monotis*, *Pseudomonotis*, *Cassianella*, *Vulsella*, *Pecten*, *Spondylus*, *Plicatula*, *Lima*, *Anomia* and *Placuna*. I now wish to consider the young of some genera belonging to other groups of *Pelecypoda* distinctly removed from those previously considered and not always closely connected with one another. Figures of the adults of most of the species described in this section are to be found in the works of Verrill and Gould.

The groups, previously studied, have been characterized by possessing *prodissoconchs of homogeneous laminar structure, but not prismatic, and with umbos directed posteriorly*. The succeeding dissoconchs have been shown to be markedly different in form from the prodissoconch, and in the earliest stages at least are characterized by *well-defined, prismatic, cellular structure*, either in both valves or the right valve.¹ In all gen-

¹ The change from homogeneous to prismatic structure was not observed in the fossils described or in *Spondylus* and *Lima*, but these genera are so united with groups that

do show it, that the absence of the feature in the few specimens observed need not be considered in this connection.

era now taken up, excepting the Unionidæ, two marked features of difference occur as compared with those previously studied. The *prodissoconchs* are directed more or less anteriorly, and the succeeding dissoconchs are not characterized by prismatic cellular structure.

The Pelecypoda is a class in which it is very difficult to find binding characters on which to make systematic divisions. The direction of the prodissoconch umbos and the condition of prismatic structure in the succeeding dissoconch, I am aware, is not wholly confined to the Aviculidæ and their allies, but these features are characteristic of the whole of that group and are not together characteristic of any other group so far as known, excepting, possibly, the Unionidæ. A thin, but well-defined, prismatic layer exists in *Pandora rostrata*, Lam.; a prismatic layer also exists in the deeper-seated portion of the periostracum of *Solemya mediterranea*, Lam., and it has been observed in limited patches in young *Ensis viridis*, Say. Carpenter observed the prismatic layer in the two former genera and mentions finding traces of it in other genera, but he was impressed with the fact that it is a marked feature in the group of the Aviculidæ and allies.

Mytilus edulis, L. This mollusc belongs to one of the oldest families of the Pelecypods extending back to early palæozoic times. It is therefore interesting to know the conditions existent in the young shell. In Pl. XXIX, fig. 9, it is shown that a well-defined prodissoconch, *p*, exists which is yellowish-brown and marked by fine concentric lines of growth. The form of the prodissoconch is evenly rounded and it has well developed umbos which are directed anteriorly. The succeeding dissoconch growth of *Mytilus* is sharply marked off from the prodissoconch stage by its changed form and color. In form the dissoconch has already acquired features characteristic of the group to which it belongs, though not of the genus itself. The hinge line is produced posteriorly in an arched line and anteriorly the lines of growth are curved inwards toward the umbonal area, but they are not crowded closely as in the adult or any species of the genus. The shell at this age reminds one strongly of forms seen commonly in the Modiomorphas, palæozoic kindred of the Mytilidæ. In color the dissoconch is distinct from the prodissoconch. Whereas the latter as stated is yellowish-brown, the dissoconch is characterized by the violet color characteristic of the adult. The transition from brown to violet color in *Mytilus* is as sharply defined as is the change from homogeneous line in the prodissoconch of *Ostrea* to the prismatic structure of the succeeding dissoconch, fig. 27, p. 314. Specimens of *Mytilus edulis* of the light horn colored variety of course do not show this change to violet with the introduction of the dissoconch period. No trace of prismatic cellular tissue has been found in the shell of *Mytilus* or other member of this family at any period of growth, but a well defined epidermis exists.¹ Lacaze-Duthiers (41) published an anatomical figure of young *Mytilus edulis* comparable to the prodissoconch stage and he notes the striking difference between the shell of that age and the adult. Lovén also published an anatomical figure of developing *Mytilus* which compares favorably in its shell form with Pl. XXIX, fig. 9.

An older specimen of *Mytilus edulis*, Pl. XXIX, fig. 10, shows no important differences from the younger specimen, fig. 9. The prodissoconch valves on account of the increased arcuateness of the umbos are not seen in side view as well as in the earlier stage, a

¹Prismatic structure is described in the inner layers of *Dreissena*, but this genus has not been studied.

necessary feature of developing bivalves. Instead of being rounded in appearance as in fig. 9, the prodissoconch valves appear flattened from perspective. The prodissoconch of fig. 10 differs from that of the earlier stage in being chalk-white, the yellowish-brown organic appearance of the earlier condition having disappeared from the wearing away of the epidermis. The same is true of older specimens as long as the prodissoconch remains intact, and it may often be found in specimens up to 4-5 mm. in length. It then appears as a little white cap at the umbo of either valve. The nepionic stage of fig. 10 is similar to that of fig. 9, except that the lines of growth anteriorly are more crowded inward toward the umbo, in this feature making a nearer approach to the condition characteristic of the adult. Verrill notes collecting abundant young specimens of *Mytilus edulis* on the 12th of April, and I have found them in July, September and December, so that this species evidently has wide limits in its breeding season.

Modiola hamatus, Verrill. This species occurs on our coast from Vineyard Sound to Mexico. A number of young and adult specimens were collected at Martha's Vineyard and Long Island Sound, also specimens were obtained from a mass of *Perna ephippium* collected at Cuba. The young *Modiola*, has a well defined prodissoconch, *p*, Pl. xxix, fig. 11, which is yellowish-brown and with umbos directed anteriorly as in *Mytilus*. The prodissoconch of *Modiola* appears flatter, less rounded than the prodissoconch of *Mytilus*, Pl. xxix, fig. 9; but this is due in part at least to perspective as noted in the older specimen of *Mytilus*, Pl. xxix, fig. 10. The hinge line of *Modiola* is produced posteriorly in a curving line and anteriorly the lines of growth approach the umbos in a sweeping curve, fig. 11. The form of this stage is not widely separated from that found in some species of the genus, but it more nearly approaches the form of the *Modiomorphas*, palaeozoic allies of the *Modiolas*. An older specimen of *Modiola hamatus*, Pl. xxx, fig. 1, shows the introduction of the plications which are characteristic of the species. The plications originate suddenly, marking a distinct stage by their introduction.

Crenella decussata, Montagu. Young specimens of this species, loaned me by the Smithsonian Institution, show distinct prodissoconchs, *p*, as shown in Pl. xxx, fig. 3, an umbonal view of a specimen. The prodissoconchs have rather highly developed umbos which are directed anteriorly and show fine concentric lines of growth. The succeeding dissoconch in its initial stages of growth is already marked by radiating plications as well as concentric lines of growth which are coarser than those of the prodissoconch.

The *Mytilidæ* are classed with the *Aviculidæ*, as heteromyarians, the connection being based on the condition of unequal adductor muscles. This basis of classification, as previously considered (Introduction), is not deemed one of high, systematic importance and is insufficient to connect otherwise differing groups. The striking differences in the prodissoconch and nepionic stages of the *Mytilidæ* and *Aviculidæ* are sufficient I think to separate these groups, and the *Mytilidæ* should be put in a group distinct from the *Aviculidæ* and their allies, which I have shown are all bound together by important features as one group.

Argina (Arca) pexata, Verrill. An extremely small specimen, Pl. xxx, fig. 2, was found in a drain-pipe trap at Buzzards Bay. The specimen was dead, but the shell was perfectly preserved. The prodissoconch is ovally rounded, very sharply defined; and has well developed umbos which are nearly central. The prodissoconch shows delicate concentric lines

of growth, and is very yellow compared with the succeeding dissoconch growth which is pure lime white, thus indicating a somewhat more marked conchyolin basis of the prodissoconch. The succeeding dissoconch has the typical hinge line characteristic of the *Arcas*. Its first stages of growth are smooth and marked by nearly concentric lines of growth; but with no plications; well defined plications exist, however, in the later growth. Taking the shell as a whole, the height (measuring from the free border of valves to the hinge line) is much greater posteriorly than anteriorly. In the middle of the ventral portion a distinct depression exists on the border of the valves and also in the preceding lines of growth. The early dissoconch before the introduction of plications differs much in appearance from the adult and bears a strong resemblance to fossil members of the *Arcidæ*. Especially does it resemble species of *Macrodon* from the Devonian as figured by Hall. The teeth on the distal limits of the hinge line of young *Argina* are oblique like those of *Macrodon*, and between these oblique teeth are the perpendicular *Area*-like teeth; but at an earlier stage of growth the perpendicular teeth were apparently wanting, and then the teeth of young *Argina* would have been closely comparable to those of *Macrodon*. *Arca ectomata*, Dall, from abyssal depths has all the teeth oblique like those on the distal limits of the hinge line in young *Argina* and like those of the early and later species of *Macrodon*.

The stage represented by the whole shell of Pl. xxx, fig. 2, differs in form from the earlier *Macrodon* stage and also from the adult, and is comparable to *Arca*, the type-genus of the family. Transitional series of specimens of *Argina pexata* older than Pl. xxx, fig. 2, show in constantly increasing degree the oblong-ovate form and shaggy epidermis characteristic of the adult. In the ontogeny of *Argina*, therefore, we find that there are four distinct stages which represent the ancestral forms from which the genus was evolved: (1) the prodissoconch representing a primitive ancestral radical, at present unknown; (2) the *Macrodon* stage, comparable to palæozoic forms of the family; (3) the *Arca* stage, comparable to the type genus of the family and, finally (4), the *Argina* stage in which the features of the genus and species are introduced and fixed. A prodissoconch and nepionic stage similar to that described in *Argina pexata* has been found in a young specimen of *Arca barbata*, L., kindly given me by Professor Verrill, and in some young *Arcas* of an undetermined species from Japan. The nepionic stage of *Parallelopipedum tortuosum*, Lam., is also similar to the same stage of *Argina*, the tortuous character of the adult shell not having been acquired at this early period of growth.

It is an important fact that members of the *Arcidæ* have a prodissoconch, because as one of the oldest living groups of Pelecypods it shows the widespread existence in time as well as genera of a distinctly marked early embryonic shell. Species of so many and such widely separated families possessing a prodissoconch in the young is strongest proof that it is characteristic of the whole class of Pelecypods. We also see that the nepionic stages in members of this family can be made use of in tracing genetic relations, as in the *Aviculidæ* and their allies.

The *Unionidæ* are naturally turned to in studies of this nature as they are characterized by a peculiar early stage called the glochidium. Although the glochidium is known by itself, I do not think the relation of this early shell to the adult has been previously studied. Through the kind intervention of Dr. Charles E. Beecher, I recently received some ma-

terial which was collected by that gentleman, from Mr. William B. Marshall of the New York State Museum. The specimens embrace glochidial stages from the gill cavities of the parent and adults with perfectly preserved umbos, so that the early embryonic shell is still intact, and thus affords the opportunity of a comparison with later stages.

Unio cariosus, Say. The glochidium stage of this species, fig. 44, p. 367, is sub-quadrate with a straight hinge line and rounded angles on the ventral border. The shell has a double line around its border, the inner line representing the limits of an earlier stage of growth. A similar double line exists in the glochidium of all Unionidæ observed, or which I have seen figured, and Dr. Lea makes the same observation. On the middle of the ventral border of the valves is a very abbreviated spur which is not, however, spinous as in *Anodon*. The single adductor muscle is situated near the hinge line and a little nearer the anterior than the posterior border of the shell.¹ The shell is granulated on its surface and presents no traces of prismatic structure, the same feature being found in the glochidium of all the Unionidæ observed. The glochidial shell of *U. cariosus* and other species of the genus is whitish and much smaller than is the glochidium in *Margaritana* and *Anodon*. The glochidium of *Unio nasutus*, Say, is similar to *U. cariosus* as described. Dr. Lea figures the glochidium from the gills of the parent in twenty-five species of *Unio*. Twenty are similar to *U. cariosus* in form with some little variation in contour. Of the five remaining species three are sub-triangular resembling some species of *Anodon*; but two have the ventral angles produced instead of rounded and each angle of either valve bears a small spur.

Unio pressus, Lea. A specimen 47 mm. in length has the umbos well preserved and still bears the early glochidial shell. This embryonic shell is sub-triangular and has the same form as is figured by Lea in a specimen from the gill chambers of the parent of this species. It is immediately succeeded by the nepionic stage of the dissoconch which has the prismatic structure and concentrically rugose growth which is characteristic of the young shell in Unionidæ and is often figured at the umbos of well preserved specimens (see Lea and other authors). The glochidial shell in its relation to the dissoconch therefore fills the requirements of the prodissoconch and may be compared with that stage as described in many genera in this paper. The *Unios* above described were collected in Albany County, New York, by C. E. Beecher.

In *Margaritana undulata*, Lea, the glochidium, fig. 45, p. 367, is sub-triangular, but the anterior end of the embryo is considerably the larger. The hinge line is straight and the valves at this area are raised in little humps indicating abbreviated umbos, not shown in the figure. The angle at the ventral border of the shell is quite sharp; it is posterior to a median line drawn perpendicularly through the shell and bears a denticulate spur on either valve similarly to *Anodon*. In other features the shell is like the glochidial stage of *Unio*. A young specimen of *M. undulata* 13 mm. long, fig. 48, has the umbos well preserved and they retain the glochidium or prodissoconch intact. The hinge line of the prodissoconch is parallel to the hinge line of the succeeding dissoconch growth and the larger end of the embryonic shell is directed toward the anterior end of the shell. The prodissoconch has the granulated surface characteristic of the glochidia of this and other

¹ The glochidial shell of all or nearly all Unionidæ is a little larger on one side than on the other of a line drawn

perpendicularly through the hinge line and middle of the ventral border of the valves.

species of the family; but the dissoconch has an external layer of prismatic tissue. Camera drawings of this specimen show that the prodissoconch is of the same size and form as are the glochidia when removed from the gills of the parent as shown in the figures, and the same observation holds in regard to the size and form of glochidia and completed prodissoconchs in every species in which I was able to make the comparison. The glochidial shell of *Margaritana marginata*, Lea, is similar to that of *M. undulata*. Lea figures the glochidium of five other species of this genus. Of these, three are similar to the glochidium of *M. undulata*; but two are less triangular and more rounded on the ventral border. A specimen of *Margaritana margaritifera*, which is 55 mm. long has the umbos well preserved and they bear at the tip the embryonic shell. As in the previous species the prodissoconch of this species is sharply marked off from the succeeding dissoconch, and in a camera drawing it coincides in form and size, with the glochidium from the gills of the parent. Specimens of *Margaritana deltoidea*, 19 mm. long, have the prodissoconch well preserved and it presents the same features in relation to the succeeding dissoconch as in the above-mentioned genera. The specimens of *Margaritana undulata* studied were collected in Albany County, New York, and those of *M. margaritana* and *M. deltoidea* at Ann Arbor, Michigan, by C. E. Beecher.

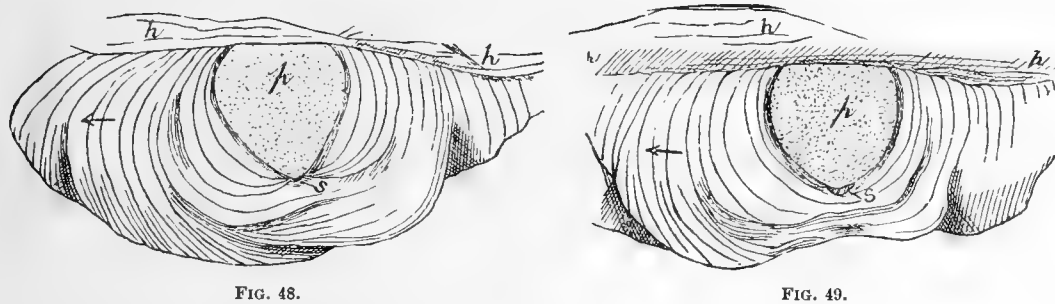
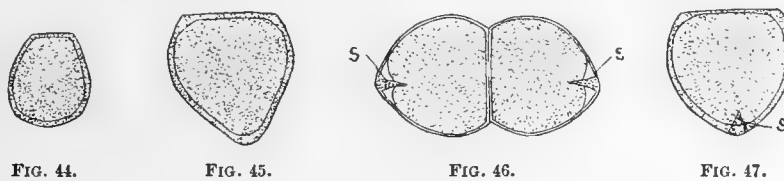


FIG. 44.—*Unio cariosus*, glochidium from the gills of the parent.
 FIG. 45.—*Margaritana undulata*, glochidium from the gills of the parent.
 FIG. 46.—*Anodon cygnea*, glochidium from the gills of the parent.
 FIG. 47.—*Anodon fluviatilis*, glochidium from the gills of the parent.
 FIG. 48.—*Margaritana undulata*, umbonal tip of a young shell, showing the prodissoconch, *p*, still in place and the nepionic stages of the succeeding dissoconch.
 FIG. 49.—*Anodon fluviatilis*, umbonal tip of a young shell showing the prodissoconch, *p*, still in place and the nepionic stages of the succeeding dissoconch.
 All the figures (except fig. 46) are of left valves. The arrows are directed toward the anterior end of the shell; *s*, glochidial spurs; *h*, hinge. All the figures $\times 50$ diam. (Drawn by the author.)

In *Anodon* the glochidium is better known than the same stage of other genera of this family, as it has been more often studied by embryologists. Schmidt studied it during the period of parasitic life which it leads on fishes, and good figures of this stage are given by that author. The glochidium of *Anodon fluviatilis*, Lea, fig. 47, is sub-triangular in

outline but is less acutely angular on the ventral border than is this stage of *Margaritana*. The hinge line is straight; the anterior end of the shell is somewhat the larger and spinous spurs exist at the ventral angle of either valve, Pl. XXIII, figs. 7-8. A double line surrounds the limits of each valve and the surface of the valves is granulated, the same characters existing in the glochidium of *Unio* and *Margaritana*. The inner line is distinct from the edge of the shell and represents an earlier stage of growth. In *A. cygnea*, fig. 46, p. 367, the double line represents the thickness of the edges of the shell, and the inner line representing an earlier stage as in fig. 47, is not seen in this view. The glochidium of *Anodon* differs from that of the other genera in the species observed in being of a brown color. A glochidium similar to that described in *Anodon fluviatilis* I have observed in glochidia from the gills of the parent of three other species, namely, *A. undulata*, *A. cylindracea* and *A. cygnea*, fig. 46. There is great constancy in size and appearance of the glochidia in the different species of *Anodon* observed, the uniformity being greater than in the other genera of the family.

A well preserved specimen of *Anodon fluviatilis* 25 mm. in length, fig. 49, p. 367, has the embryonic shell or prodissoconch still in place. The prodissoconch in a camera drawing of this specimen coincides in size and form with the glochidia from the gills of the parent, no increased growth being observed. The larger end of the embryonic shell is directed anteriorly and the hinge line is parallel to the hinge line of the succeeding dissoconch. The dissoconch has the rugose fluting characteristic of the young (frequently figured at the umbos in well preserved specimens by Lea and others) and presents well defined prismatic structure. The glochidia of *Anodon fluviatilis* described and the older specimen of the same species as also the glochidia of *A. undulata* and *A. cylindracea* were collected in Albany County, New York, by C. E. Beecher. The glochidia of *A. cygnea* are from Belfast, Ireland, and were loaned to me by the Smithsonian Institution.

The fact that the larger end of the prodissoconch is directed anteriorly in all the species of *Margaritana* and *Anodon* in which it was still found in place at the umbos of the valves, is convincing proof of the correctness of Schmidt's observation that the larger end of the embryo of *Anodon* is the anterior end. It is a remarkable fact that the completed prodissoconch in the various species observed has the same form and size as does the glochidial stage of the same species when removed from the gills of the parent. We know from the observations of Balfour and Schmidt that after quitting the gills of the parent the embryos of *Anodon* (and probably, from analogy, other genera of the family as well) lead a parasitic existence in the gills, fins, etc., of fishes. During this period of parasitism considerable anatomical changes take place, yet these changes are not accompanied by any noticeable modification or increase in size of the embryonic shell.

It is seen that the glochidial shells of the genera of the Unionidæ described are sub-triangular or subquadrate; but always with a straight hinge line. But a single adductor muscle exists and other anatomical features are in a very early condition of development. This stage is directly the equivalent of what I have described as the phylembryonic stage (p. 291) of development in Pelecypods and it may be compared to the embryos of *Modiola*, *Cardium* and *Montacuta*, Pl. XXIII, figs. 9-11, also of *Ostrea*, fig. 25, p. 300, and Pl. XXIV, figs. 13-15. The anatomy of the glochidium from the gills of parents is less advanced than is the same (phylembryonic) stage in other genera, as shown in the figures cited; but this is explained as a peculiarity due to the specialized development of this type.

It is a striking fact that the embryonic shell of the completed prodissoconch period of the Unionidæ has not changed in form or size from the condition it had when ready to leave the gills of the parents. This fact and the correlated fact that umbos have not developed, although they exist in the prodissoconch of the twenty-six other genera described in this paper, are proof of the extreme reduction of the embryonic shell. The completed prodissoconch of the Unionidæ, therefore, has not progressed in the features of the shell beyond the phylembryonic stage, which is found only in early embryonic stages of other genera. This high reduction is probably to be explained by the condition of parasitism which exists at this period in the development of the embryo. While the prodissoconch of the Unionidæ is in all cases granulated on the surface and shows no prismatic tissue, the succeeding dissoconch is characteristically prismatic. This condition is comparable to what I have described in the Aviculidæ and their allies, but differs from what I have found in other genera.

