ART. LV.—*On the Hinge of Pelecypods and its Development, with an attempt toward a better subdivision of the group;* by WM. H. DALL, Paleontologist, U. S. Geol. Survey, and Curator Dept. of Mollusks, U. S. National Museum.

THE attempt to divide the class *Pelecypoda* or *Lamellibranchiata* into orders has so far been unsuccessful, or at least the subdivisions adopted have from time to time been found unsatisfactory, on account of the discovery of forms which combine in their organization characters which had previously been regarded as diagnostic of important subdivisions, such as orders.

This has resulted from the selection of characters as diagnostic which are really not fundamental in the evolutionary history of the minor groups. As we gradually become acquainted with the mutability of the adductor muscles, the gills, the arrangements for retracting the siphons and other factors in the mechanics of these organisms, the classification based upon their mutations has gradually ceased to satisfy students though one phase or another of it may still retain a place in ordinary text books.

* Reference is not here made to the "Dinosaur Sands" which lie at the base of the Comanche Cretaceous upon both sides of the Paleozoic area in Texas. These beds I have provisionally included in the Lower Cretaceous, but it is probable that they represent the Potomac formation of the Atlantic coast region, and it is regarded as possible that they represent the uppermost Jurassic of Europe.

To cite a few examples it will be remembered that the most persistent of the early systems for classifying these animals was based on the number of adductor muscles or the scars upon the shell by which they might be traced. At first the groups of Monomyarians or forms with one adductor, like the oyster, and Dimyarians with two adductors, like the ordinary edible clam, seemed sufficiently well distinguished. Later when transitional forms like the mussel and its allies were carefully studied a new group, *Heteromyaria* was erected for those which would not fit into either of the others.

But when it is considered that there are forms like *Dimya*, in which with a monomyarian organization two distinct adductors are found, one at each end of the shell; that in *Chlamydoconcha* we have a specially modified animal with no adductors at all; that in *Mulleria* we have the young (not larval) animal typically Dimyarian, and becoming in its adult stage as typically monomyarian in its muscular apparatus as an oyster; then it is sufficiently evident that better and more fundamental diagnostic characters should be found or the so-called orders given up.

Again, an attempt has been made to use the characters of one of the most mutable parts of the whole organism, namely the gill, as a basis for primary divisions of the group. I have shown elsewhere,* I venture to think conclusively, that this selection is ill-advised and cannot successfully solve the problem.

The simplicity or sinuation of the pallial line has been regarded as a character of high importance and has been used as diagnostic of divisions of primary importance. I have recently shown that, in certain groups, long siphons may exist with a simple pallial line, as in *Cuspidaria;* that in species without long siphons, members of the same family (*Poromyidæ*), and perhaps of the same genus, may show a simple or a strongly sinuated pallial line according to the modifications of certain muscular elements which certainly cannot be claimed to have any high systematic importance.

The question is further complicated by the fact that certain characters, which in general are indicative of very early evolutionary divergencies, may be simulated or assumed as very modern special modifications brought about in animals of diverse groups by natural selection under the influence of special circumstances. Species thus lately modified will very naturally be classed with those which bear the same or similar characters as the early result of very ancient ancestral divergencies, and, as a consequence, other characters not harmonizing, the systems are thrown into confusion. These are difficul-

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ties among which the sum total of the organic characters must be our guide in attempting to decide. Only too often we may find, as knowledge increases, that our first judgment was more or less in error.

In reflecting upon the origin of the complicated mechanical arrangements in bivalves which we call the hinge, I have come to the conclusion that here, as in the cases of the mammalian foot and tooth, elaborated so clearly by Cope and Ryder, we have the result of influences of a mechanical nature operating upon an organ or apparatus in the process of development.

The hinge of a bivalve, reduced to its ultimate terms, consists of two more or less rigid edges of shell united by a flexible membrane or ligament.

The ligament may be wholly external or may be supplemented by an internal addendum (called the cartilage), which exerts a stress in the same direction within certain limits. The movements of the hinge are dependent upon the elasticity of the ligament and cartilage and upon force exerted by one or more adductor muscles uniting to the valves

The rigid edges or cardinal margins of the valves may be simple or modified by the presence of interlocking processes known as teeth, whose purpose is to regulate the direction of the valves in opening and closing.

There are three fundamental types of hinge: 1, the simple edentulous margin closing by simple apposition of the edges of the two valves; 2, the hinge in which the teeth are developed in a direction transverse to the cardinal margin; 3, the hinge in which the direction of the teeth is parallel to the margin. The mechanical features of the second and third types may be more or less combined in a single hinge, but the affinities of the particular form in which this may occur are usually not difficult to determine on a general survey of all its organic characters.

I am disposed to think that the time relations of the different types are those of the order in which I have cited them; the most perfect hinge, morphologically speaking, would be one which should combine the most effective features of the second and third types.