What the affinities of the Unionidæ are is a puzzle, for they are not clearly related to any other family. The peculiar form, the spurs and absence of umbos in the prodissoconch are special features, apparently due to the peculiar environment of the developing embryo. Although it cannot be supposed to fully represent in the ontogeny of the individual any ancient ancestral form, yet certain data can be gathered from this early shell. As the prodissoconch of the Unionidæ has no prismatic tissue, it is doubtless the representative of an early ancestor which was without that structure (the same comparison that is made in the prodissoconch of the Aviculidæ). The radical ancestor, of which this prodissoconch is the inherited representative, probably had umbos directed posteriorly, for though the prodissoconch of the Unionidæ has no umbos, the more rapid growth on the anterior border would have pushed umbos posteriorly had they existed. That this ancestor was dimyarian might be conjectured; but is fully implied by the fact that the completed prodissoconch has two adductor muscles, for Balfour's and Schmidt's figures of a mature glochidium of *Anodon* from a fish have two adductors. The nepionic stages of the Unionidæ, though peculiar, do not so far as I am aware indicate kinship with early predecessors of the group.

Sphærium securis, Adams. This species was collected in a culvert at Medford, Mass., in November. The adults were crowded with large embryos, and as many as fourteen were taken from the gills and mantle cavity of the parent. The embryos, Pl. xxx, fig. 4, show no traces of a velum as far as discerned, but have a well-developed foot and crawl actively when removed from the parent. The foot has a prominent otocyst as figured in *Cyclas* by Ziegler and other investigators; but no byssal gland was observed as described in that genus. Two adductor muscles, palps and filamentous gills exist. The mantle border is produced posteriorly in a single siphon, fig. 4, but is free throughout the rest of its exposed margin. In older specimens and the adult, two siphons exist, an excurrent and an incurrent. This was not seen in the young of the age under consideration, but as the point was not in mind when studying the specimens, it is possible that two might be found. If not, it is an interesting character, for the adult of *Pisidium* has but one and the existence of one in young *Sphærium* would appear to be of genetic significance. The shell of *Sphærium*, Pl. xxx, fig. 4, represents an incompleated prodissoconch stage. In Pl. xxx, fig. 5, also from the gills of an adult, a completed prodisso-

conch, *p*, exists and is succeeded by considerable dissoconch growth. The prodissoconch is globose and almost circular, slight umbos being developed. When young, fig. 4, it is very translucent of a light horn color, but in older specimens, fig. 5, the shell is thickened by shell deposition, and it is darker and more opaque. The prodissoconch in *Sphærium* is of gigantic size compared with the prodissoconch found in other Pelecypods described and figured in this paper. Pl. xxx, fig. 5*a*, is a young specimen magnified only ten times in order to show the large size of this early shell. By definition, the prodissoconch in Pelecypods is the shell of the completed embryonic period, and it is natural that in *Sphærium* we should have a large prodissoconch because of the relative great size of the embryo in that genus.

Besides in *Sphærium securis*, a similar strongly marked prodissoconch has been observed in *S. partumeium*, Say, *S. rhomboideum*, Adams, and *S. transversum*. The specimens of these species observed are in the choice Beecher collection of fresh water shells, in the New York State Museum.

Echinochama (Chama) arcinella, L. In a specimen sent me by Dr. Beecher, a prodissoconch was found intact. It is ovally rounded with umbos directed anteriorly. The nepionic stage is pink in color, is ovately drawn out, and truncated posteriorly. Concentric ridges mark the nepionic period and as pointed out by Fischer, this early stage resembles a *Venerupis* in form. The shell of the nepionic stage is equivalvular as observed in several specimens in the collections of the Boston Society of Natural History. As soon, however, as the right valve becomes attached to a foreign body (which occurs when the shell is about 3 mm. in length), both valves immediately change their form and assume the irregular growth characteristic of the *Chamas*, and soon the spines and pit-like depressions characteristic of the species are introduced. We find in this case a full substantiation of our views on the modifying effects of the conditions of fixation on shell form as fully discussed in section VIII, p. 322.

Petricola pholadiformis, Lam. At Nantucket in July, 1889, a large number of young specimens of this species were collected, varying from very small to 12 mm. in length. The largest individuals had the adult characters fully developed. The specimens were burrowing in shallow *Mytilus* beds which covered rocks between tide marks. In the youngest specimens found, Pl. xxx, fig. 6, also in some older individuals, a distinct prodissoconch, *p*, exists at the umbos. It is not widely different from the succeeding dissoconch in form, but is sub-ovately rounded and appears like a cap on account of its whiteness compared with the succeeding grayer dissoconch. The whiteness of the prodissoconch is noted in several genera in this section, and as described in *Mytilus* it is doubtless due to the wearing away of the organic epidermis of the valves and consequent exposure of the chalky-white lime basis. The early dissoconch of *Petricola*, Pl. xxx, fig. 6, is strikingly different from the adult. It is oblong, anteriorly roundly compressed and posteriorly slightly truncated. The lines of growth indicate an earlier more oval form. In this early stage the ligament, *l*, projects from the hinge line as in the later stage, Pl. xxx, fig. 7, and in the adult; but no plications of the shell exist until considerably later. The specimens, although taken from their burrows in the *Mytilus* bed, proved to be active crawlers having a highly developed foot, fig. 6. The siphons of this early stage fig. 4, are separate for the entire length produced beyond the limits of the shell. The

incurrent siphon as in later periods is the longer of the two and the two tubes are widely divergent as in the figure. The excurrent siphon is not retracted and extended periodically as described in *Mya*, Pl. xxx, fig. 13, and no tentacles surround the base of either siphon tube in *Petricola*. The distal tips of the tubes in *Petricola*, fig. 6, are fringed by a few simple unbranched tentacles.

An older specimen of *Petricola pholadiformis* than that just considered is shown in Pl. xxx, fig. 7. The umbos are too arcuately incurved to show the prodissoconch if it were existent, and as a fact, it is not, being eroded away before this period is reached. The younger portion as indicated by the lines of growth is oval and marked by coarse concentric lines. A distinct stage is indicated in the oval portion of this specimen and similar stages are common, but variable in individuals. The umbos are progressively pushed anteriorly during the younger growth. Rugose plications originate suddenly, the earliest stages having none. From the period of the introduction of plications, the shell rapidly assumes features characteristic of the adult, differing principally in not being so elongate, differing also of course in that the rugose plications of the adult are produced nearly to what then becomes the umbo of the shell. The siphon tubes of *Petricola* of the age of fig. 7, are long and are capable of being extended to a length considerably greater than the total length of the shell. They are separate throughout their length beyond the shell borders as in the younger specimen, fig. 6. In the adult, on the contrary, Verrill says they are united for about a quarter of their length. In specimens of the age of fig. 7, the branchial siphon, Pl. xxx, fig. 8, is surrounded at its tip by tentacles which branch laterally, intermediate with which are some simple unbranched tentacles. The dorsal excurrent siphon of the same and of similar specimens on the contrary has no branching tentacles, all being simple as in fig. 6. This condition of the orifices is similar to that of the adult described by Verrill, excepting that he says some branching tentacles exist at the orifice of the excurrent siphon though fewer than at the orifice of the branchial siphon.

Venus mercenaria, L. I secured a number of young shells of this species in the drain-pipe traps at Buzzards Bay. The youngest specimen, Pl. xxx, fig. 9, has a sharply defined prodissoconch which is yellowish-white, covered with a delicate epidermis and bears fine concentric lines of growth. It is separated from the succeeding dissoconch growth by the changes then introduced in the marking of the shell, angles of curvature and color, which though covered with a thin epidermis is nearly chalk-white. The first stages of the dissoconch are marked by the series of concentric ridges and furrows characteristic of young shells of this species, but which are wanting in the adult. This feature is shown at the umbos of Dr. Gould's figure of the species. Ridges and furrows like those found in young *Venus mercenaria* are characteristic of the adult in some species of the genus, as *Venus rugosa*, Chem., of the West Indies. The same feature is shown in a high degree in the closely allied genus *Chione*, and its occurrence in young *Venus mercenaria* is evidently of genetic significance. In its earliest growth, Pl. xxx, fig. 9, the dissoconch shows only faint traces of a lunule (which was unfortunately overlooked when the figure was drawn) but it is a marked feature in the older specimen, Pl. xxx, fig. 10, and is characteristic of the adult.

Tottenia gemma, Perkins. A few young specimens were collected in August at Buz-

zards Bay. The prodissoconch is oval, rounded and not sharply defined from the succeeding dissoconch, as both have nearly the same shape and the same peculiar violet color. The prodissoconch is marked by a fine pitted structure which partially obscures the lines of growth. The dissoconch bears closely crowded lines of growth and is violet or amethyst color over its whole surface. In the adult, on the other hand, the shell is mostly white or rosy, the amethyst color being limited to the umbonal and posterior portion of the shell. Gould says this species is commonly taken for the fry of *Venus mercenaria* on account of the color of the tip (young). This is an unnecessary mistake as the lunule, elevated ridges and white color of young individuals of that species (Pl. xxx, figs. 9-10) are wanting both in the young and adult of *Tottenia*.

Scrobicularia tenuis, Pl. xxx, fig. 11, illustrates a specimen from the collections of the Smithsonian Institution. It has a distinct prodissoconch which is not, however, as sharply defined as in many genera because the succeeding dissoconch is so like it in form that no marked contrast is produced by the introduction of that later stage. The prodissoconch shows concentric lines of growth and its limits are defined by a varix of growth indicating the close of the stage.

Saxicava arctica, Desh. Young specimens were collected on the roots of *Laminaria* at Cohasset and Chelsea Beach in September, 1889. A very sharply defined prodissoconch exists at the umbos, fig. 50. It is ovate with umbos directed anteriorly and shows

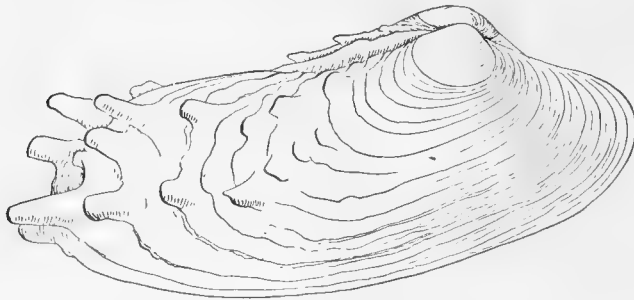


FIG. 50.—Young *Saxicava arctica*, showing oval rounded prodissoconch and succeeding spinous dissoconch. The ligament is external and prominent. $\times 38$ diam. (Drawn by J. H. Emerton.)

fine concentric lines of growth. The succeeding dissoconch is oblong, covered with a delicate epidermis, as is the prodissoconch and bears comparatively coarse strongly defined lines of growth. The ligament is external and forms a prominent feature of this early stage as well as in the adult. Two ridges which extend posteriorly from the limits of the prodissoconch valves are ornamented with spines. The spines vary in size and number, but persist in specimens up to four or five millimeters in length after which they were not observed. Their existence is noted in the young of *Saxicava* in Binney's Gould.

Mya arenaria, L. A number of young living individuals of this species were found actively crawling on the glass slides in the drain-pipe traps at Buzzards Bay during August, 1888; the specimens varied from 0.6 mm. to 5 mm. in length. At Chelsea Beach, Mass., in September, 1889, many clams were also collected, from very young to those having the adult characteristics fully developed. The specimens varied from 1.5 mm. in length upwards, and instead of being free crawling, as were those collected at Buzzards Bay, they were for the most part burrowing in a bed of dead eel grass where the roots and mud formed a comparatively solid mass. The burial was superficial and so abundant were the little clams that a handful of the material might contain fifty specimens more or less.

In very young *Mya*, Pl. xxx, fig. 13, a remarkable condition of the siphon tubes exists.

The tubes are divided from the base beyond the shell margins and are not coalesced at any point visible when fully extended. The relation between this condition and that found in the adult is of much interest and was fully illustrated in the specimens which I studied alive. The excurrent tube, Pl. xxx, fig. 13, is composed of most delicate transparent tissue. It is prolonged in a proboscis-like fashion and is frequently extended and retracted with a jerky irregular motion. Water is expelled intermittently, and between the expulsions the siphon tube is somewhat retracted. The tube has a small contracted orifice and a tentacle was noticed at its base. More tentacles at this region doubtless existed, for many are found in the next stage, but they were not observed. The incurrent branchial siphon tube, fig. 13, is much shorter than the excurrent tube. It has thicker walls, bears a circle of simple tentacles at its orifice and does not take part in the frequent extensions and retractions characteristic of the excurrent tube. The siphon of an older specimen measuring about 7 mm. in length is represented in Pl. xxx, fig. 14. Short termini of the excurrent and incurrent siphon tubes similar to those of fig. 13 exist at the tip; but between these and the shell, a massive coalesced growth of the tubes has developed by interstitial growth of the extended mantle border. Thus the portions of the siphons which are found in fig. 13 are now pushed out to the terminus of what may be called the massive siphon. The massive siphon is pigmented in dots, especially near the terminus which approaches nearest to the light, and it is covered by a delicate epidermal layer as in the adult. Tentacles fringe the free, distal border of the massive tube around its entire circumference, and a line of black pigment closely underlies the tentacles. The excurrent terminus, as in fig. 13, is composed of delicate tissue, is extensible and has a small contracted orifice which is plain, bearing no tentacles. Under higher magnification small dots regularly placed were observed on the walls of the excurrent terminus. The incurrent siphon terminus, as in fig. 13, is shorter than the excurrent. It is composed of thicker tissue and is constantly extended, not intermittently extended and retracted as is the excurrent terminus. Tentacles surround the orifice of the incurrent siphon and between the tentacles is black pigment bordered by orange; the tentacles also are themselves slightly pigmented. The pedal orifice of the mantle border in specimens of this age bears short papillose tentacles.

The development of the siphon from the condition just described, Pl. xxx, fig. 14, to the adult condition is merely a series of mechanical changes. The massive siphon elongates proportionately until, as Verrill says, in the adult it can be extended to the length of a foot or more. The termini of the tubes described in the young exist in the adult, but are so reduced in proportion to the entire siphon that they are hardly noticeable. The incurrent terminus is so short that it appears, as I have seen it described, that two rows of tentacles exist at this opening, whereas the fact is that one row surrounds the tip of the massive siphon and the other the free border of the incurrent siphon terminus as in fig. 14. The true condition of the parts in the adult is clearly figured by Morse, in his "First Book of Zoölogy."

A condition of the siphons, similar to that of Pl. xxx, fig. 14, exists in adult *Mya truncata*, as figured by Forbes and Hanley, and a condition similar to that of the earlier stage of *Mya arenaria*, Pl. xxx, fig. 13, is found in the adults of several genera, some closely allied to *Mya* and some not. Most important to us is the fact that this early condition of

the siphon exactly corresponds to what is found in the adult of *Corbula* (see Fischer, fig. 855). *Corbula* presents in the adult many features found in the early development of *Mya* and as it is the most ancient member of the *Myidæ*, being known from the Trias up, these facts are features of genetic importance in *Mya*. The great development of the siphon in *Mya arenaria* is most distinctly a correlation of structure induced by its habit of deep burial, and in the development of the individual we find that with increasing age as the individual burrows deeper the siphon elongates.

Professor Ryder (63), in a paper recently published, announces the discovery of a byssated condition in young *Mya arenaria*. Specimens studied at Buzzards Bay did not show this feature, although kept alive for several days; the clams from Chelsea Beach, however, did show it. I had them in glass dishes and many became attached to the sides and bottom. The byssus is produced from the ventral border of the foot at about the position of its point of extrusion from the shell in Pl. xxx, fig. 13. The animal attached itself as observed by a few (1-4) colorless threads of great delicacy. The threads were not expanded in disc-like distal termini as in the byssus of *Pecten* and *Mytilus*, but were glued to the glass for a considerable part of their length. Sharp angles in the line of the attached portion often existed, and separate threads often coalesced proximally. Byssal fixation occurred in specimens varying from 2.7 mm. to 9 mm. in length, and it was evidently a strong habit, for when detached, in a few minutes the fixation was again effected. A byssal cleft is characteristic of *Corbula* and *Sphenia*, near allies of *Mya*, according to authors, and Forbes and Hanley state that a byssal cleft exists in the foot of *Mya truncata*. In a very young specimen of *Mya arenaria* studied alive, the gills were filamentous, ciliated and expanded at their tips as shown in the gills of young *Ostrea*, Pl. xxiv, fig. 3. I did not determine certainly whether cross-bars united the tips or not.

A young specimen of *Mya arenaria*, Pl. xxx, fig. 12, shows the prodissoconch, *p*, clearly. The prodissoconch is rounded in outline, with umbos directed anteriorly. It is glistening and translucent, covered by a delicate epidermis and marked by fine concentric lines of growth. The prodissoconch may be retained in well preserved specimens, much older than fig. 12, even in those which are several millimetres in length; but commonly it is lost early from erosion. The prodissoconch is not so sharply marked off from the succeeding growth in *Mya* as in many genera, because the dissoconch growth has no striking features which originate with its introduction. It is, however, perfectly clear when preserved.

Professor Ryder (63) in his paper on *Mya arenaria*, published January, 1889, says that he did not find an embryonic shell in young clams such as is characteristic of young oysters. Since that time I have sent him specimens showing the embryonic or larval shell (prodissoconch) of *Mya*, and he acknowledges their existence in a letter, saying: "The specimens which you have been good enough to send show the larval shell very distinctly indeed, much more plainly than my own materials, in fact."

The dissoconch growth of *Mya arenaria* is covered with a delicate epidermis and is much whiter than the prodissoconch. I did not find any trace of prismatic cellular tissue in the young shell of *Mya*. The early dissoconch growth, Pl. xxx, fig. 12, is rounded in outline anteriorly, but truncated posteriorly and marked by fine concentric lines of growth. An older specimen of a clam is seen in Pl. xxx, fig. 13. The prodissoconch

of this later stage, on account of the arcuateness of the umbos, is not seen so clearly in side view as in the younger stage. The shell differs much from the adult in form, being less rounded anteriorly and less pointed posteriorly, also the valves gape less proportionately than in the adult. An angular ridge runs from the umbos posteriorly to the ventral border of the valves, emphasizing a flattened area above it. The features described are found in older young specimens, but gradually fade out and in successive growth give place to the characteristics of the adult.

The young shell of *Mya arenaria* bears a marked resemblance to some species of *Corbula* (leaving out of consideration the inequality of valves in many species of that genus); especially does it resemble *C. contracta*, Say, of our coast. The anatomy of young *Mya* also bears a close resemblance to the adult of *Corbula* (see Fischer's fig. 855) in possessing a similar siphon, Pl. xxx, fig. 13, papillose tentacles on the mantle border at the point of extrusion of the foot and a byssated foot. As *Corbula* is the oldest known genus of the Myidæ, being found from the Triassic upwards, and as it presents similar features to those found in the young of *Mya*, it is probably in the line of ancestry of the *Myas* and is a near representative of the form from which they have descended.¹

XV. ON THE GENETIC RELATIONS OF THE PRODISSOCONCH.²

In the development of Pelecypoda at an early embryonic stage, which I have described as the phylembryo stage, the two valves of the shell are sub-circular or saucer-shaped; but flattened into a straight line at the hinge area where they are joined by a ligament. This stage is characteristic of many developing Pelecypods (Pl. xxiii, figs. 7-11; Pl. xxiv, figs. 13-16 and fig. 25, p. 300)³ and apparently represents a primitive ancestral condition common to the whole class. Embryology shows that the Pelecypod shell originates from a single shell gland and that the two valves doubtless arose from the splitting on the median line of a primitive univalvular ancestral form. If that ancient univalvular radical had a saddle-shaped shell as in young *Dentalium*, Pl. xxiii, fig. 13, or a cup-shaped shell as exists in very early stages of cephalous mollusca,⁴ the first result of the introduction of a median hinge would be to straighten the shell on the hinge line. This is a simple problem in mechanics; for, if one tries to break by flexion a piece of metal which is saddle-shaped or cup-shaped, the metal will tend to form a straight

¹ Since this paper was in press, a prodissoconch has been discovered in a number of genera not considered in the foregoing pages. An ovably rounded prodissoconch has been found in *Nucula proxima* and in *Tellina*. In both genera the umbos of the prodissoconch are directed posteriorly as in the adults. A prodissoconch has also been discovered in *Chione*, *Cardita*, *Cardium*, *Mactra* and a number of undetermined genera belonging to other families of Pelecypods. In these latter the umbos of the prodissoconchs are directed anteriorly, and the succeeding dissoconch is destitute of prismatic cellular tissue.

² This section and the next one, xvi, have been considerably altered and added to since this paper was offered as a thesis at Harvard University on May 1, 1889. The additions are not indicated excepting by this note.

³ It is also described in *Teredo* by Hatschek. Exceptions to the rule occur as in *Pisidium*, where according to Lankester (43) the early embryonic valves are triangular. I think such cases may be considered exceptions in which the straight hinge period is skipped by acceleration of development.

⁴ The shell of Gasteropods, as I have observed in studies of *Sycotopus*, is cup-shaped before it acquires the spiral form of the completed protoconch, and a similar condition is shown in Lankester's (43) figures of *Aplysia*. The shell of Pteropods and Cephalopods is also at first cup-shaped as is obvious in studying the changes that must take place in the building up of the completed protoconch, Pl. xxiii, figs. 15-18.

line on the axis of flexion. A directly parallel case is the condition existent in bivalvular crustaceans. These originate by the introduction of a hinge in the median line of the carapace of a normal crustacean. The ancient Ostracoda,—Leperditia, Aristozae, etc., have a straight hinge line and sub circular valves which are united on the hinge line by a ligament. Thus, the resulting form of the bivalvular shell in these two entirely distinct classes is strikingly similar.