The archetypal form of bivalve may be imagined as small, with nearly equilateral, symmetrical, sub-circular valves with edentulous cardinal margin and a short external ligament nearly central between the umbones. This is the character of many larval bivalves at the present day, though it is probable that many of the forms now edentulous in the adult state, have passed through an evolutionary stage in which they had a more or less denticulate hinge-margin, while their present condition is one in which the hinge has diminished in complexity or, in other words, undergone degeneration.

Very few of the earliest known bivalves appear to have hinge teeth, yet this may be on account of our imperfect knowledge of many of them since they are often represented by fossils in which no evidence of the hinge structure is discernible. It is highly probable that the evolution of hinge-teeth closely followed the differentiation of the Pelecypod class and that the segregation of the muscular apparatus for closing the valves into two bunches or adductors was accomplished very early in its history.

The first bivalves are all small, as far as known, when compared with a majority of their descendants. It is highly probable that they possessed a developed foot and that their gills were either lamelliform on either side of an arterial stem, as in *Nucula*, *Solenomya* and many Gastropods, or filiform, as in *Dimya* and certain Pectens. The siphons were probably little developed and the lobes of the mantle rather widely separated or perhaps entirely free.

As long as the shell remained small and subglobular, the ligament short and wholly external, the imperfect character of the hinge was of less importance. With the essential difference between the anterior and the posterior halves of the animal, and especially with any material increase in the magnitude of the adult, more or less discrepancy would develop itself between the two ends of the shell, the subglobular form would disappear, and certain other consequences would follow. Either the ligament must increase with the size of the shell and become longer or its power would become inadequate for the proper performance of its functions.

Here I will turn aside for a moment from the direct line of argument to describe the mechanical relations of ligament and shell, a proper understanding of which is very necessary to the comprehension of the whole question.

With a wholly external ligament the operation of the valves is that of two appendages to the free ends of a C-shaped spring. The action of the muscles in pulling the valves together includes the bringing nearer to each other of the two extremities of the ligament which the latter by its elasticity resists, consequently the operation of the ligament is in the direction of opening the valves to a certain distance. Beyond this distance the separation of the valves tends to compress the ligament, which again resists, and therefore beyond the normal distance of separation the action of the ligament tends to prevent the valves from opening. This very simple matter may be observed by any one who will examine an ordinary clam with the ligament in fresh condition and whose adductor muscles have been severed.

When the ligament, in harmony with the elongation of the cardinal margin, becomes elongated it must be either straight or angulated. For obvious reasons a ligament forming a curve or the arc of a circle is mechanically impossible This any one may prove to his own satisfaction by putting two light wooden saucers edge to edge, convexity outward, and attaching a leather or paper ligament by cement. A curved ligament when the valves open will tear or break at once, either itself or the edge to which it is fixed. In other words, the axis of motion of the hinge must be in a straight line. If any part of the ligament diverges from the axial line, it must cease to take part in the axial motion and must be capable of stretching to an extent which will neutralize its angulation, or it will be broken or torn away. But if the thickness of the ligament increases ventrally, as may be the case when it is situated between the valves rather than as an arch above them, a certain portion may extend to and beyond the axial plane in a downward direction. The portion thus projecting will then partake of the axial motion in an opposite sense to that portion which remains above the axial line. It will be compressed when the latter is stretched by the closing of the valves and will expand as the opening of the valves allows the external portion to contract. This change may be brought about by a downward angulation of one end of the ligament (as in *Solenomya*) or as a simple downward growth, which may be central (as in *Neilonella* or *Galeomma*). The former may be the result of an angulation of the hinge-margin consequent on elongation or ventral extension. Its result is to separate a terminal segment of the original ligament, which segment may be totally detached or remain physically connected; while in either case its mechanical function has undergone a reversal of direction.

The second mode likewise removes a segment but in a vertical direction. This segment may be physically continuous throughout its upper portion with the lower portion of the superjacent ligament, it may be wholly detached, or it may be attached by one extremity while the other is separated; in the last case its direction will be oblique or at an acute angle with that of the original ligament. This detached segment whatever its position has always similar mechanical relations to the movement of the hinge and is called the cartilage. The separation of the cartilage from the ligament is generally either central or toward the shortest end of the hinge, which is usually the anterior, owing to the fact that when the size of a lamellibranch increases, the siphons, the ovaries, the visceral mass or the gills are the organs where proportionally increased growth is most likely to occur, and these are usually central or posterior to the umbones. In *Solenomya*, which is exceptional in having a posterior cartilage, the posterior portion is shortest.