The next stage in the development of the Pelecypod shell is the loss of the early straight hinge line which is superseded by a curving of the hinge line and a centralization of connecting tissue and teeth of the two valves in the median line of the hinge.¹ The necessary form of the valves of an equilateral bivalve, freely crawling on the ventral border, is curved in section. Therefore, more or less arcuate umbos would develop during successive growth. This condition of growth would bring the shell to the form of the completed prodissoconch stage which is the representative of ancestral type radicals in the ontogeny of the individual. A close parallel of this later stage of shell growth is again to be found in bivalvular crustaceans. Some genera, as *Estheria*, have a curved hinge line, more or less arcuate umbos, and bear a close resemblance to Pelecypods. In this consideration of the mechanical origin of the Pelecypod shell, especial attention should be called to a highly interesting and important paper by Dr. Dall,² in which he demonstrates in a most striking manner the mechanical relations of the ligament and cartilage to the hinge in Pelecypods, and the progressive, mechanical development of systems of hinge teeth in this class.

The form of the shell up to the close of the prodissoconch stage seems to be the natural outcome of the bivalvular condition. I think the muscles which close the valves may be demonstrated to be the necessary consequent of the mechanical conditions of a bivalve shell. The anterior adductor muscle in Pelecypods is reduced and finally disappears when it comes into such position that its functional activity is lost, *e. g.*, *Ostrea*, *Pecten*, *Mulleria*, etc. (section v). The posterior adductor also may disappear through disuse. In *Aspergillum*, where the two valves have united so as to form a simple tube,³ and therefore, of course, the action of the adductor muscles is lost, the posterior adductor has disappeared and the anterior is reduced to a few disconnected shreds (Fischer). In the phylembryo stage of Pelecypods, fig. 25, p. 300, Pl. XXIII, figs. 7–11, the valves are closed by a single adductor muscle, the simplest condition mechanically possible to effect the desired end. This adductor does not seem to be homologous with any muscle in other classes of molluscs, and it probably developed as a necessary consequence of the

¹A straight hinge line is characteristic of many Pelecypods and it is not easy to perceive what causes led to the adoption of a curved one in the primitive radicals of the class. That it was adopted, however, is predicated by the form of the completed prodissoconch as described in these pages. See Plates XXIV–XXX. The prodissoconch of the Unionidæ has a straight hinge line, the reasons for which are discussed on p. 368.

²On the hinge of Pelecypods and its development, with an attempt toward a better subdivision of the group. By Wm. H. Dall, *Am. Journ. Sci.*, Vol. XXXVIII, pp. 445–462. Published since this paper was in press.

³The tube of this and similar genera is commonly spoken

of as if it were something separate and distinct from the shell, whereas it is a modified condition of the shell and should be so considered. In the young of *Aspergillum* every step can be traced between the typical bivalvular stage and the period when the two valves merge into one another by concrescence and form the truly univalvular condition characteristic of the genus. This concrescence of the apposed borders of the two valves in *Aspergillum* is paralleled by the concrescence of the two sides of the embryonic saddle-shaped shell of *Dentalium*, Pl. XXIII, fig. 14, which unite to form the tubular shell of the adult, as described by Lacaze-Duthiers (42).

conditions of the case.¹ In support of this view, the bivalvular crustaceans may again be cited as they have an analogous adductor muscle, developed, of course, on an entirely different line of descent, but under closely similar mechanical conditions. In the completed prodissoconch of all Pelecypods there are two adductor muscles, Pl. xxiv, figs. 1-2, Pl. xxx, fig. 4,² thus arriving at what may be called in this respect the *typical condition of the class*. During later life the anterior, the posterior, or both adductors, may be retained, reduced or lost, according as the persistence or changes in correlated features of anatomy retain in use or bring into disuse the muscles in question.

The preceding studies show the existence of an embryonic shell to which I have given the name of prodissoconch (p. 311) in many widely separated genera of Pelecypoda. We will now consider this early shell and see if any close connection can be traced between it and ancestral forms of which it is the representative in early stages of development.

Two classes of prodissoconchs and succeeding shell structure are described in the preceding pages. In the first division the prodissoconch has umbos directed posteriorly and is not prismatic, but is succeeded by a dissoconch having an external layer of prismatic cellular tissue which is more or less developed, but exists at least in the early nepionic stages of one valve. These features are characteristic of the Aviculidæ, Ostreidæ, Pectinidæ and Anomiadæ, as shown by representative genera. The second division is less well defined; but with one exception can be separated from the first. The prodissoconch of this second division has umbos which are directed more or less anteriorly. It has no prismatic cellular layer and is succeeded by a dissoconch which has no prismatic layer. Such features are characteristic of genera representing the families Mytilidæ, Arcidæ, Chamidæ, Petricolidæ, Cycladidæ, Veneridæ, Glycimeridæ, Scrobicularidæ and Myidæ. The young of the Unionidæ as described (page 305) does not come under this second section but in some features approaches the first. Only a part of the families of Pelecypods are included under these two divisions. Whether other families will come under one or the other, or yet new divisions, must be proven by future investigations (see note, p. 375).

The first of the divisions above considered embraces a group of families (the Aviculidæ and allies) intimately bound together as I have attempted to show in this paper. It will probably prove to be a group of ordinal value and *I shall limit myself to this group in considering the derivation of the prodissoconch*. The prodissoconch of the second division has doubtless a different ancestral kinship or perhaps several lines of ancestral kinship as the case may be.

The features by which a possible connection may be traced to the radical ancestor from which the prodissoconch form is inherited includes features of shell structure and anatomy, for we know both in a measure from the results of the studies in this pa-

¹The mantle of molluscs often has a highly developed muscular system, and it seems probable that the adductors of the Pelecypod arose from a modification of mantle muscles. A somewhat similar modification of these muscles is seen in the retractor muscles of the siphon, characteristic of many Pelecypods, as the clam, Pl. xxv, fig. 9.

²Also figures by Lovén, Schmidt and other investigators of marine and fresh-water Pelecypoda. The fact of the two adductors is also attested by the form of the prodissoconch in the genera figured on Plates xxxvi-xxx inclusive.

per. These two lines of inquiry linked with the proper palæontological sequence are found to point directly to a form which fills the necessary requirements of such an ancestor. Data for the inquiry. *The shell.* In *Avicula*, *Perna*, *Ostrea*, *Pecten*, *Anomia* and allies a prodissoconch exists in which the structure is homogeneous and laminar, sub-nacreous, not prismatic, though succeeded by a dissoconch having well-defined prismatic structure. The umbos of the prodissoconchs are directed posteriorly, and the hinge line is curved. The only genus in which we know the prodissoconch before any dissoconch growth has taken place, so to enable us to determine features of the hinge line, at this stage is *Ostrea*. In *Ostrea edulis*, fig. 26, p. 312, the prodissoconch has teeth at right angles to the hinge line, and these teeth closely resemble the teeth of *Nucula*, when a shell of that genus is viewed from the umbonal region as in the figure cited. In *O. virginiana*, however, no teeth were observed. *The anatomy* as illustrated by the various genera yields points of great synthetic value. The prodissoconch has two adductor muscles as proven in *Ostrea*, Pl. xxiv, figs. 1-2, and inferred in the other genera from the form of the prodissoconch valves and the kinship to *Ostrea* (see studies of *Perna*, *Avicula*, *Pecten* and *Anomia*). In the prodissoconch stage of *Ostrea* the gills are simple unpaired filaments and they are evidently simple filaments at first in other genera as indicated in our studies of *Anomia* and *Pecten*.¹ The mantle border of the prodissoconch is free around its entire margins except at the hinge line in *Ostrea*, and bears no tentacles or siphons. A similar condition of freedom exists in the youngest stages we know of related genera, and the development of tentacles and eyes described in *Pecten* indicates that at a very early period the border was without them in that genus. A foot evidently exists in the typical prodissoconch, for though wanting in *Ostrea*,² it is present and highly developed at the close of the prodissoconch period in the young of many related genera (*Avicula*, *Perna*, *Pecten*, *Anomia*, etc.), as I have shown. The foot where known is marked by a proximal byssal cleft and a distal cleft which latter is flattened out when crawling, giving the foot a disc-like, clinging power (see *Pecten* and *Anomia*, sections IX and XII).

With the above described prodissoconch features as known characters we have to seek for possible kinship with ancient forms. These characters are found to be combined in a remarkable degree in the ancient genus *Nucula* which, though living to-day, extends back to very early fossiliferous formations, fifty species (Tryon) being known from the palæozoic. *Nucula* is one of the few genera known which has the umbos of the shell directed toward the posterior end of the body.³ The shell of *Nucula* is oval, nacreous, not prismatic⁴ and has a curved hinge line with teeth at right angles to its axis. A triangular, central cartilage pit is a characteristic feature of the *Nuculidæ*, and though it is not definitely known to exist in the prodissoconch it may exist at that stage in some genera, and is a marked feature of the succeeding dissoconch in all the ascendent series

¹ A simple, filamentous condition of the gills as first described by Lacaze-Duthiers in *Mytilus* is considered by embryologists as characteristic of all developing Pelecypoda.

² The absence of the foot in *Ostrea* is fully discussed in previous pages.

³ The only genera outside the *Nuculidæ*, in which the um-

bos are directed posteriorly as far as I have found from the conchological manuals, are *Anatina*, *Donax* and *Tellina*, the two latter belonging to one family.

⁴ Traces of prismatic cellular structure are noted in *Nucula* by Carpenter, but he equally notes it in many other genera of Pelecypods, as sometimes seen in slight patches though not a feature of the shell as in *Avicula*, etc.

of the Aviculidæ and their allies. *Nucula* is dimyarian, an adductor muscle existing at either end of the equal valves. The gills are in two pairs, composed of simple, disunited filaments¹ (Mitzukuri). The mantle borders are plain, without tentacles or a siphon, and free around the margins. The foot is marked by a longitudinal cleft; accordingly it can be flattened into a circular disc (Mitzukuri) and it has been observed crawling up the sides of a glass of sea water (Tryon) indicating considerable clinging capacity of the foot. All these characters coinciding so closely with the features of anatomy and shell structure known in the prodissoconch, together with the fact that *Nucula* is known in very early fossiliferous formations combine to render it extremely probable that *Nucula* or a *Nuculoid* form is the type we are seeking as the early ancestral radical represented by the completed prodissoconch in the development of *Avicula*, *Perna*, *Ostrea*, *Pecten*, *Anomia* and their allies.

The fact that *Nucula* is found in the Lower Silurian formations and still lives up to the present day without sufficient changes in its shell structure to make these extremely separable forms in time generically separable, argues strongly for a very high antiquity for this genus. It was so firmly established in its earliest known forms that it must at that time have been an ancient genus. It may therefore well have been the primitive ancestral radical toward which the prodissoconch of the genera under consideration points as the archetype, still indicated in the development of a modern individual.

I have, therefore, from the results of these studies been able to trace, to *Nucula* or a *Nuculoid* form as a probable type-ancestor, the prodissoconch which I have found to be characteristic of developing *Avicula*, *Perna*, *Ostrea*, *Pecten*, *Anomia* and their allies. In the next section (XVI) the relationship existing between these several genera and their allies is traced as far as I am able to do so with my present understanding of the groups.

XVI. GENEALOGICAL CONNECTION OF THE AVICULIDÆ AND THEIR ALLIES.

It is shown in section XV that the prodissoconch, which is characteristic of the Aviculidæ and their allies, as represented by typical genera, can be traced to *Nucula* or a *Nuculoid* form as a probable ancestral radical of the whole group. In this section later stages of shell growth are considered in their phylogenetic bearing and a tabular view is given which represents the genealogical connection of the several genera as it is understood from the results of these studies. Frequent reference is made to the preceding text for a full consideration of points only briefly alluded to, and many genera not previously studied are introduced.

The early nepionic stage of *Avicula*, figs. 32-33, p. 330, *Perna*, Pl. XXVII, fig. 1, and *Pecten*, Pl. XXVIII, fig. 9, is closely alike in many species, indicating a common line of ancestry for these genera. The points of resemblance are as follows:—The body of the shell is sub-rhomboidal, oblique, the hinge line straight; the posterior wing is rounded and is not produced beyond the margin of the body of the shell. Anteriorly the straight hinge extends beyond the limits of the prodissoconch, and is terminated by a moderate auricle as in *Avicula* and *Pecten*, or the auricle may descend directly from the umbonal area without any anterior extension of the hinge line as in *Perna*. In the several genera

¹*Nucula* has been considered a primitive prototypal Pelecypod by several investigators on account of the sim-

plicity of the gills, which are paralleled in the early stages of many genera of Pelecypods.

the ligament joins the valves on the hinge line and a triangular cartilage pit extends inwards from the limits of the prodissoconch valve as shown in young *Perna*, fig. 30, p. 329. Teeth may exist on the hinge line as in *Avicula* and *Perna*, or not, as in *Pecten*. The right valve in the young of these genera has a byssal sinus originating in the initial stages of the dissoconch growth on the border of the prodissoconch valve, thence progressively produced to the free border of the valves, fig. 33, p. 330; Pl. xxvii, figs. 2, 3, 7, 8, 9, and Pl. xxviii, fig. 10.

The form of the young shell as above described is found to be closely similar to that characteristic of the adults of many *Aviculoids* from the Lower and Upper Silurian formations. Especially is it comparable to early *Aviculoids* figured by Barrande. These early forms differ widely from *Avicula* and require one or more distinct generic names. The Devonian *Aviculoids* have been subdivided generically by Professor Hall, but none of his genera suffice to cover the types which are here referred to. I would, therefore, introduce a new genus—*Rhombopteria*.

Rhombopteria, gen. nov.¹ A group of Lower and Upper Silurian *Aviculoids*, in which the shell is sub-rhomboidal, oblique, with umbos in the anterior half. The hinge line is straight, less than the length of shell, and is commonly produced anteriorly as well as posteriorly from the umbos. The borders of the valves posteriorly descend in a curved line from the terminus of the hinge without having any posterior extension of the wing. Anteriorly the borders of the valves descend from the hinge, forming an auricle close to the hinge line. In some species the auricle may be in close proximity to the umbos without any anterior extension of the hinge line, as in *Rhombopteria* (*Av.*) *glabra*, sp. Munst. Two adductor muscles and lateral teeth exist in closely related forms and probably are characteristic of this genus; but the features are not definitely known. It is quite possible, also, that a cartilage pit exists, although it also is not known, as the internal characters of the genus have not been ascertained. Type—*Rhombopteria* (*Av.*) *mira*, sp. Barr., fig. 51. For other figures of this species see Barrande's *Système Silurien de la Bohème*, Vol. VI, Pl. 226. Besides the type several species figured by M. Barrande come under the genus *Rhombopteria*, among which should be mentioned: *R. pseudomira*, sp. Barr.; *R. cognata*, sp. Barr.; *R. scala*, sp. Barr.; *R. patricia*, sp. Barr. and *R. glabra*, sp. Munst, all of which are figured on Plates 226–228 inclusive.

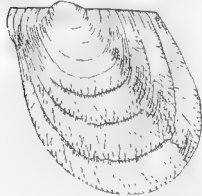


FIG. 51—*Rhombopteria mira*, formation E (upper Silurian), système Silurien. (After Barrande.)

Rhombopteria is the nearest approach to a primitive *Aviculoid* that has been found in studying fossil species. Not only can the nepionic stages of modern *Avicula*, *Pecten* and *Perna* be closely compared to this type, but camera drawings of the young of *Aviculopecten*, *Leptodesma* and other palæozoic and mesozoic allied genera bear a close resemblance to *Rhombopteria* as well. The American Lower Silurian species, *Avicula?* *trentonensis*, Con., *A.?* *gregaria*, Ulrich, and *A.?* *demissa*, Con., are near allies of *Rhombopteria*, especially the species *trentonensis*. In *Aviculoids* as a rule, the younger the specimen or the older the geological formation from which a specimen is obtained the nearer does it approach to the features of the genus *Rhombopteria*. In the comparisons of young *Avicula*, *Perna*, *Pecten*, etc., to *Rhombopteria*, it will be observed that there

¹ ῥομβος, a rhomb, and πτερον, a wing.

is a discrepancy in that the right valve of these genera has a well defined byssal sinus, whereas no byssal sinus exists in any of the figures of Rhombopteria cited. Dr. Beecher writes me that young *Avicula? demissa* has a byssal sinus and this species is a near approach to Rhombopteria, especially when young, but differs in having the posterior wing produced in the adult. It is quite possible that species of Rhombopteria may be found which have a byssal sinus; but if no such species should be found, it would not seriously affect our comparison of young *Aviculas*, etc., to this early type. The byssal sinus acquired in later periods of the development of a group might well be pushed back to the nepionic stages in the ontogeny of an individual by acceleration of development, also the existence of the character is quite variable in some genera, as in *Aviculopecten*.

The genetic relations expressed in the following pages and table must be looked at as a first attempt to classify the various groups and genera in their serial connections, for such I believe it is. Changes may and probably will be necessary in parts, but as a whole I believe it represents a close approximation to the true phylogenetic sequence of the genera considered.

The dimyarian prodissoconch characteristic of the early stages of this whole group is the representative in development of a dimyarian Nuculoid radical as discussed in section xv. Therefore a Nuculoid form makes a basis from which to start our phylogenetic series.

These studies tend to show that the primitive *Aviculoid* ancestor came off directly from the Nuculoid radical because the first nepionic stages of *Avicula*, *Leptodesma*, *Perna*, *Pecten*, *Aviculopecten*, etc., correspond closely with the earliest and simplest known *Aviculoid*. If intermediate forms existed between the Nuculoid radical and the earliest known *Aviculoid*, traces of it are not indicated in the shell, so that such possible transitional steps cannot be ascertained with our present knowledge. Therefore Rhombopteria, as the most primitive known *Aviculoid*, is considered the next step upward in the phylogeny of the group.

From this point up the phylogeny of the various groups is on divergent lines as expressed in the tabular view, and in the following pages we shall consider the groups in succession as indicated in the table, p. 391.

Leptodesma,¹ Hall, is a genus embracing a group of Devonian *Aviculoids* characterized by an oblique body. The posterior wing is more or less produced beyond the borders of the valves; anteriorly the shell is acute or nasute. The hinge is narrow with a slender, lateral tooth. The posterior adductor muscle is large, subcentral, but the anterior is not figured by Hall and is therefore presumably very reduced. The genus forms a natural passage from Rhombopteria to the true *Aviculas*. As Professor Hall says, the species present a remarkable assemblage of forms. At one extreme the shell has a well-developed posterior wing, acute anterior border and byssal sinus closely resembling *Avicula*. From this extreme it passes ". . . through various phases in form, proportions, etc., until the wing becomes nearly obsolete, the byssal sinus obscure and the anterior end rounded. . . ." This other extreme brings the form very close to our genus

¹For a consideration of this and other palæozoic genera I am greatly indebted to Professor Hall's fine work on Devonian Lamellibranchs in the Natural History of New

York, Vol. v, Parts I-II. I am also recently indebted to that venerable palæontologist for the opportunity to study his collections and types at Albany.

Rhombopteria. *Leptodesma orus*, Hall, is a species with a well-developed posterior wing but a camera drawing of the young is rhomboidal and bears much resemblance to Rhombopteria. The same comparison may be made in a degree by noting the differences in the younger and older specimens figured by Hall in several species as *L. matheri* and *L. jason* and it may also be observed by following the lines of growth in many of his figures. *Leptodesma* is therefore considered the next step in the ascendent phylogenetic series.

Avicula, the representative of the family, is clearly derived from *Leptodesma*-like forms. Using *Avicula hirundo*, L., the type species of the genus, as our basis of comparison we find that *Avicula* differs from *Leptodesma* in having a highly produced posterior wing, a deep byssal notch in the right valve, and small cardinal teeth. A more or less well-developed triangular cartilage pit exists in all *Aviculas*. In species with a narrow hinge line, as *A. sterna*, the pit is only prominent in the young; but in others, as in the sub-genus *Meleagrina*, it is a marked feature of the adults.¹ In the ontogeny of the individual we find that *Avicula* at the prodissoconch stage is referable in ancestry to the Nuculoid radical of the group. In the early nepionic stage, fig. 32, p. 330, it is referable to Rhombopteria; in the later nepionic stage, fig. 33, p. 330, a considerable wing has developed and the form approaches near to the winged *Leptodesmas*. Later still the full *Avicula* features are acquired. Thus the ontogeny of the individual represents very fully the phylogeny of the genus. The first appearance of true *Avicula* in the geological horizon is uncertain as many early types called *Avicula* certainly do not properly belong to that genus and the limitations of the genus in the past have not been fully ascertained. It probably is truly represented as early as the Devonian or Carboniferous. From *Avicula* many genera and sub-genera are derived, a part of which only we are prepared to discuss. (Further consideration of *Avicula*, see p. 330.)

Pseudomonotis. The young, as observed in *P. echinata*, has a prodissoconch and nepionic stage like the same period of *Avicula*, figs. 32-34, p. 330. Later, the hinge line becomes relatively shorter and very moderate abbreviated wings are differentiated. *Monotis* occurs later in time and has features closely comparable to *Pseudomonotis*, therefore it is considered provisionally as derived from that genus. *Daonella* and *Halobia* are genera which are sub-rhomboidal in form and present a high reduction of *Aviculoid* characters. They are unquestionably side-issues off the ascendent line of the group and should probably be associated with *Monotis* or *Pseudomonotis*, but as I have not had specimens for study they are not further considered. (Further description of *Monotis* and *Pseudomonotis*, see pp. 331, 332.)

Oxytoma, a genus near to *Avicula*, has a short hinge line with moderately developed ears and a slight obliquity of the body of the shell. It seems to be a variation from *Avicula*, in the same line as *Monotis* and *Pseudomonotis*. Some features of the young are shown in Pl. XXVII, fig. 7. (Further description of *Oxytoma*, see p. 332.)

Cassianella is highly inequivalvular; the young has a prodissoconch and nepionic stages like the young of *Avicula*, as shown in *C. decussata*, fig. 35, p. 332. The hinge line is of moderate length, the wings are moderately produced and cardinal teeth are

¹A cartilage pit is characteristic of the *Pecten* division of this group and it is probably characteristic of Rhombop-

teria and *Leptodesma*. In all it may be inherited from the Nuculoid ancestor in which it is a characteristic feature.

well developed. Provisionally, *Cassianella* is considered a branch from *Avicula*, in the same line as *Pseudomonotis*, etc. (Further description of *Cassianella*, see p. 332.)

Vulsella, when young, fig. 36, p. 332, bears a considerable resemblance to young *Avicula*, fig. 32, p. 330, as it has a similar prodissoconch and nepionic rhombic form. Later, the resemblance is lost, as wings are wanting, the hinge line is highly reduced and often produced in a curve around the deeply-sunken cartilage pit. *Vulsella* is evidently a side-issue from the *Avicula* stock and provisionally is placed on the same branch as *Malleus*.

Malleus is a genus closely allied to *Avicula*. The main features of difference are the great development of prismatic cellular tissue, loss of teeth, deep cartilage pit and contorted form. In the young it resembles *Avicula*, as pointed out by Woodward. It should be observed, however, that it is the young of *Avicula*, fig. 32, p. 330, which the young *Malleus* most nearly resembles, as shown at the umbonal region or early growth of fig. 52. The irregular, contorted growth of adult *Malleus*, Pl. xxvii, fig. 19, and also the relative great development of prismatic cellular tissue and extreme reduction in area and thickness of nacreous tissue, are features of the adult which point toward the probability that *Malleus* is a degenerate or retrograde genus.

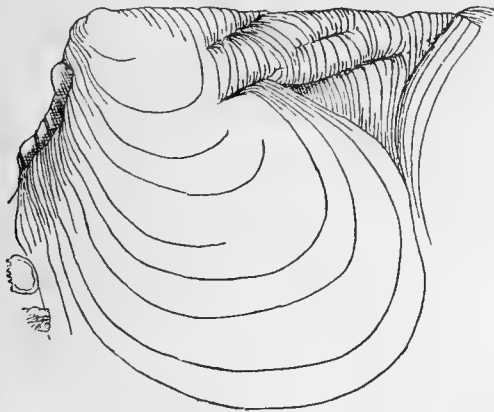


FIG. 52.—*Malleus vulgaris*, L. Tip of left valve showing the form of the young. $\times 13$ diam. (Drawn by the author.)

On another line of descent we find *Meleagrina*. When young it resembles young *Avicula*, fig. 32, p. 330, but it has then no teeth. The cartilage pit descends from the limits of the prodissoconch as in *Avicula* and *Perna*, fig. 30, p. 329. With increasing age the oblique form of the body of the shell decreases and the characteristic rhombic form of the adult progressively increases. The rhombic form characteristic of the adults of this and

some other genera is not necessarily to be considered as an inheritance from Rhombopteria. It is rather an approach to a form normal to the group and which is frequently repeated in genera not closely akin. (Further description of *Meleagrina*, see p. 331.)

Perna is an unquestionable branch from *Avicula*. The nepionic stage of *Perna*, Pl. xxvii, fig. 1, is similar to the same stage of *Avicula*, fig. 32, p. 330, the main difference being that the anterior auricle descends directly from the prodissoconch without an anterior extension of the hinge line. At this age but a single triangular cartilage pit exists, fig. 30, p. 329, and cardinal and lateral teeth like those of *Avicula* underlie the hinge line. Later, new cartilage pits develop on the hinge line, fig. 31, p. 329, and in successive growth they assume the perpendicular form characteristic of the pits of the genus, Pl. xxvi, fig. 16. The number of pits is variable, but twenty or more exist in some fossil species. Wings may or may not develop in *Perna*, Pl. xxvi, figs. 16-18, but the body of the shell is produced obliquely or vertically as in *Avicula* or *Malleus*, Pl. xxvi, fig. 19. In no species are teeth known in the adult and they seem to be purely hereditary characters limited to early stages of development. The microscopic shell structure of *Perna* is identical with that of *Avicula*, and the anatomy of the two genera is alike as far as

observed. The numerous and peculiar cartilage pits, loss of hinge teeth and form of the shell point out clearly that *Perna* is a side branch, off the ascendent line of the *Aviculan* series. In these studies *Perna* is considered the main stem from which important branches are given off. (Further description of *Perna*, see pp. 326, 327.)

Bakewellia appears to be a branch from *Avicula*, in the same line of variation as *Perna*, on account of the series of cartilage pits. The form of adult *Bakewellia* is very similar to the young of *Perna*, Pl. XXVII, fig. 1, so that it might appear to be in the line of ancestry of *Perna*. An objection to this assumption is the high development of both adductor muscles, whereas neither *Avicula* nor *Perna* has more than a slight development of the anterior adductor. A dimyarian condition has been shown to be characteristic of the prodissoconch stage of *Ostrea*, *Pecten*, *Avicula*, etc., and in *Bakewellia*, we merely have to assume that the early anterior adductor was retained instead of abandoned in the ontogeny of the individual. A similar case of the retention of the anterior adductor is seen in *Dimya*, which has two adductors in the adult though belonging to a typical monomyarian group. The form of *Bakewellia* is sub-rhomboidal, oblique and is quite comparable to *Rhombopteria*. The cartilage pits, primitive form of the valves and large anterior adductor muscle, point to the conclusion that *Bakewellia* is a specialized and partially retrogressive genus.

Gervillia has important characters of form and cartilage pits connecting it with *Perna* from which genus it was probably derived. *Hornesia*, an allied genus, is apparently a modified branch from *Gervillia* differing principally in its inequivalvular form.

Inoceramus was probably derived from *Perna*, through the intermediation of *Gervillia*. The forms of the genus which are rhomboidal and the most equivalvular, as *Inoceramus crispi*, Mant., are to be considered the more normal, least modified forms of the genus as they approach nearest to the condition found in ancestral genera. The oval and plicated genus *Actinoceramus* is a modified branch from *Inoceramus*. *Volviceramus* is a still more modified, oval and highly involute genus probably derived from *Actinoceramus*.

Pernostrea from the Jurassic is a descendant of *Perna* which attached itself by the umbo of the left valve and the consequent conditions of fixation modified the shell, inducing an ostrean form. The shell has a series of cartilage pits like *Perna* and a form which closely resembles an oyster. (Further description of *Pernostrea*, see p. 325.)

From the studies on the development of the oyster, sections IV-VII, we have come to consider *Ostrea* as close akin to and derived from *Perna* (pp. 326-327). The points of likeness are features in the anatomy of the soft parts, the prodissoconch and the structure of the right, free, least modified valve. The points of difference are the absence of the foot, the highly modified attached valve and the single cartilage pit of *Ostrea*. The first two features of difference are paralleled in *Pernostrea* and are ascribed to the effects of the condition of cemented fixation (section VII). The oyster is a highly modified form and the reduction of the several cartilage pits of *Perna* to a single one in *Ostrea* is considered as part of the specialization of the genus. When young, *Perna* also has but a single cartilage pit like the oyster; compare fig. 30, p. 329 with Pl. XXIV, fig. 19. *Ostrea* is the least modified member of the *Ostreadæ*, as it nearest approaches to *Perna* from which it was apparently derived. *Gryphæa* is a more highly modified genus and

Exogyra is the most highly modified member of the family. Therefore they are considered as derived from *Ostrea* and are in the ascendent series of this peculiar group. The marked sinuosity in the left valve of *Gryphæa* and *Exogyra* is compared to a similar sinuosity in young *Ostrea*, Pl. xxv, figs. 5-6, and is ascribed to the local retraction of the mantle border at that area where excurrent action takes place (p. 307).

Exogyra is compared to the adult of species of *Chama* (the base of the *Chamidæ*) and to the young of *Caprinula*, Pl. xxv, fig. 20, *Hippurites* and *Radiolites* (extremes of the same group) which in external form it closely resembles. The form of all these genera is believed to be built up as the result of cemented fixation with its accompanying influences of environment. When a Pelecypod becomes attached by cemented fixation the first form induced by the new conditions is a form like *Ostrea*. A further modification in this line of variation is a form like *Exogyra*. The next step in the same line of variation is a form like *Caprotina* or *Caprinula*, Pl. xxvi, figs. 10 and 8. Finally the last step in the same line of variation is a form like *Hippurites* or *Radiolites* which are conical or cup-shaped with a considerable degree of superficial radial symmetry (see section VII, and especially foot-note, p. 322).

Alectryonia which is strongly plicated in both valves and adherent by recurved clasping spinous processes, is undoubtedly a side issue from *Ostrea* and not in the ascendent line of the family.

I have not had opportunity to study the *Pinnidæ* satisfactorily as attempts to obtain very young specimens have so far failed. The following is offered as the probable genetic relations of the family. *Palæopinna* (Hall) in form is not far removed from some species of *Leptodesma* and it can be naturally derived from that genus by reducing the posterior extension of the wing and increasing the length of the antero-posterior axis. From *Palæopinna* or *Aviculopinna* to *Pinna*, is a natural step introduced by an increased acuteness anteriorly and a greater curvature of the lines of growth posteriorly. In support of this view we find that young *Pinnas* (20 mm. more or less in length), fig. 53, are obtuse anteriorly, and posteriorly have an obtuse abbreviated extension of the hinge line, like *Aviculopinna*. These features gradually fade out in succeeding growth and give place to the acute anterior and roundly curved posterior border of the valves which is characteristic of the genus. The *Pinnidæ* should, I believe, be considered a degradational group because of the great development of prismatic cellular tissue and loss of nacreous tissue (a weakening character), loss of teeth on the hinge line, and relatively large development of the anterior adductor muscle (a larval character, highly reduced or wanting in the ascendent series of related groups).

Atrina is a peculiar genus of the *Pinnidæ* of twisted irregular growth. In the later growth of the shell there is a direct fusion of the two valves both on the dorsal and ventral border though in less degree on the latter. In a specimen of *A. saccata* sp., L. in my collection, 114 mm. in length, the fusion dorsally occupies a length of about 50 mm.

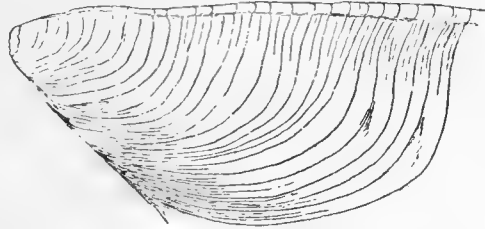


FIG. 53.—Tip of young *Pinna*, sp. *indet.* from Panama. Original in Yale University Museum. Cat. No. 2327. $\times 4$ diam. (Drawn by the author.)

and in this area the lines of growth pass directly across from one valve to the other without any indication of the hinge line. The nacreous tissue is highly reduced in extent. The shell has become in a physiological sense a flattened tubular univalve which may be compared in a measure in its resultant form to an *Aspergillum* (*vide* note 3, p. 376). In the young of *Atrina* the two valves are perfectly separable and have not yet acquired the twisted abnormal features characteristic of the adult. *Atrina* should be considered a very retrograde genus as it is weak and abnormal to a high degree.

Trichites, another genus derived from *Pinna*, is peculiar for its excessive development of prismatic cellular tissue which may reach an inch or more in thickness. It is an extreme modification of the *Pinnidæ* of highly irregular growth and without hinge teeth. The great development of prismatic cellular tissue in the *Pinnidæ* disproves the statement commonly made in text-books that this structure is only formed by the edge of the mantle. The formation of prismatic tissue commonly is limited to that portion of the shell built by the edge of the mantle, as in *Avicula*, *Ostrea*, *Anodon*, etc., the deeper-seated portions of the mantle in such cases building nacreous or sub-nacreous tissue. In *Pinna*, *Atrina*, *Trichites* and *Malleus*, however, the deeper seated parts of the mantle as well as distal edges must build prismatic tissue or this structure would not attain the thickness that it does, and further we may actually see in fresh specimens that the nacreous structure, as in *Atrina* and *Malleus*, is limited to a very small area near the umbonal portion of the shell.

Pterinea is closely related to *Aviculoid* types and yet is not in the ascendent line of *Avicula* proper. The shell is nasute anteriorly and the wing may or may not be produced posteriorly. The ligamental area of the valves is striated longitudinally (compare with *Meleagrina*); but no cartilage pit is differentiated, although this is characteristic (either as a single or several pits) of *Avicula* and all its various descendants as represented in the accompanying table. The young of *Pterinea* as shown by Goldfuss¹ in *P. lævis* is rhombic in form and bears a very close resemblance in contour to *Rhombopteria*, fig. 51, p. 380. *Pterinea* is considered as a side branch, probably derived from *Rhombopteria*.

Actinopteria (Hall) and *Ptychopteria* (Hall) are genera described by Professor Hall as differing from *Pterinea* in the absence of a strong striated ligamental area and in the absence of cardinal and lateral teeth. Following his figures and descriptions, it is seen that *Actinopteria* more nearly approaches to the characters of *Pterinea* than does *Ptychopteria*; therefore, in our table they are arranged in that serial order. Both genera appear to be on a side branch from *Pterinea*; not in a direct line of ascent because they are characterized by a loss, not an accentuation or modification of *Pterinean* features.

Pterinopecten (Hall), a Devonian genus of the *Aviculopecten* group, is characterized by a long hinge line, with ears not well defined, being simple expansions or extensions of the hinge line. The various species are frequently described by Hall as sub-rhomboidal, especially when young, and he mentions that some species resemble the young of *Aviculopecten* and *Lyriopecten*. *Pterinopecten dignatus*, Hall, *P. conspectus*, Hall, and similar species bear a close resemblance to the young of *Pecten irradians*, Pl. XXVIII, figs. 12-13. They resemble the figures cited in both valves as the right valve has a deep byssal sinus. The young of *Pterinopecten* is similar to the adult of *Rhombopteria* as I have observed in *P.*

¹ *Petrefacta Germaniæ*, Pl. CXIX, fig. 1a.

intermedius, Hall, *P. vertumnus*, Hall, and *P. conspectus*, Hall. Pterinopecten is naturally derived from Rhombopteria by the introduction of slight ears on the hinge line. It is the simplest known form of the Pectenidæ and is traceable in the early stages of development of Aviculopecten and Pecten; therefore, I shall consider Pterinopecten as directly descended from Rhombopteria and as the base of the Pectenidæ from which all later forms were derived. (Further discussion of Pterinopecten, see p. 346.)

Aviculopecten (McCoy), as amended by Hall, includes forms with a hinge usually shorter than the transverse diameter of the shell and with both ears well defined. A cartilage pit is described by Hall in several species of this genus, also in Lyriopecten and other allies. A deep byssal sinus occurs in the right valve of many species of Aviculopecten and diverging furrows exist on the hinge line in some species similar to those found in certain recent Pectens as *P. maximus*. A finely preserved specimen of *Aviculopecten fasciculatus*, Hall, shows that when young (3 mm. in height) the shell was rhomboidal and in its general contour, resembled Rhombopteria. During later growth a long hinge line and moderately developed ears develop, making the shell at this stage comparable to Pterinopecten; later still, the characters of a shorter hinge line and pronounced ears give the shell the characters of the genus Aviculopecten. Similar observations have been made on the development of *Aviculopecten princeps*, Hall, and a few other species. Aviculopecten, when young, resembles Pterinopecten and when adult resembles the young of Pecten, Pl. xxviii, fig. 2. It is, therefore, unquestionably intermediate between these two types. (Further discussion of Aviculopecten, see p. 346.)

From Aviculopecten we pass to Pecten in the direct line of ascent. Pecten has a relatively short hinge line, both ears well defined, but the ventral (anterior) a little larger; either a slight or no byssal sinus exists in the ear of the right valve. The ligament and cartilage are as in Aviculopecten. In the development of *Pecten irradians* and other species (sections IX-X) we have shown a remarkable series of phylogenetic characters which may be briefly alluded to. The prodissoconch, *p*, of Pecten is dimyarian, Pl. xxvii, figs. 8-9, Pl. xxviii, figs. 9-10, and is traced to the Nuculoid radical of the whole group (see table). The first nepionic stage, Pl. xxviii, fig. 9, is rhomboidal, oblique, and is traced to Rhombopteria; the later nepionic stage, Pl. xxviii, figs. 12-13 has a long hinge line, and ears which are simple expansions of the hinge margin; these features and the deep byssal sinus are traceable to Pterinopecten. The nealagic stage of Pecten, Pl. xxviii, fig. 2, has a relatively shorter hinge and well developed ears, and this stage is traceable to Aviculopecten. Only when the individual has advanced considerably in age are the full characters of the adult, fig. 37, p. 333, acquired. The first appearance of Pecten geologically is doubtful as the limitations of the genus among palæozoic fossils has not been fully worked out. All of Professor Hall's Devonian Pectenidæ are, however, referable to other genera and we will provisionally consider Pecten as dating from the Carboniferous. From Pecten as a base many genera have sprung as will be presently considered.

Lyriopecten (Hall) differs from Aviculopecten in possessing a short hinge and a small anterior ear. It also differs from Pecten in this last character and it is considered as a side branch from Aviculopecten. In support of this view we find that a specimen of *Lyriopecten orbiculatus* Hall, which had a short hinge in the adult, in the young (as ascer-

tained by following the lines of growth) had a long hinge line, with a comparatively slight development of the ears.

Crenipecten, Hall, is a genus like *Aviculopecten* in form, but with crenulations on the hinge margins. *Pernopecten*, Winchell, has a large triangular cartilage pit and a crenulated hinge plate. The crenulations in these genera are described as cartilage pits. A crenulated hinge plate is found in the young of *Pecten tenuicostatus*, fig. 38, p. 348, and *P. monotimeris*. It has also been found more or less developed in the young of several recent species of *Pecten* by Dall (16). He considers the crenulations as an order of dentition¹ and the crenulations in the fossil genera cited are probably of similar significance. As evidence against the view of considering them as cartilage pits, it should be observed that in *Perna*, etc., where numerous cartilage pits are typical, the primitive pit as well as succeeding ones assumes the perpendicular sides characteristic of the pits of the genus, figs. 30-31, p. 329, and Pl. xxvi, fig. 16. *Crenipecten* and *Pernopecten* are considered as side issues from *Aviculopecten*.

Lima has many features of anatomy and shell form linking it with *Pecten*; it is, therefore, presumably a side issue from the early members of this genus. (Further description of *Lima*, see p. 353.)

The genus *Chlamys* (Bolton), characterized by the great development of the ventral (anterior) ear and correlated reduction of the dorsal ear, is an undoubted branch from *Pecten*. When young, Pl. xxviii, fig. 14, both ears are nearly equally developed as in *Pecten*. *Chlamys* is a swing in one direction as *Lyriopecten* is a swing in the other direction, for the latter has the anterior ear very reduced and the posterior ear largely developed. (Further description of *Chlamys*, see p. 348.)

Vola (Klein) is a near ally of *Pecten*; in the adult it is highly inequivalvular, the right valve is deeply concave, while the left valve is flat or even slightly concave. When young, however, it is nearly or quite equivalvular. In a finely preserved specimen from Japan, a prodissoconch and nepionic stages were observed in both valves, similar to those characteristic of *Pecten irradians*, Pl. xxviii, figs. 9-12.

Amusium (Schumacher) (see Dall) is characterized by radiating, internal ribs, a short hinge line, nearly equal ears and a high reduction or complete absence of the byssal notch. The ears of the right valve may be produced beyond the limits of those of the left, on the hinge border, as in *Amusium japonicum*, thus making an abbreviated approach to the condition characteristic of the genus *Eutolium*, Meek. Commonly a pair of ridges diverge from the hinge line and terminate in tubercular processes close to the auricular sinus of either ear. Dall has named them auricular cruræ. Cruræ similar to those of *Amusium* may be traced in most species of *Pecten*, though they are often very reduced, the terminal tubercle at the auricular sinus alone existing. The function of the cruræ is not understood. Dr. Dall, in his studies of deep-sea *Amusium*, notes the existence of prismatic structure in several species, in which, however, it was not limited to the right valves, as shown in our studies of young *Pecten* (section x). *Amusium* is considered a side issue from *Pecten*, rather than in the line of ascent of the group.

Anomia is doubtless a side issue from *Pecten* as discussed (section xiii). In the young there is, as in *Pecten*, a deep byssal sinus in the right valve, Pl. xxix, fig. 6.

¹ See reference to a paper by W. H. Dall, foot-note, p. 376.

Later the byssal sinus becomes enclosed to form the byssal foramen as described (fig. 41, p. 354). The peculiarity of the shell and many features of anatomy are clearly attributable to the special conditions of environment of the animal (full discussion, sections XII-XIII).

Ænigma is an extreme modification in the *Anomia* line of variation. The right valve is very attenuated, the umbos are far removed from the hinge line, and the byssal foramen is sub-central. A specimen of *Ænigma ænigmatica*, Chemn., in my collection is obliquely oval, closely resembling the form found in young *Anomia*, Pl. XXIX, fig. 5. The left (upper) valve from the umbo to the periphery of the shell shows the fusion of the lines of growth that takes place at that area as in young *Anomia*, Pl. XXIX, fig. 8. *Ænigma*, therefore, though with full probability a descendant of *Anomia*, in some characters resembles the nepionic period of that genus.

Placunanomia differs from *Anomia* in the calcareous union of the borders of the byssal foramen anteriorly; it also differs in the development of diverging lamellæ from the hinge border. By the encroachment of the borders of the byssal foramen the byssus in later life tends to become solidly fixed in the lower valve. In *Placunanomia macrochisma*, Desh., the byssal foramen is open in specimens two inches in height and is only partially closed in specimens somewhat over four inches in height, as far as observed in the few specimens at command. In the single specimen of *Placunanomia rudis*, Brod., observed, the byssal foramen is entirely closed. *Placunanomia* is off the direct line of ascent in the *Anomia* order of modification, and is transitional between *Anomia* on one side and *Carolia* and *Placuna* on the other, as demonstrated by Fischer.

Carolia is a genus which seems clearly to be intermediate between *Placunanomia* and *Placuna*, as demonstrated by Fischer. When young, *Carolia* has a deep byssal sinus like adult *Anomia*. Later the sinus becomes progressively deeper like *Ænigma*, then the borders of the notch become joined on the anterior border like *Placunanomia* and finally the byssal foramen is cut off by shelly growth, when the shell approaches to the condition of *Placuna*.

Placuna in its anatomy is essentially like *Anomia* but the mantle border has a curtain, like *Pecten*, as shown by Woodward. The structure of the shell is also very similar to *Anomia*. In the New York State Museum I observed an inclosed byssal plug in young specimens of *Placuna sella*. The plug occupies the base of a foramen which is filled up by calcareous growth similarly to *Anomia*; but in the specimens observed the plug was already cut off from the body of the animal by a calcareous secretion that had taken place on the proximal side of that area. A similar condition to that observed in *Placuna sella* is described and figured by Fischer in young *P. papyracea*. The cruræ of *Placuna*, though existing only in the right valve of the adult (the left valve having corresponding depressions), are equally developed in both valves of the young. The cruræ of *Placuna* seem to be a modification and posterior extension of the knob-like cartilage support found in the right valve of *Anomia*. (Further discussion of *Placuna*, see p. 362.)

Dimya, on account of some features of anatomy and shell structure, is placed by Dr. Dall near to *Pecten*. The shell being ostreaform, he considered that the genus lay between *Pecten* and *Ostrea*. I have shown I think conclusively that the ostrean form of

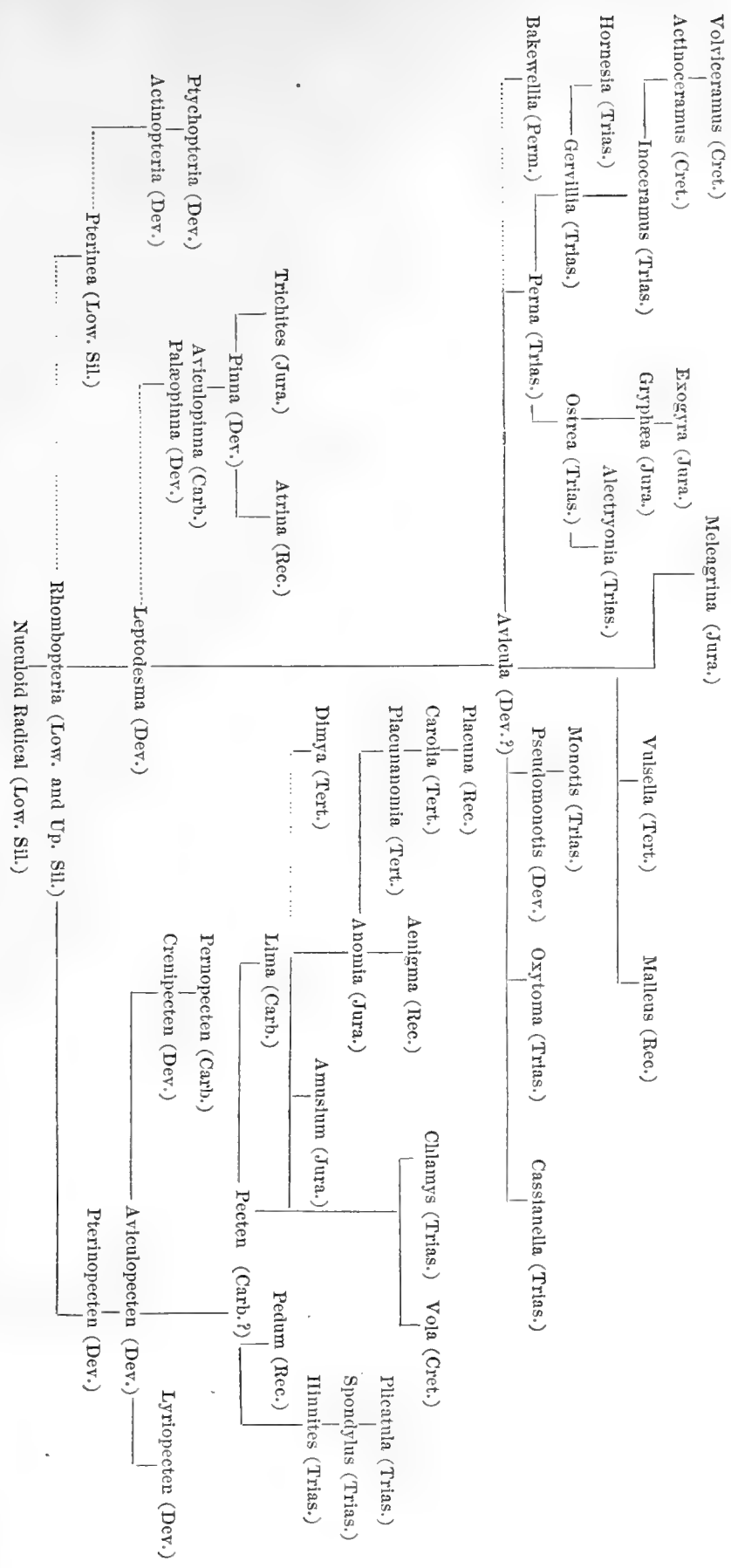
shell is induced by the conditions of fixation in any attached Pelecypod; therefore *Dimya* should be considered as a highly modified branch from *Pecten*, which is ostreaform because attached. It is shown in this paper that the prodissoconch of *Ostrea*, *Pecten*, etc., is dimyarian, therefore we may fairly infer that the existence of two adductor muscles in adult *Dimya* is due to the retention of both muscles which are doubtless existent in the prodissoconch stage of that genus. It is to be noted also that the gills of *Dimya* are in an archaic condition of simplicity as described by Dall. It is shown in the table of genera, p. 391, that *Pecten* and *Ostrea* are very widely separated genera, therefore no one genus can properly be considered as intermediate between these two types. *Dimya* is considered as a side-issue from *Pecten*, possessing many archaic and modified features which render it a highly retrogressive or degradational form. (Further description of *Dimya*, see pp. 306, 324.)

Pedum is evidently a descendant of *Pecten*. In the nepionic period, *Pedum* is purely pecteniform in both valves, not yet having acquired the peculiarities of the genus. Later, the byssal sinus is enclosed so as to become, in a measure, foraminal, and the shell is apparently closely related to the object of byssal attachment. The right valve is the most highly modified, although both valves are modified, and in the adult condition bear little resemblance to *Pecten*. The peculiar form of the shell of *Pedum*, it may be reasonably inferred, is due to the habit of close byssal fixation.

Hinnites, as already discussed, is an important genus in our conclusions. Up to the nealagic period, it is free or attached by a byssus and pecteniform, Pl. xxvi, figs. 3-4. It then becomes permanently attached by soldering the right valve to an object of support and with this change in habit we find that the irregular ostreaform growth is introduced as fully discussed (section VII). *Hinnites* is an undoubted descendant from *Pecten* and owes the peculiarity of its form to its adopted habit of fixation. (Further description of *Hinnites*, see pp. 324, 350.)

Spondylus, like *Hinnites* in its nepionic stage, is pecteniform, Pl. xxvii, fig. 4; then becoming attached at this early stage, the irregular growth characteristic of the genus is introduced and the shell becomes spondyliform. The right attached valve is the most highly modified, and the left valve is the least modified and nearest approaches to *Pecten* in form (discussed in sections VII and XI). *Spondylus* is considered as descended from *Hinnites* and is more highly modified than that genus because it earlier adopts the condition of fixation. The degree to which a talon is developed in *Spondylus* varies, being least developed in species which are most nearly equivalvular (p. 352). The peculiar interlocking teeth of *Spondylus* are believed to be a modification of the auricular cruræ characteristic of most *Pecten*s and especially *Amusium*. The several teeth of *Spondylus* in the young seem directly traceable to the knob-like processes of the cruræ existing at the auricular termination of the cruræ in *Pecten*. In *Spondylus* apparently by the shortening of the cruræ, the distal knobs of the same are brought in close proximity to the hinge line, where they are further modified so as to produce interlocking, articulating processes. If this assumption in regard to the teeth of *Spondylus* is correct, they are teeth of different morphological nature from ordinary cardinal teeth and are to be compared to those only as to mechanical equivalents. (Further consideration of *Spondylus*, see pp. 318, 323 and 351.)

GENEALOGICAL TABLE OF THE AVICULIDÆ AND THEIR ALLIES.



Plicatula is an undoubted ally of *Spondylus*, as usually considered. As we have shown, the shell of *Plicatula* becomes attached at the close of the prodissoconch stage, and at once assumes the ostrean form, thus eradicating features of the nepionic stage which (as in *Spondylus* and *Hinnites*) might render that stage comparable to *Pecten*. *Plicatula* is considered the farthest removed from *Pecten* of its group, for in it the ostrean form is earliest acquired and most completely emphasized in the shell. (Further description of *Plicatula*, see p. 352.)

The table on the preceding page represents graphically the genetic relations expressed at various places in this paper and especially in the present section. When genera are considered as derived from other genera and in the ascendent line of the group, they are placed directly over one another, as in the case of *Gryphæa* and *Ostrea*. When a genus is derived from another, but is not considered as in the ascendent line of the series then it is placed as a side branch, as *Alectryonia* from *Ostrea*. Broken lines are used where the affinities expressed appear to be open to doubt. With each genus is expressed in brackets its earliest geological appearance, the data for these statements being for the most gathered from Zittel's *Palæontology*. The following abbreviations are used: Low. Sil., Lower Silurian; Up. Sil., Upper Silurian; Dev., Devonian; Carb., Carboniferous; Perm., Permian; Trias., Triassic; Jura., Jurassic; Cret., Cretaceous; Tert., Tertiary; Rec., Recent.

ERRATA.

Page 281, note, the prodissoconch is described in a few genera not included in this list. For such additions see sections VIII, X and XIV.

Page 291, paragraph 5, line 5, for *Apysia*, read *Aplysia*.

Page 291, paragraph 6, attention should have been called to Dr. W. Branco's monograph: *Beitrage zur Entwicklungsgeschichte der fossilen Cephalopoden*. *Palæontographica*, B. 27, 1880-81.

In section IV, at several points the oyster is spoken of as showing concentration of development, or as a concentrated type. In these cases for *concentration*, or *concentrated*, read *acceleration*, or *accelerated*, as that word is more in accord with the principle involved.

Page 314, line 14, for *overlying*, read *underlying*.

Page 330, line 5, for *Leioptera*, read *Leiopteria*.

Page 333, line 8, from bottom of page, for *shortening its length*. *It*, read *then shortening its length, it*.

Page 334, paragraph 3, line 13, for *exists*, read *were existent*.

Page 335, paragraph 3, line 10, for *at that time*, read *therefore*.

Page 336, paragraph 3, line 8, for *specimen if kept*, read *specimen kept*.

Page 336, paragraph 3, line 12, for *condition*, read *stage*.

Page 337, paragraph 2, line 4, for *If one break the byssus loose it*, read *If the scallop breaks loose, the byssus*.

Page 338, paragraph 2, line 6, for *over*, read *at*.

Page 345, line 6, for *Actinoptera*, read *Actinopteria*.

Page 361, description of cut, for *60*, read *30*.

Page 366, line 3, for *adults*, read *young shells*.

Page 370, paragraph 3, line 12, for *VIII* read *VII*.

XVII. LIST OF PAPERS QUOTED OR REFERRED TO IN THE TEXT.

In the text, numbers in parentheses referring to this list are appended to references when there is need of it, as when there are several references from one author in this list, or when with few references, there might be ambiguity as to which one is referred to. When but one reference is given in the list, or the reference intended is clear from the context, no number is appended in the text.

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XVIII. EXPLANATION OF PLATES.

The figures which illustrate this paper were drawn by Mr. J. H. Emerton or the author, with a few exceptions which are noted in the descriptions. All figures of microscopic material were either drawn directly from specimens with the aid of a Zeiss camera lucida, or were redrawn from camera drawings. The locality and date of collecting specimens are indicated in the description of figures excepting cases where those facts are given in the text. The magnification of figures and the principal references to the pages in the text where the figures are described or discussed are given as an aid to readers. Specimens figured in the plates or text, unless otherwise mentioned, are in the collection of the author. I have to thank Mr. Emerton for the pains he has taken in drawing the figures which largely illustrate this paper.

Besides the plates the following figures illustrate the text:

Figs. 1-8. <i>Orthoceras elegans</i> and <i>O. politum</i> , protoconch and apex of conch, by kindness of Professor Hyatt,	p. 292.
Fig. 9. <i>Vermetus radricula</i> , adult,	p. 294.
Figs. 10-18. <i>Ostrea edulis</i> , embryology,	p. 295.
Figs. 19-22. " " " "	p. 297.
Figs. 23-24. " " " "	p. 299.
Fig. 25. " " " "	p. 300.
Fig. 26. <i>Ostrea edulis</i> , prodissoconch,	p. 312.
Figs. 27-29. <i>Ostrea edulis</i> , the spat,	p. 314.
Figs. 30-31. <i>Perna ehippium</i> , young,	p. 329.
Figs. 32-34. <i>Avicula sterna</i> , "	p. 330.
Fig. 35. <i>Cassianella decussata</i> , young,	p. 332.
Fig. 36. <i>Vulsella rugosa</i> , young,	p. 332.
Fig. 37. <i>Pecten irradians</i> , adult,	p. 333.
Figs. 38-39. <i>Pecten magellanicus</i> , young,	p. 348.
Fig. 40. <i>Pecten dislocatus</i> , shell structure of young,	p. 348.
Figs. 41-42. <i>Anomia glabra</i> , adult,	p. 354.
Fig. 43. <i>Anomia aculeata</i> , young,	p. 361.
Fig. 44. <i>Unio cariosus</i> , glochidium,	p. 367.
Fig. 45. <i>Margaritana undulata</i> , glochidium,	p. 367.
Fig. 46. <i>Anodon cygnea</i> , glochidium,	p. 367.
Fig. 47. <i>Anodon fluviatilis</i> , glochidium,	p. 367.
Fig. 48. <i>Margaritana undulata</i> , young,	p. 367.
Fig. 49. <i>Anodon fluviatilis</i> , young,	p. 367.
Fig. 50. <i>Saxicava rugosa</i> , young,	p. 372.
Fig. 51. <i>Rhombopteria mira</i> , adult,	p. 380.
Fig. 52. <i>Malleus vulgaris</i> young,	p. 383.
Fig. 53. <i>Pinna</i> sp. indet., young,	p. 385.

Figs. 9, 37, 41 and 42 are electrotypes furnished by the kindness of Professor A. E. Verrill. Figs. 10 to 24 and 26 to 29 inclusive are electrotypes furnished by the kindness of Colonel MacDonald, United States Commissioner of Fisheries.

PLATE XXIII.

- Fig. 1. Embryo of *Patella* in the morula or mesembryo stage. Fig. 1a is an optical section of a similar stage (after Patten). p. 291.
- Fig. 2. Embryo of *Paludina*, gastrula, or metembryo stage: *g*, gastrula invagination; *m*, mesoderm cells (after Butschli). p. 291.
- Figs. 3-4. Embryo of *Patella*, trochosphere or neoembryo stage viewed from the dorsal side. In the middle of this region the shell gland appears. Fig. 4 is a similar specimen viewed from the opposite or ventral side: *b*, blastopore (after Patten). pp. 288, 291.
- Fig. 5. Embryo of *Pisidium pusillum*, typembryo stage: *s*, shell gland; *m*, mouth; *a*, anus; *f*, foot. p. 291.
- Fig. 6. Embryo of *Pleurobranchidium*, typembryo stage: *s*, shell gland and beginning of shell; *v*, velum; *m*, mouth; *f*, foot. p. 291. (Figs. 5-6, after Lankester.)
- Figs. 7-8. Glochidium of *Anodon fluviatilis*, from the gill cavities of the parent: *ad*, adductor muscle. This period is referable to the phylembryo stage. The shell has a straight hinge line, and the remarkable spurs, *sp*, on its ventral border. Fig. 8 is a different view of a similar specimen. Medford, November, 1888. × 75 diam. pp. 301, 312, 367.
- Fig. 9. Developing *Modiolaria marmorata*, phylembryo stage: *ad*, anterior adductor muscle, which alone exists at this stage; *m*, mouth; *s*, shell, which has a straight hinge line.
- Fig. 10. Developing *Cardium exiguum*, phylembryo stage: *ad*, anterior adductor, which alone exists at this stage; *v*, velum; *m*, mouth; *i*, intestine; *a*, anus; *s*, shell, which has a straight hinge line.
- Fig. 11. Developing *Montacuta ferruginosa*, phylembryo stage: *ad*, anterior adductor muscle, which alone exists at this stage; *v*, velum; *m*, mouth; *a*, anus; *f*, foot; *r, r, r*, retractor muscles of the velum; *s*, shell, which has a straight hinge line. (Figs. 9-11 after Lovén.) Figs. 9-11, pp. 280, 289, 291, 312, 375.
- Fig. 12. Adult *Slava fibrosa*, showing a very marked change in form of the shell: *n*, neologic stage; *e*, epheboic stage (after Barrande), life size. pp. 293, 294.
- Fig. 13. Developing Dentalium, phylembryo stage: *v*, velum; *s*, saddle-shaped shell. pp. 289, 291.
- Fig. 14. Developing Dentalium, older than fig. 13. The completed periconch stage, comparable to the period of the completed protoconch in Gasteropods, etc.: *v*, velum; *s*, shell. (Figs. 13-14, after Lacaze-Duthiers.) pp. 289, 293.
- Fig. 15. Young *Goniatites compressus*: *p*, ovoid protoconch, succeeded by true conch.¹ pp. 291, 311, 375.

¹From Hyatt (27) after Sandberger.

- Fig. 16. Young *Goniatites canaliculatus*, var. *gracilis*: *p*, globular protoconch, succeeded by true conch.¹ pp. 291, 311.
- Fig. 17. Young Pteropod: *p*, ovoid protoconch (after Bronn). p. 291.
- Fig. 18. *Tentaculites acuarius*, Richter: *p*, protoconch (after Fischer). p. 291.
- Fig. 19. Developing *Sycotopus canaliculatus*, completed protoconch stage: *h*, heart; *f*, foot; *v*, velum. The shell shows distinct lines of growth (after camera drawing by the author). × 24 diam., pp. 289, 291, 375.
- Fig. 20. Developing *Sycotopus canaliculatus*, a period much later than the close of the protoconch stage yet still retaining a velum, *v*, which is enormously developed, and has a ramifying muscular system, shown in the figure: *f*, foot; *t*, tentacles; *e*, eyes and *m*, mouth. × 12 diam., p. 289. Figs. 19–20 from egg cases, Buzzards Bay, September, 1889 (after camera drawing by the author).
- Fig. 21. Young *Crepidula fornicata*: *p*, spirally twisted protoconch, succeeded by the sub-conical nepionic growth. Buzzards Bay. × 24 diam., pp. 292, 293.
- Fig. 22. *Crepidula fornicata*, a series of adult specimens growing on one another and with axes arranged in relation to currents. An oyster is attached to the base of the colony. Buzzards Bay. Life size, p. 354.
- Fig. 23. *Crepidula fornicata*, much younger than fig. 21: *p*, the protoconch, which is sharply defined, is succeeded by the early nepionic growth. Nantucket, July, 1889. × 24 diam., pp. 292, 311.
- Fig. 24. Young *Acmaea testulinialis* var. *alveus*. Interesting as showing instead of a protoconch, a plug-like cicatrix, *c*, formed where the protoconch delisced. The cicatrix corresponds in form with the base of a typical protoconch. (Compare with fig. 23). × 87 diam., pp. 292, 293.
- Figs. 7, 8, 17, 18, 23 and 24 drawn by the author; all others drawn by Mr. J. H. Emerton.

PLATE XXIV.

- Fig. 1. Embryonic *Ostrea virginiana*, growing on a plate of glass from a drain-pipe trap. It is the completed prodissoconch stage and dimyarian: *a. ad*, anterior adductor muscle; *p. ad*, posterior adductor; *g*, gills, which consist of simple filamentous processes (compare with fig. 6); *v*, velum; *pl*, palps; *a*, anus; *m*, mantle border, which is broad and bears no tentacles. The shell is wholly prodissoconch growth, no spat growth having taken place, and is cemented to the glass by the ventral border of the left valve. The early straight hinge line similar to that of *Ostrea edulis*, fig. 25, p. 300, is lost and superseded by a curved one. × 120 diam., pp. 282, 300, 308, 378.
- Fig. 2. Same specimen as fig. 1, viewed from the left side through the glass to which attached; lettering as in fig. 1.
- Fig. 3. *Ostrea*, the same specimen as figs. 1 and 2, but three days older: *pl*, palps; *r*, rectum; *g*, gills, which at this stage are composed of filaments connected at the tips by cross connecting bars; *m*, mantle border, broad and not yet possessing marginal tentacles; *p*, the prodissoconch, which equals nearly half the entire height of the shell. Redrawn from camera drawing by the author. p. 304.
- Fig. 4. *Ostrea virginiana*, young spat growing on glass: *ad*, adductor muscle; *pl*, palps. The body is permeated with liver follicles; *g*, gills. Three gill lamellæ are in view, *A*, *A'*, *B'*, for an understanding of which see fig. 8. In the early growth of the right, outer gill *B'*, no corresponding gill *B* exists on the left side; *st*, stomach; *int*, intestine; *a*, anus; *h*, heart; *v*, large blood vessel passing to mantle border; *c, d*, foramina through which afferent blood passes to heart; *m*, mantle border fringed with tentacles; *rm*, radial muscles which retract the mantle; *s*, a sinuosity in the upper right valve, exists at this point; the mantle is constantly retracted and all excurrent action takes place through this sinuosity as indicated by arrows; *p*, prodissoconch. Redrawn from camera drawing by the author. × 12 diam., pp. 305, 307.
- Fig. 5. Gill plate from a young oyster of age of fig. 4, showing filaments joined by cross connecting bars. p. 305.
- Figs. 6–12. Diagrams of gills of developing *Ostrea* and adult *Perna*, *Anomia* and *Pecten*. The filaments in all are lettered the same so as to show the relation of the several diagrams: *A*, direct filament of inner gill of left side; *a*, reflected border of same filament; *A'*, direct filament of inner gill of right side; *a'*, reflected border of same filament; *B*, direct filament of outer gill on left side; *b*, reflected border of same filament; *B'* direct filament of outer gill of right side; *b'*, reflected border of same filament.
- Fig. 6. Gills of young *Ostrea virginiana*, age of figs. 1–2, this plate, pp. 301, 303.
- Fig. 7. Gills of *Ostrea*, later stage, age of fig. 3, this plate, p. 304.
- Fig. 8. Gills of *Ostrea*, still later stage, age of fig. 4, this plate, p. 305.
- Fig. 9. Gills of adult *Ostrea*, see Pl. xxv, fig. 12, p. 306.
- Fig. 10. Gills of adult *Perna ephippium*, see Pl. xxv, fig. 11. pp. 304, 326.
- Fig. 11. Gills of adult *Anomia glabra*, p. 358.
- Fig. 12. Gills of adult *Pecten irradians*, pp. 336, 341.
- Figs. 13–16. *Ostrea edulis*, early phylembryonic stage of shell growth; 13, viewed from the right side; 14, from the ventral border; 15, from the left side; and 16, in end view. Compare with fig. 25, p. 300, an anatomical figure of about the same age. The shell has a straight hinge line and only a slight indication of umbos. From the gill chamber of the parent. × 120 diam., pp. 299, 312, 375.
- Fig. 17. *Ostrea virginiana*, completed prodissoconch stage, viewed from the upper right side, the specimen being already cemented to an object of support: *r*, right valve; *l*, left valve. Compare with fig. 26, p. 312. × 87 diam., pp. 312, 378.
- Fig. 18. A specimen slightly older than fig. 17, viewed from the anterior end: *l*, left valve; *r*, right valve; *s*, spat growth, which has begun along the margin of the prodissoconch valves. × 87 diam., pp. 312, 315.
- Fig. 19. Young *Ostrea virginiana*. Tip of left valve from inside whorls of a dead *Sycotopus*, where it was preserved from

¹From Hyatt (27) after Sandberger.

all eroding action: *p*, prodissoconch; *s*, spat growth; *l*, cartilage pit; *f*, flange-like extension of margin of the shell extending over the object of fixation; *b*, border of shell proper, exclusive of flange. $\times 87$ diam., pp. 315, 329.

Fig. 20. Young *Ostrea virginiana*, growing on glass, viewed from right side, showing *p*, left and right valves of prodissoconch, and *s*, the first stages of spat growth. $\times 24$ diam., p. 315.

Fig. 21. Same specimen as fig. 20, viewed from the left side through the glass to which attached: *p*, prodissoconch; *s*, spat growth. p. 315. Figures 17 to 21 are of specimens from Buzzards Bay.

Fig. 22. *Gryphæa arcuata*, umbos of shell showing flat area of early fixation in left valve and corresponding convex area of right. Specimen from Lower Lias; in Museum of Comparative Zoölogy. $\times 11$ diam., p. 317.

Fig. 23. *Gryphæa culceola*, var. *nebrascensis*, showing a flat area of early attachment in this highly arcuate species and a prodissoconch, *p*. Jurassic of Wyoming, specimen No. 1881, U. S. National Museum. $\times 11$ diam., pp. 313, 317.

Fig. 24. Same specimen as fig. 23, viewed from in front.

Figs. 3-4 and 22-24 drawn by Mr. J. H. Emerton; figs. 17-18 drawn by Mr. F. W. Cobb; all other figures drawn by the author.

PLATE XXV.

Fig. 1. Young *Ostrea virginiana*, growing on glass, viewed from the right side: *p*, left and right valves of prodissoconch; *1s*, *2s*, limits of first and second spat or nepionic stages.

Fig. 2. Same specimen as fig. 1, viewed from the left side through the glass to which attached: *p*, left valve of prodissoconch; *1s*, *2s*, limits of first and second spat or nepionic stages; *l*, margin of left valve, beyond which the right (upper) valve extends. Figs. 1 and 2, $\times 24$ diam., p. 315.

Fig. 3. Young *Ostrea virginiana*, viewed from the hinge area: *p*, prodissoconch; *lc*, left valve; *rc*, right valve; *s*, early spat growth. The left valve has not yet flattened to the object of attachment. $\times 120$ diam., p. 315.

Fig. 4. Young *Ostrea virginiana* viewed from right side, the specimen being attached to a shell: *p*, prodissoconch, succeeded by *s*, the early spat or nepionic growth. $\times 98$ diam., pp. 311, 315

Fig. 5. Young *Ostrea virginiana* separated from a glass slide on which it had grown and viewed from right upper side: *p*, prodissoconch; *1s*, *2s*, *3s*, *4s*, four spat or nepionic stages of growth clearly indicated in this specimen; *si*, a sinuosity in the right valve where excurrent action takes place. Compare with left view of same specimen, fig. 6. $\times 8$ diam., pp. 307, 316.

Fig. 6. Same specimen as fig. 5, but viewed from the left side, by which it was attached to the glass before removal. The left valve is seen to overhang the right on its free borders; at *si*, the excurrent sinuosity of the right valve is very noticeable in this figure, and four nepionic stages are marked in this valve as in the right valve. p. 316. Figs. 1-6, inclusive, are of specimens from Buzzards Bay.

Fig. 7. Young *Ostrea virginiana* from Provincetown, Massachusetts, showing nepionic or spat stages of growth of the right valve (*1s*, *2s*, *3s*, *4s*, *5s*). The first two stages were drawn from a younger specimen, as they were worn off in the specimen at hand. $\times \frac{1}{3}$ diam. p. 316.

Fig. 8. *Ostrea virginiana*. Two adult individuals fixed to the same object of attachment. The left hand specimen is growing in the normal position with the right valve uppermost, and the left valve lowermost. The right hand specimen is growing in a reversed position with the right valve lowermost, and the left valve, uppermost; in both the same relative form of the valves is maintained. Buzzards Bay. $\times \frac{1}{3}$ diam., pp. 316, 321.

Figs. 9-12. Revolution of the axes, showing the relations of the axes of the body to the shell in typical Pelecypods, and the serial mechanical relation of the same. Lettering in the figures: *ap. ax.*, antero-posterior axis, drawn through the mouth and middle of the posterior adductor muscle; *h. ax.*, hinge axis, the axis of motion of the valves; *a. ad.*, anterior adductor muscle; *p. ad.*, posterior adductor; *m*, mouth; *pl*, palps; *a*, anus; *g*, gills; *pd*, pedal muscles; *f*, foot; *b*, byssus; *h*, heart.

Fig. 9. *Mya arenaria*, p. 309.

Fig. 10. *Modiola plicatula*, p. 309.

Fig. 11. *Perna ephippium*, pp. 309, 329.

Fig. 12. *Ostrea virginiana*, pp. 305, 308, 327.

Fig. 8, drawn by the kindness of Mrs. J. W. Elliot; all other figures drawn by the author.

PLATE XXVI.

Fig. 1. *Spondylus hippuritarum*, having a highly modified, deep, attached valve and less modified free valve. European Cretaceous (after d'Orbigny). pp. 319, 323, 351.

Fig. 2. *Chamostrea albida*, showing an ostreaform, cemented valve and flatter free valve (after H. & A. Adams). p. 323.

Fig. 3. *Hinnites cortesi*, right valve, showing an early nealagic, regular pecteniform stage, possessing a byssal sinus, which is succeeded, when the shell becomes attached to a foreign body, by an irregular ostreaform growth, possessing no byssal sinus, and losing almost entirely the features characteristic of early stages. pp. 282, 293, 294, 324, 350 and 390.

Fig. 4. *Hinnites cortesi*, left valve, showing an early regular pecteniform shell, as does the right valve, fig. 3. When the

shell becomes attached, the left valve, acting in sympathy with the right, becomes somewhat irregular in growth; but is less modified than the right by the new condition of cemented fixation. Life size, p. 324. Both specimens from the European Tertiary, in the Museum of Comparative Zoölogy.

Fig. 5. *Mulleria lobata*, showing adult oyster-like form and at the tip of umbos a regular Anodon-shaped shell preceding the attached stage (after H. & A. Adams). pp. 310, 324.

Figs. 6-7. *Mulleria lobata*. Tips of the valves magnified to show the early stage, viewed from the dorsal and left side (after Bronn). pp. 310, 324.

Fig. 8. *Caprinula boissyi*, having a deep, conical, rugose, attached valve and an arcuate, plain, free valve. European Cretaceous. pp. 282, 319, 323.

Fig. 9. *Monopleura marcida*, showing a highly modified attached valve and a normal free valve. American Cretaceous (after White (74), slightly modified). pp. 319, 323.

Fig. 10. *Caprotina semistriata*, showing a deep, rugose attached valve and shallow, plain, free valve. European Cretaceous. Compare with fig. 20, a young specimen of this species. pp. 319, 323.

Figs. 11-12. *Radiolites fleuriausa*, having a highly modified, cornucopia-shaped, attached valve, fig. 12, and a less modified flattish free valve, fig. 11. European Cretaceous, pp. 319, 324 (figs. 8 and 10-12, after d'Orbigny).

Fig. 13. *Ostrea virginiana*, section showing the deep, concave, cemented valve, and flat free valve: *l*, lacunæ in the sub-nacreous structure are filled with chalky lime; *ad*, adductor muscle, which makes a purple scar at its area of insertion in the valves. The black line indicates the position of the adductor at different periods of growth, and is very noticeable in the section, being marked by a continuous purple line. An instructive section to show action of adductor muscle, ligament, growth of shell and change of base of the muscle in successive growth. Buzzards Bay. Life size, p. 320.

Figs. 14-15. *Davidsonella rugosa*, sp. d'Orb., showing rugose, lower, attached valve (fig. 14) and a flat free valve (fig. 15), indicating that cementation in Brachiopods produces a similar result to that in Pelecypods. European Cretaceous (after d'Orbigny). p. 320.

Fig. 16. *Perna ephippium*, adult, pp. 327, 329, 383.

Fig. 17. *Perna isogonum*, p. 327.

Fig. 18. *Perna vesperilio*, p. 327.

Fig. 19. *Malleus albus*, adult. pp. 327, 383 (figs. 16-19 after Reeve, reduced).

Fig. 20. Young *Caprotina semistriata*, from the Cretaceous. The lines of growth are introduced according to judgment to render the parts clear, as the specimen is too much eroded to show them. Compare with the adult, fig. 10, this plate. Specimen No. 2902 in collections of the Museum of Comparative Zoölogy. × 24 diam. pp. 319, 385.

Fig. 20 drawn by the author; all others drawn by Mr. J. H. Emerton.

PLATE XXVII.

Fig. 1. Young *Perna ephippium*, viewed from left side, showing, *p*, prodissoconch and succeeding dissoconch growth. Compare with *Pecten*, Pl. xxviii, fig. 9 and *Avicula*, fig. 32, p. 330. The form of the shell is strikingly different from the adult, Pl. xxvi, fig. 16. Specimen from Museum of Comparative Zoölogy. × 50 diam. (another view of this specimen, see Pl. xxviii, fig. 11). pp. 328, 379, 383.

Fig. 2. Young *Perna ephippium*, viewed from the right side, showing, *p*, prodissoconch and succeeding dissoconch growth. The byssal notch originates at the close of the prodissoconch period in the initial stages of dissoconch growth. The figure shows the margin of left valve extending beyond the right in the byssal area and several threads of the byssus. Specimen from Boston Society of Natural History Collections. Cat. No. 2989. × 24 diam., p. 328.

Fig. 3. *Perna ephippium*, same specimen and view as fig. 2, showing the prodissoconch, *p*, and the early stages of growth of the right dissoconch valve. It is seen in figs. 2 and 3, that as in *Pecten* the left valve in early stages is larger than the right, and overhangs it at the umbos. × 87 diam., p. 328.

Fig. 4. Young *Spondylus asperimus*, tip of right attached valve: *p*, prodissoconch; the succeeding early dissoconch growth is pecteniform with a deep byssal notch; as soon as attached the growth becomes irregular, the pecteniform shape and byssal notch being eradicated. Compare with *Hinnites*, Pl. xxvii, fig. 3. Specimen in Boston Society of Natural History, Cat. No. 8494. × 50 diam., pp. 351, 390.

Fig. 5. Young *Plicatula marginata*, viewed from the left side, showing a prodissoconch, *p*, and succeeding dissoconch growth. Specimen in Museum of Comparative Zoölogy. × 50 diam., pp. 325, 352, 392.

Fig. 6. Young *Lima elliptica*, showing, *p*, prodissoconch, succeeded by the dissoconch growth. Specimen in Smithsonian Institution. From drawing made when at that Museum. Magnified, pp. 353, 388.

Fig. 7. *Oxytoma inequivalvis*, Sow., umbonal region of right valve showing *p*, prodissoconch, succeeded by a dissoconch which has a byssal notch in its initial stages of growth, and a triangular cartilage pit. Compare with *Pecten*, several figs., Pl. xxviii, and *Avicula*, fig. 33, p. 330. Specimen from the Middle Lias in the Museum of Comparative Zoölogy, Cat. No. 9222. × 50 diam., pp. 332, 382.

Fig. 8. *Chlamys islandica*, hinge area of same specimen as Pl. xxviii, fig. 14, viewed from the right side, showing, *p*, prodissoconch, and the byssal notch originating in the initial stages of dissoconch growth. Compare with *Pecten irradians* Pl. xxviii, figs. 10 and 13. The left valve is larger than the right. × 87 diam., p. 344.

Fig. 9. *Pecten irradians*. Umbonal view from left side of a similar specimen to that in Pl. xxviii, fig. 10, more enlarged, showing *p*, prodissoconch, and the byssal notch originating at the close of the prodissoconch stage. × 87 diam., p. 342.

Figs. 4 and 6 drawn by the author; all others drawn by Mr. J. H. Emerton.

PLATE XXVIII.

Fig. 1. Young *Pecten irradians*, viewed from the left side: *ad*, adductor muscle; *g*, gills; *i*, intestine; *a*, anus; *h*, heart; *f*, foot; *p r*, posterior retractor of the foot; *m*, mantle border bearing eyes, *e*; and alternating tentacles, *t*. The shell bears a prodissoconch, *p*, and is of about the age of fig. 12, this plate. Redrawn from camera drawing by the author. $\times 40$ diam., p. 333.

Fig. 2. *Pecten irradians*, older than any other young *Pecten* figured. Shows an active extensible foot; the mantle border bears a single eye in each plication of the shell and alternating with each eye two tentacles (tentacles are omitted in the right mantle lobe for the sake of clearness). Under the dorsal ear a special protrusion of the mantle border (pseudosphon) exists, and at this point all excurrent flow takes place as indicated by the arrow. The shell shows no prodissoconch, but the smooth early nepionic stage is indicated. The plications are as in the adult, fig. 37, p. 333, in number and form. The hinge line is relatively long, and but slight ears are developed. $\times 16$ diam., pp. 335, 345, 387.

Fig. 3. *Pecten irradians*, diagram of a gill filament of adult: *a*, direct border; *a'*, reflected border; *s*, septum connecting direct and reflected border of about every fifteenth filament; *bl*, blade commencing when septum diminishes. Compare with Pl. xxiv, fig. 12. p. 341.

Fig. 4. *Pecten*, diagrammatic section of adult, to show relations of mantle wall and tentacles: *s*, shell; *lig*, ligament; *ad*, adductor; *m*, mantle; *m w*, mantle wall; *e*, eye; *t*, marginal tentacles; *gt*, guard tentacles. p. 338.

Fig. 5. Faces of *Pecten*, seen in section and longitudinally. p. 340.

Fig. 6. *Pecten*, mantle border of fig. 1 enlarged, showing cup-shaped eyes alternating with single papillose tentacles; no mantle wall or guard tentacles are yet developed on the mantle border. pp. 335, 337.

Fig. 7. Young *Pecten*, diagram of foot. In forming the byssal attachment it may lay hold of a foreign object at its tip and at the point of the byssal cleft, arching up between those points as in the figure. p. 337.

Figs. 8, 8a. *Pecten*, diagram to illustrate the swimming. Arrows indicate the several currents of water ejected in swimming as described in the text. p. 339.

Fig. 9. Young *Pecten irradians*, viewed from left side: *p*, prodissoconch, succeeded by the early nepionic stage of the dissoconch. The form of the shell is distinct and differs from all later stages. Compare with *Perna*, Pl. xxvii, fig. 1, and *Avicula*, fig. 32, p. 330. $\times 50$ diam., pp. 333, 342, 379, 387.

Fig. 10. *Pecten*, same specimen as fig. 9, but viewed from the right side. The byssal notch originates with the initial stages of dissoconch growth, it is deep, and has a marginal tooth. The left valve overhangs the right on its free border. Compare with Pl. xxvii, fig. 3, and Pl. xxix, fig. 6. pp. 328, 342.

Fig. 11. *Perna ephippium*, same specimen as Pl. xxvii, fig. 1, viewed from umbonal region: *lv*, left valve; which is slightly larger than *rv*, the right valve. The umbos of the prodissoconch, *p*, are directed posteriorly. $\times 50$ diam., p. 328.

Fig. 12. *Pecten irradians*, older than figs. 9-10, viewed from the left side: *p*, prodissoconch, succeeded by smooth early nepionic growth which gives place to a plicated later growth. The hinge line is proportionately longer than in earlier stages, figs. 9-10, and is also relatively longer than in the adult, fig. 37, p. 333. Very slight indications of ears exist at this stage. $\times 40$ diam., pp. 345, 387.

Fig. 13. *Pecten*, same specimen as fig. 12, viewed from the right side. Description of shell as in fig. 12. A deep byssal notch exists in this valve, originating at the close of the prodissoconch period. Four teeth exist on the border of the notch instead of one as in fig. 10. At this age the left valve has ceased to be produced beyond the border of the right on its free margins, as in fig. 10. The shell as viewed from both sides differs markedly from earlier and later stages in form. p. 345.

All the specimens of *Pecten irradians* figured were collected at Buzzards Bay, August, 1888.

Fig. 14. Young *Chlamys islandica*, viewed from left side, showing, *p*, prodissoconch, and a smooth early nepionic growth, succeeded by a plicated later growth. The plications are like those of the adult and mark a stage by their introduction. The hinge line is longer relatively to the width of the shell at this stage than in the adult as noted in *Pecten irradians*, and has slightly developed ears. Specimen No. 27294, Smithsonian Institution Catalogue. $\times 23$ diam., pp. 349 and 388. An enlarged umbonal view of this specimen seen from the right side, *vide* Pl. xxvii, fig. 8.

Figs. 3-8 drawn by the author; all others drawn by Mr. J. H. Emerton.

PLATE XXIX.

Fig. 1. Young *Anomia glabra*, growing on glass, viewed from the left side: *ad*, adductor muscle; *p r*, posterior retractor and *a r*, anterior retractor muscles of the foot; *f*, foot; *pl*, palps; *a*, anus; *b*, body permeated with liver follicles; *g*, gills. Two gill lamellæ are seen from this side, *A* and *B* (compare with diagram, Pl. xxiv, fig. 11); *s*, sheath supporting gills; *h*, heart; *v, v*, blood vessels; *m*, mantle border; *p*, prodissoconch. p. 355.

Fig. 2. *Anomia*, same specimen as fig. 1, viewed from the right side through the glass to which attached: *ad*, adductor muscle; *a r*, anterior retractor muscle of the foot, attached to the left upper valve, but seen through the glass; *bs*, calcifying byssal tip composed of separate discs of lime which unite to form parallel lines, as shown in the figure; *f*, foot; *pl*, palps, showing slightly in this view; *g*, gills of which three lamellæ, *a, A', B'*, are visible from this side (compare with Pl. xxiv, fig. 11); *s*, sheath which supports the gills; *h*, heart, a ventricle and auricle are visible from this side; *a*, anus; *c*, cæcum, highly produced; *m*, mantle border; *rv*, border of right valve which by a sinuosity encloses the byssus; *lv*, border of left valve. Figs. 1 and 2 magnified about 20 diam. Redrawn from camera drawings by the author. p. 355.

Fig. 3. Diagrammatic cross-section of fig. 1, to show action of the muscles; lettering as in fig. 1. p. 355.

Fig. 4. *Anomia glabra*, very young, viewed from the left side: *p*, prodissoconch, which is on the border of the valve, not yet being enclosed by the dissoconch growth. $\times 50$ diam., p. 359.

Fig. 5. Young *Anomia glabra*, viewed from the left side: *p*, the prodissoconch, is not yet surrounded by dissoconch growth. Compare with figs. 4 and 8. The dissoconch is sub-oval and an extensible foot, *f*, exists. $\times 50$ diam., pp. 355, 389.

Fig. 6. *Anomia*, same specimen as fig. 5, viewed from right side; *p*, the prodissoconch, shows indications of a byssal sinus in the lines of growth. The dissoconch is extremely thin, surrounds the byssal notch and anteriorly has grown around the prodissoconch covering its umbo. The method of growth is indicated by the lines of growth. pp. 359, 388. Compare with Pecten, Pl. xxviii, fig. 10.

Fig. 7. Young *Anomia glabra*, umbonal region of right valve: *p*, the prodissoconch, shows indications of a byssal notch which is accentuated in the succeeding dissoconch growth; the latter finally grows around the byssus so as to enclose it. Compare with fig. 6, this plate, also with Pl. xxvii, fig. 3, and Pl. xxviii, fig. 10. $\times 50$ diam., p. 360.

Fig. 8. *Anomia*, tip of valve, older than figs. 4 and 5 and in the same view. The dissoconch growth has now enclosed the prodissoconch, *p*, and the borders of the opposing sides form a marked area by their ingrowth at the umbo. $\times 50$ diam., pp. 359, 389. Specimens of *Anomia*, figs. 1-8, were collected at Buzzards Bay, August, 1888.

Fig. 9. *Mytilus edulis*, very young: *p*, the prodissoconch, succeeded by early nepionic growth. Beach Bluff, Mass. $\times 50$ diam., p. 363.

Fig. 10. *Mytilus edulis*, older than fig. 9; *p*, prodissoconch, succeeded by nepionic growth. Nantucket. $\times 47$ diam.

Fig. 11. Young *Modiola hamatus*: *p*, prodissoconch, succeeded by a smooth nepionic stage. Later, the smooth nepionic stage is succeeded by the plicated growth typical of the species as shown in Pl. xxx, fig. 1. Specimen on oyster shells from Baltimore, collected at Martha's Vineyard. $\times 50$ diam., p. 364.

Figs. 3, 5, 6, 9, 10 and 11 drawn by the author; all others by Mr. J. H. Emerton.

PLATE XXX.

Fig. 1. *Modiola hamatus*, older than Pl. xxix, fig. 11: *p*, prodissoconch, succeeded by an early plain nepionic stage, which is again succeeded by a plicated later stage. Attached to a cluster of *Pernas* in Museum of Comparative Zoölogy. $\times 50$ diam., p. 364.

Fig. 2. *Argina pexata*, very young, showing a prodissoconch, *p*, and succeeding dissoconch growth. Buzzards Bay, September, 1888. $\times 87$ diam., p. 364.

Fig. 3. *Crenella decussata*: *p*, prodissoconch, succeeded by the early dissoconch growth. Specimen from Smithsonian Institution. $\times 23$ diam., p. 364.

Fig. 4. *Sphærium securis*: embryo from gills of the parent. The whole shell of this specimen represents the prodissoconch period: *a. ad.*, anterior adductor; *p. ad.*, posterior adductor; *g*, gill filaments; *pl.*, palps; *f*, foot; *ol.*, otocyst; *si.*, siphon. Medford, Mass., Nov. 1888. \times about 60 diam., p. 369.

Fig. 5. *Sphærium securis*, a little older than fig. 4, viewed from left side: *p*, prodissoconch, succeeded by early dissoconch growth. \times about 25 diam., p. 369.

Fig. 5a. *Sphærium securis*, a little older than figure 5, viewed from right side: *p*, prodissoconch. $\times 8$ diam., p. 370.

Fig. 6. Young *Petricola pholadiformis*, showing *p*, prodissoconch and succeeding nepionic stage which is strikingly different from later stages: *f*, foot; *m*, mantle border; *si.*, siphons, both with simple, unbranched tentacles. $\times 47$ diam., p. 370.

Fig. 7. *Petricola pholadiformis*, older than fig. 6, shows early nepionic smooth stage succeeded by the later characteristic plicated and elongate features typical of the adult. $\times 8$ diam., p. 371. Figs. 6-7, of specimens from Nantucket, July, 1889.

Fig. 8. *Petricola*, tip of branchial siphon of a specimen of about the age of fig. 7, showing the arborescently branching tentacles which surround the orifice. $\times 19$ diam., p. 371.

Fig. 9. Young *Venus mercenaria*: *p*, prodissoconch, succeeded by early dissoconch growth. $\times 87$ diam., p. 371.

Fig. 10. *Venus mercenaria*, an older specimen than fig. 9, showing a prodissoconch *p*, and succeeding nepionic growth. $\times 40$ diam., p. 371. Figs. 9-10 from Buzzards Bay.

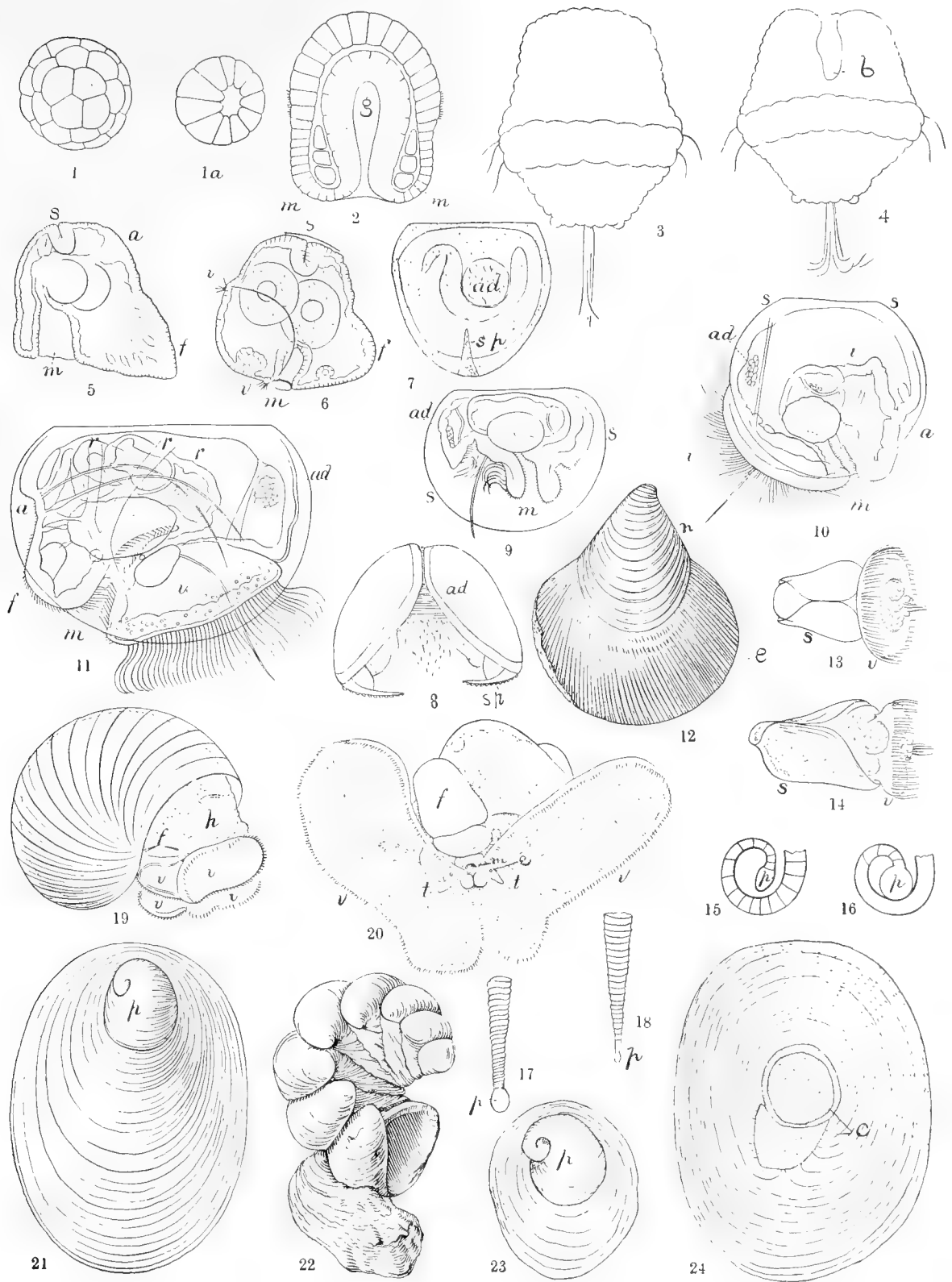
Fig. 11. *Scrobicularia tenuis*: *p*, prodissoconch succeeded by early dissoconch growth. The prodissoconch is not so sharply defined as in many genera, because the early dissoconch is not characterized by markedly differing features. Specimen from Smithsonian Institution. $\times 50$ diam., p. 372.

Fig. 12. *Mya arenaria*, very young: *p*, prodissoconch, and well defined succeeding dissoconch. Buzzards Bay, 1888. $\times 87$ diam., p. 374.

Fig. 13. *Mya arenaria*, older than fig. 12: a prodissoconch, *p*, less clearly defined than when younger, exists at the umbos. The dissoconch growth has acquired characteristics of the genus in form. A large active foot exists. The siphon consists of an extensible excurrent and a short non-extensible incurrent tube. Buzzards Bay. $\times 20$ diam., p. 372.

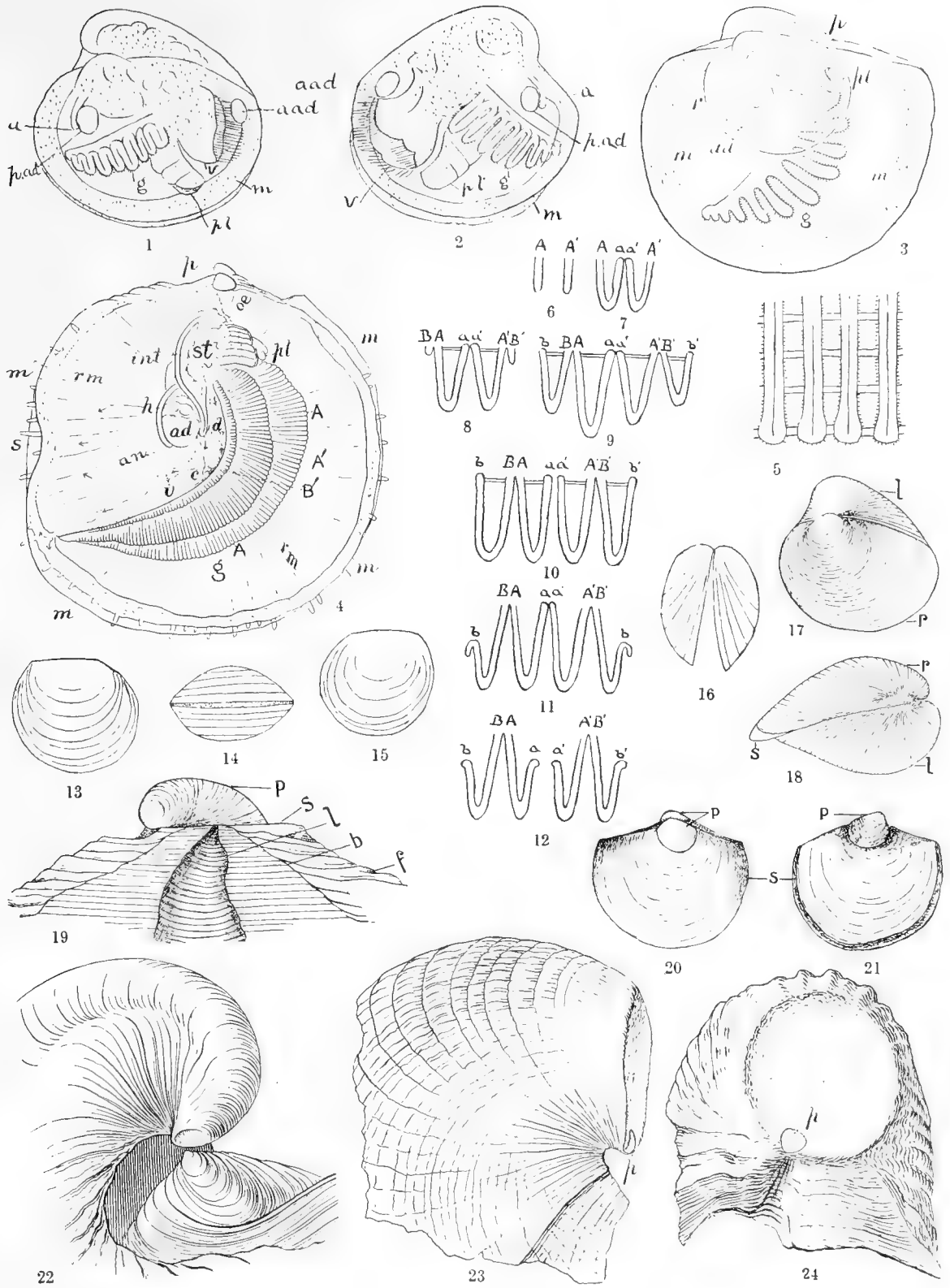
Fig. 14. Siphon of a young clam older than fig. 13. The massive siphon is fringed with tentacles. The incurrent tube is also bordered by tentacles, but the excurrent tube bears none; it is thin walled and retractile: *s*, border of shell from which the siphon extrudes. Chelsea Beach. $\times 10$ diam., p. 373.

Figs. 4 to 8 inclusive, and fig. 14 drawn by the author; all others drawn by Mr. J. H. Emerton.

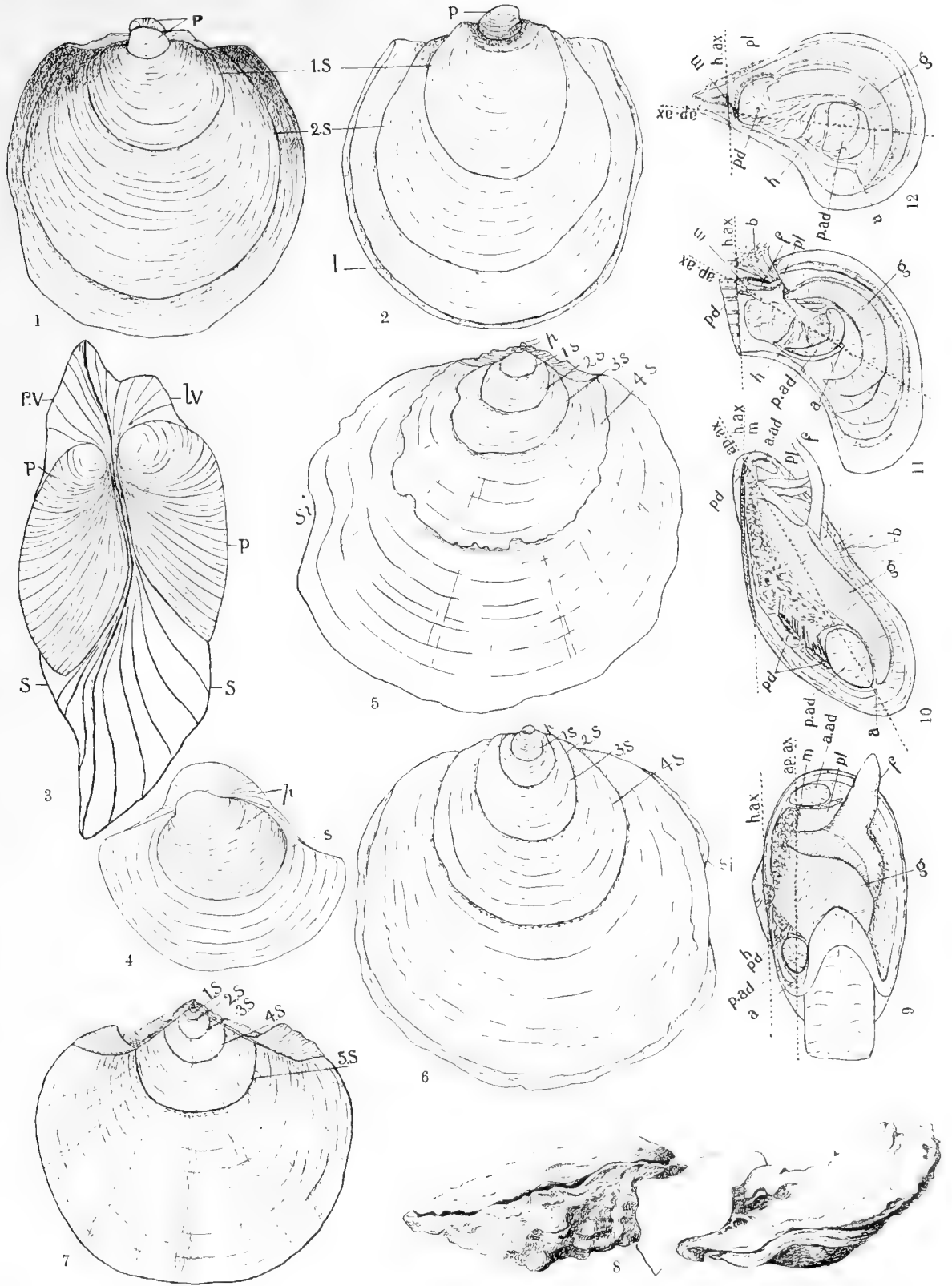


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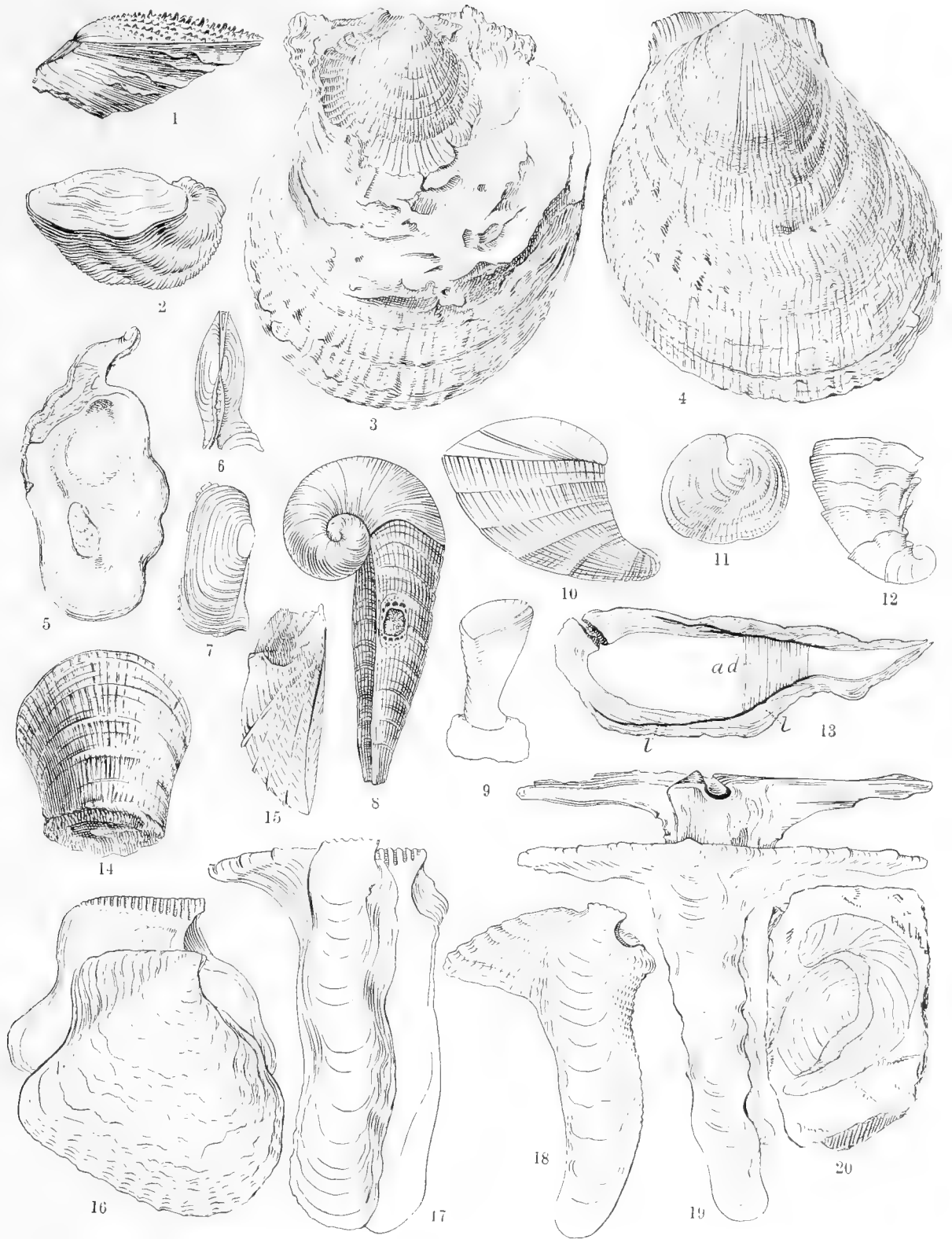


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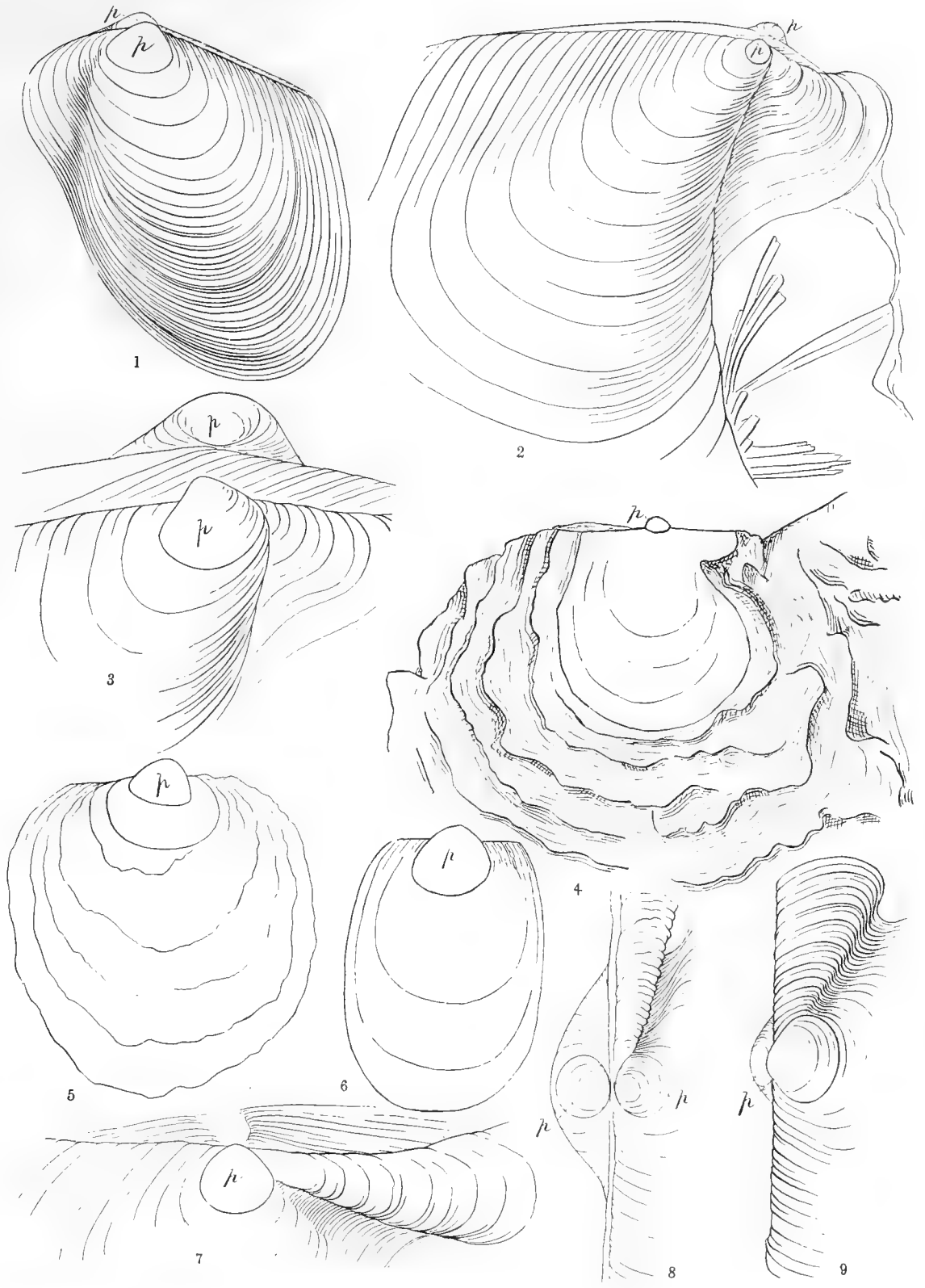
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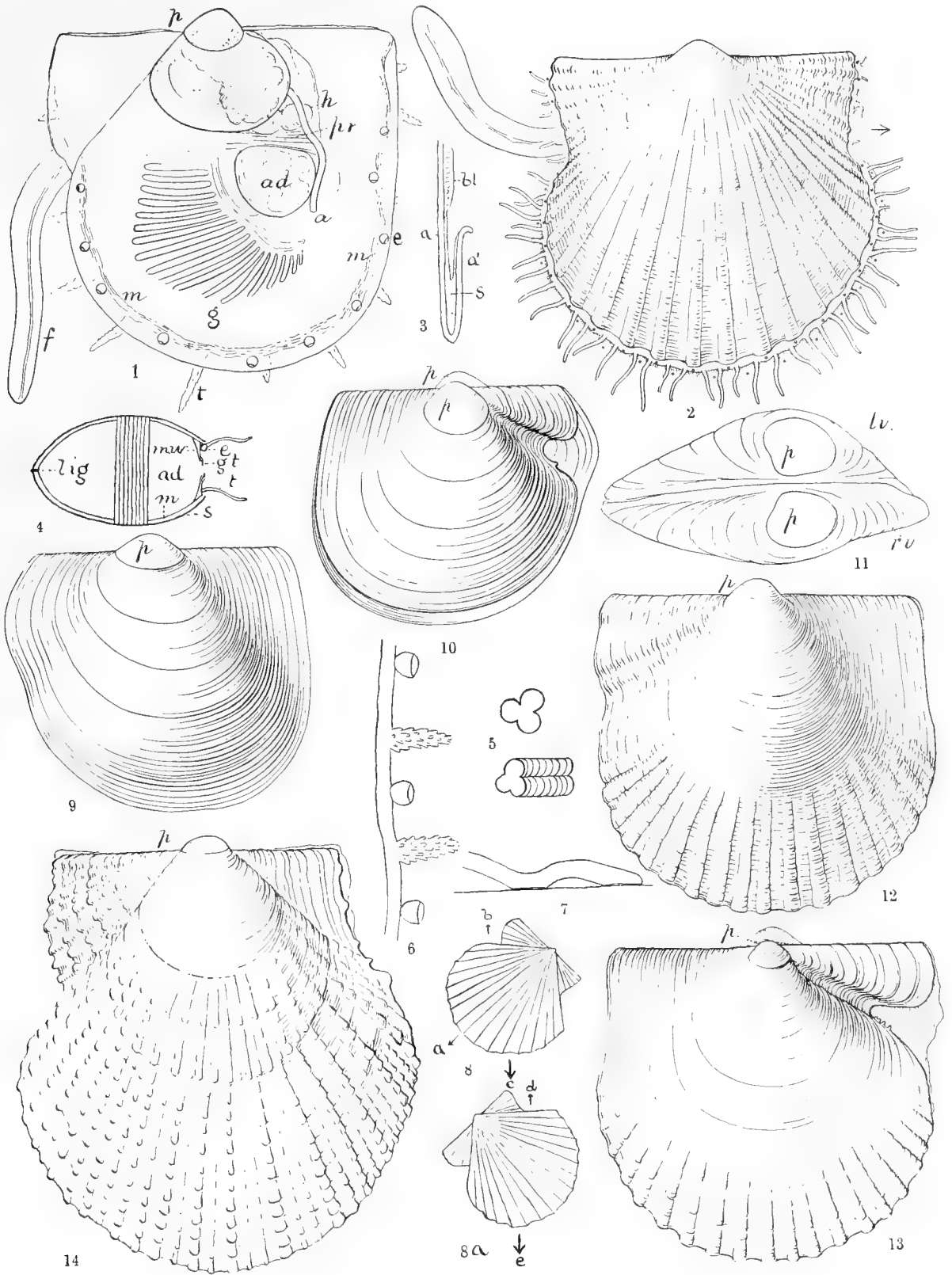


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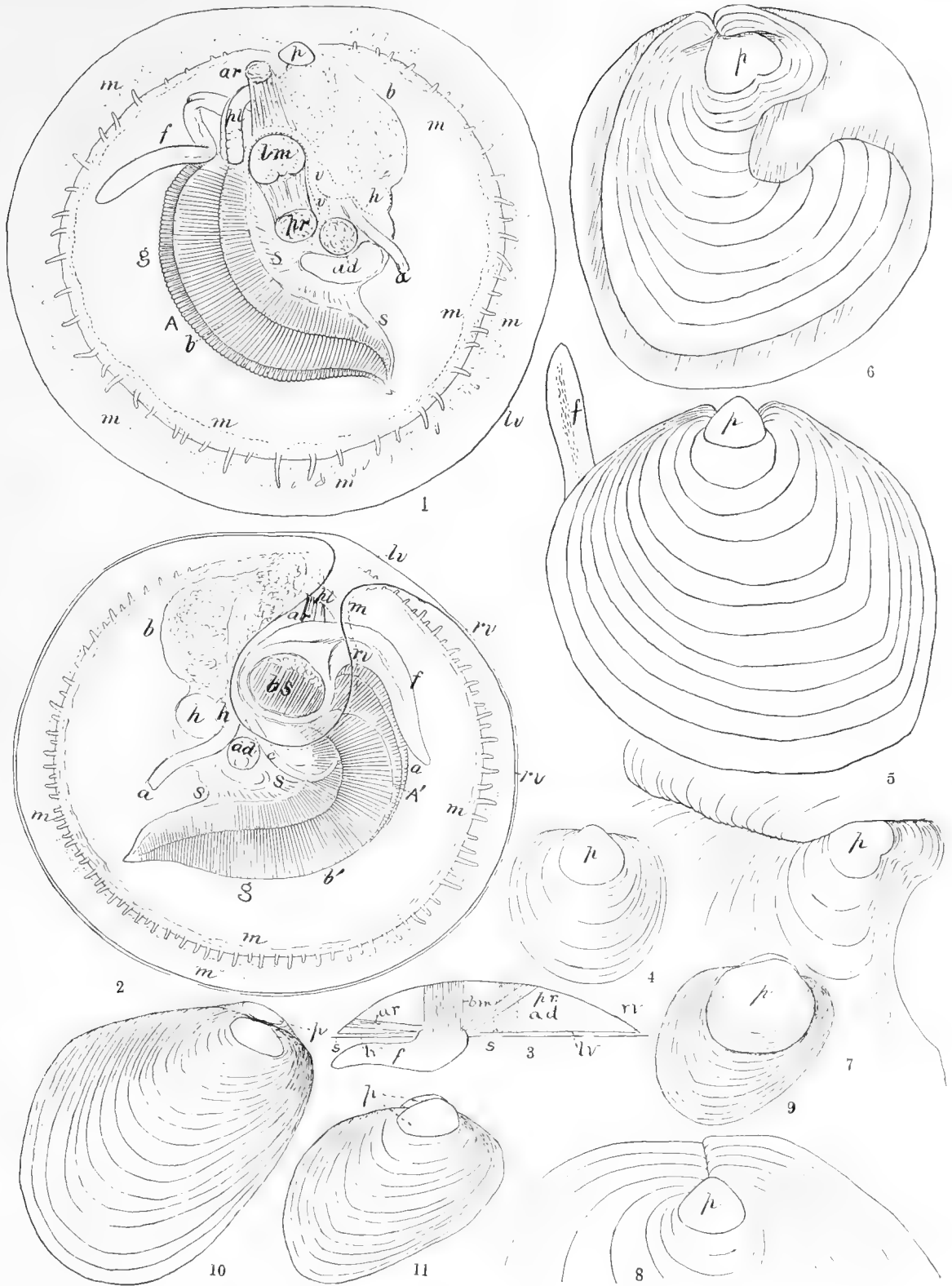


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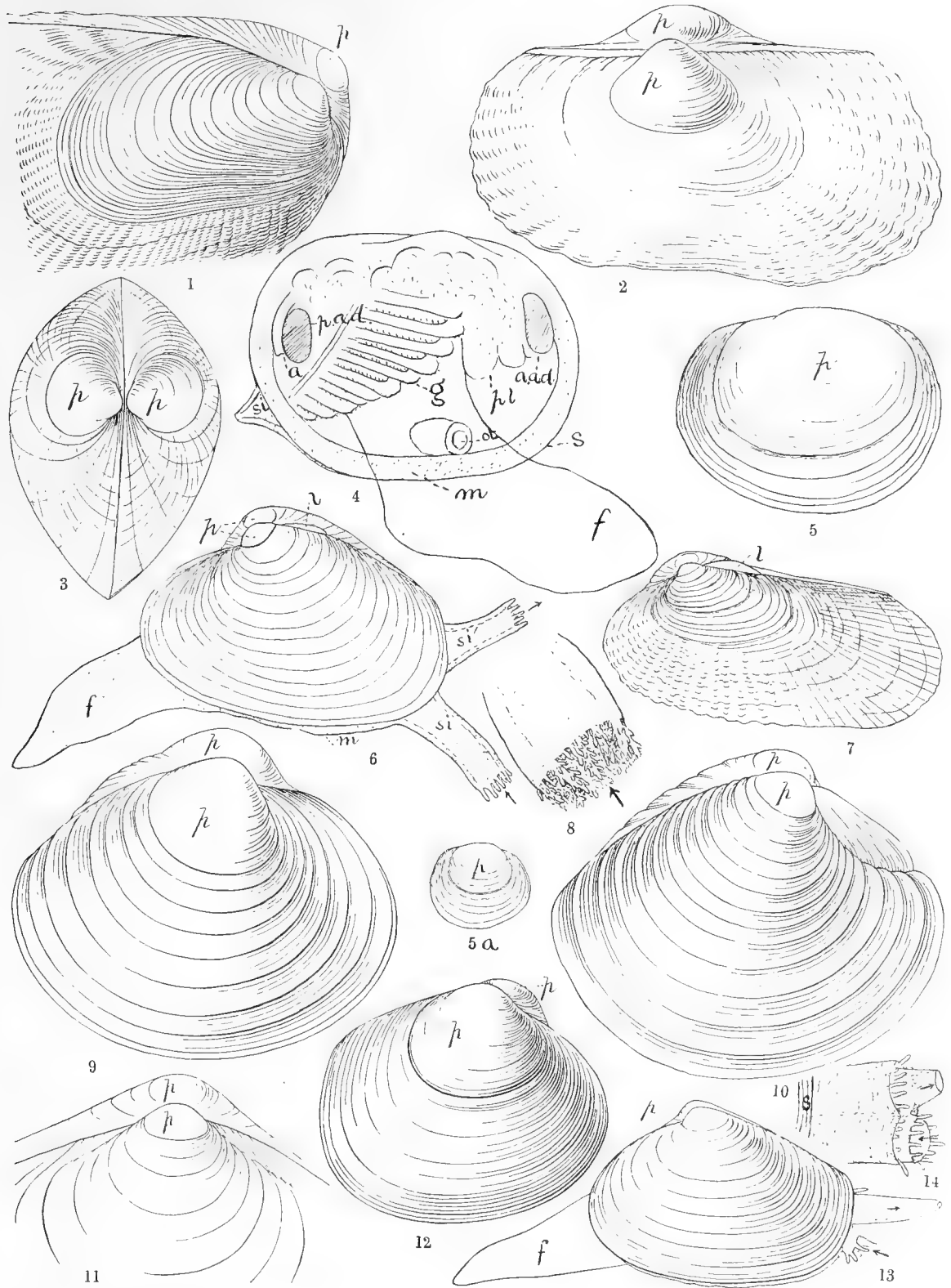


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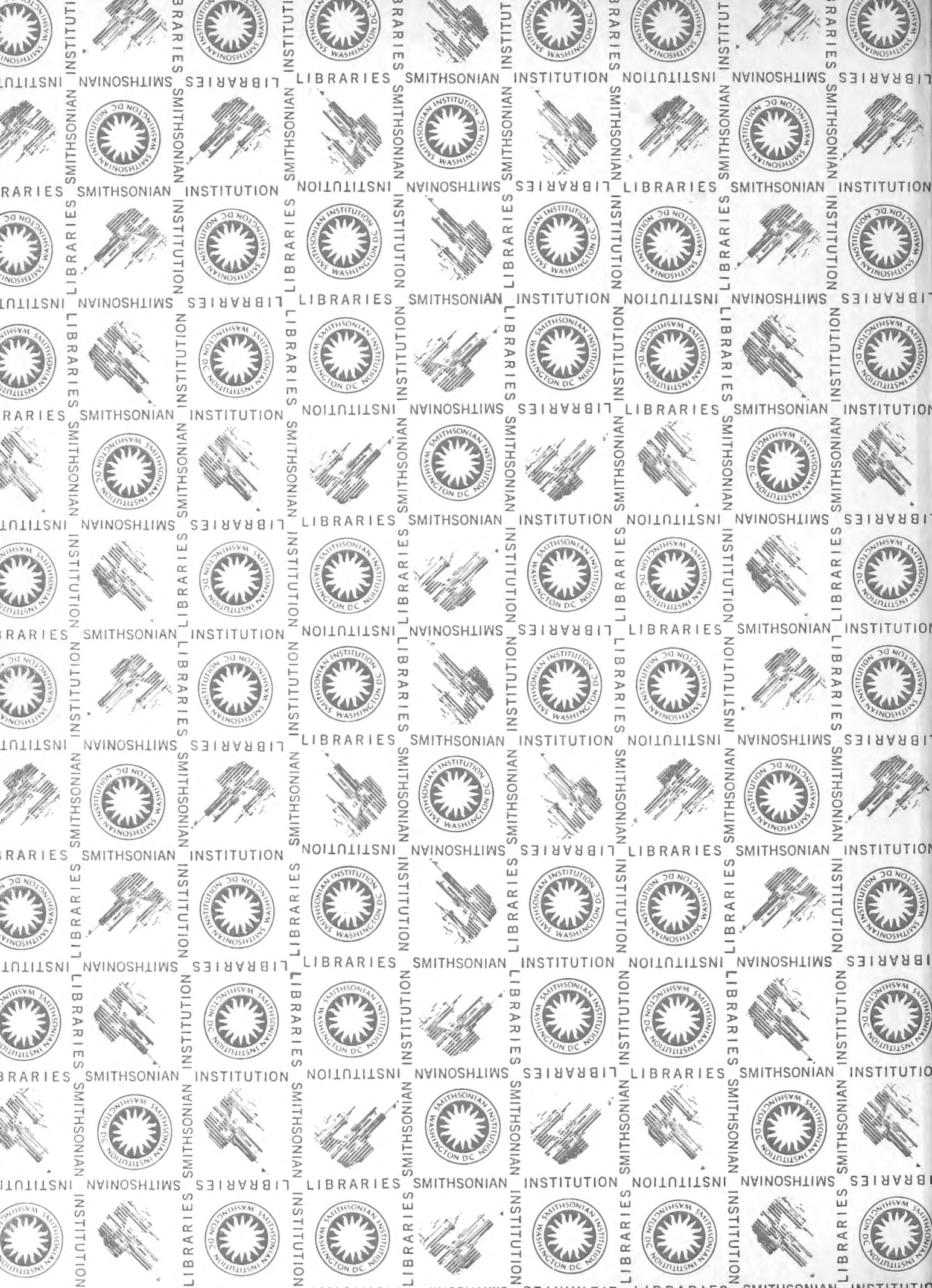
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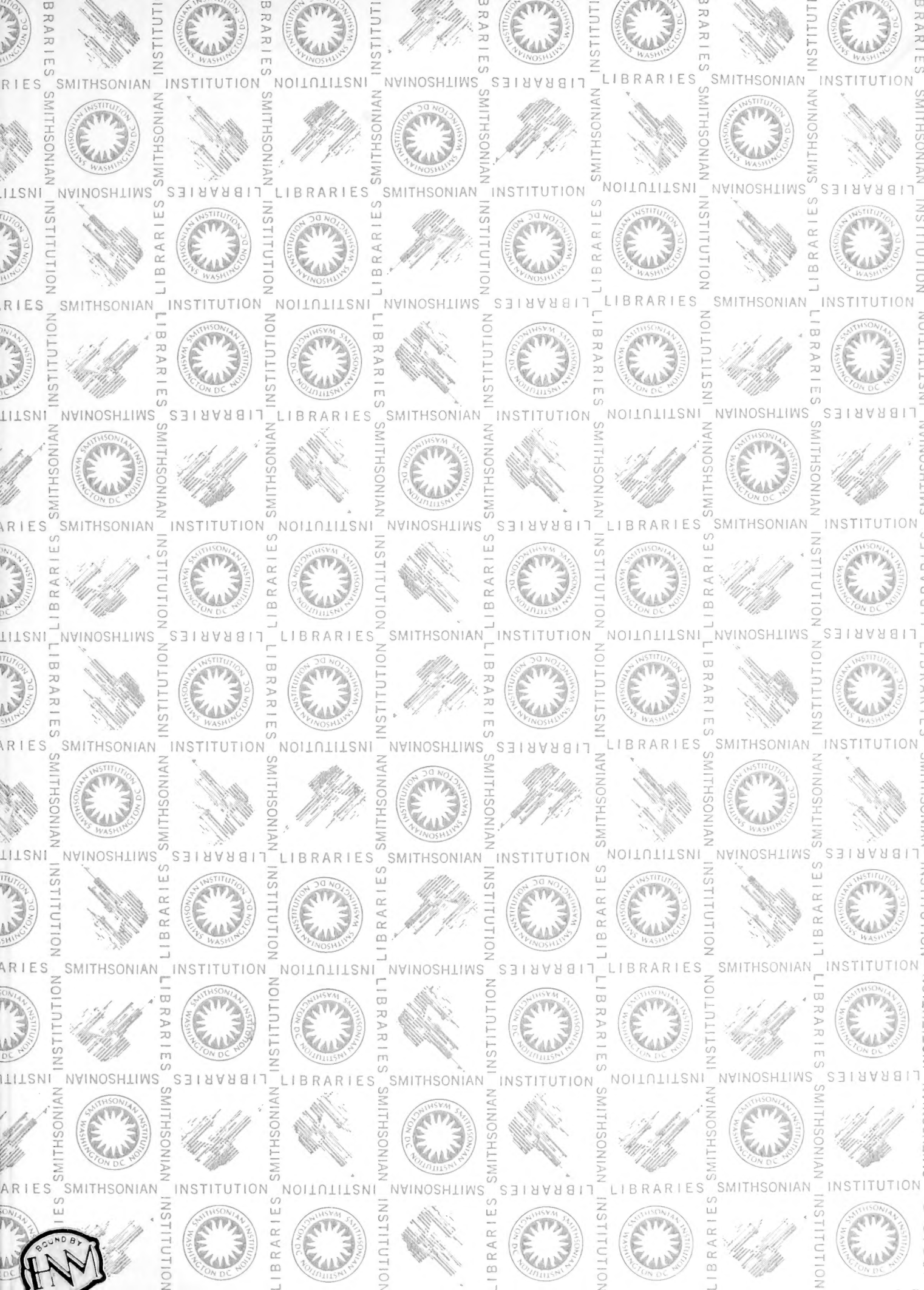
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