The amount of shifting required to put part of the ligament on the ventral side of the axis of hinge motion, or cardinal axis, is extremely small. All stages of the changes involved may be observed in the *Nuculacea*, even to one not hitherto mentioned where the cartilage has been developed and has subsequently become obsolete or altogether disappeared (*Malletia*), while leaving some traces of its former presence in the shape of an empty and degenerate fossette (*Pleurodon*). It is noteworthy that this suborder, in which the shell gives us so many hints as to processes which we may imagine to be of great antiquity, should on other grounds be regarded as among the few which best retain traces in the soft parts of archaic stages of development.

With the lengthening and angulation of the cardinal margin the ligament gradually shifted to a point where it became posterior to the beaks. Perhaps it would be better to say that the portion in front of the beaks either became segmented off as a cartilage, or became obsolete and vanished, while the portion on the posterior side gradually elongated, as the elongation of the posterior hinge-margin rendered a longer ligament more useful. It has already been pointed out that a curved ligament would involve stresses leading to its own destruction. The curvature of the cardinal margin, now the common property of a vast majority of bivalves, was inevitable with increase in size and a symmetrical development of the anterior and posterior ends of the body. Consequently that the ligament should be shifted was a mechanical necessity, unless the evolution of the group was to be confined within extremely narrow limits as regards hinge characters.

The infolding of the ligament and the development of a cartilage and its supports would be especially likely to occur in forms with a thin edentulous hinge, where the least shifting would be necessary (*Solenomya*, *Anatina*) rather than in those with a broad flat hinge-margin. In harmony with this proposition we find the archaic forms with internal cartilage have generally a narrow edentulous cardinal border, the exceptions belonging to the more recently specialized types (*Mactra*, *Spondylus*); while the groups without an internal cartilage contain the broadest and heaviest types of hinge (*Pectunculus*, *Veneridæ*.)

The infolding of a cartilage which arose by longitudinal segmentation would leave a line of weakness in the arch of the umbones. In thin shells with strong adductors there would be a tendency to fracture here. This singular feature has been perpetuated in what may be termed the normal umbonal fissure of *Solenomya*, *Periploma* and similar forms. Traces of it are evident in *Thracia*, while the unfractured suture itself is visible in *Isocardia*, *Pachyrisma*, *Pecchiolia*.

In the thin-shelled *Cuspidariidæ* a special buttress is often developed to support the shell at this weak point. In the *Isocardiidæ* an independent cartilage was possibly never developed, but the infolding of the anterior part of the ligament went far enough to leave permanent traces on the shell. That it did not result in a cartilage if this was the case may possibly be due to the fact that, owing to the great size and spiral character of the umbones, the anterior part of the ligament was turned up instead of downward, and therefore did not tend to shift toward the interior.

If it is not clear how the thickening or vertical extension of the ligament below the cardinal axis should cause its separation into two parts, I need only recall the familiar experience of every one in breaking off a wire or piece of tin by bending it backward and forward on the line of the desired fracture. The mechanical principles and results in the two cases are precisely similar.

When finally developed in the same individual the ligament and cartilage work in identically the same manner but in different directions. The resistance of the ligament to compression prevents any straining of the adductors by a too wide opening of the valves. The same resistance in the cartilage prevents the ventral margins from crushing each other by sudden and violent contractions of the adductors when the animal is alarmed, and closes its valves.

The nymphæ, or processes to which the ligament is attached, and the fossette, or socket of the cartilage, have been strengthened and regulated by the development of various buttresses and other devices, varying in different groups. The cartilage in turn has its rigidity and strength increased in many species by the special development of shell substance known as the ossiculum.

To return to the development of the cardinal margin. The asymmetry of the shell and ligament relative to a vertical transverse plane passing through the umbones, would be promoted not only by the natural discrepancies between the anterior and posterior halves of the body, but by the mechanical effect of the projecting umbones. Where a shell opens laterally, in the strict sense of the word, unless the beaks are very inconspicuous, or are separated by a wide projection of the cardinal border (as in *Arca noæ*), they will strike against and wear out one another. This abnormal or accidental result is very constantly observable in many *Anatinidæ*, such as our own *Thracia Conradi.* But it must be a source of weakness and danger to the animal. If the ligament is shifted posteriorly the valves must open more obliquely, with a result that this dangerous friction will be avoided in most cases.

In a protective armor like the valves of bivalves, other things being equal, it will be obviously beneficial if not absolutely essential that it should offer as few weak joints or open spaces as possible. Burrowing animals, who themselves serve as a supplementary defence of their burrow, may be able to perpetuate gaping shells and exposed siphons without serious danger from their enemies. Those animals which burrow but slightly or live in material which enemies may also easily penetrate in their forays, will unquestionably benefit greatly by an accurate and exact closure of the valves. The intrusion of solid bodies can be to some extent guarded against by the action of the cilia or processes of the mantle margin, but such intrusion would be greatly facilitated by any organization of the hinge which would permit an independent rocking motion of the valves with respect to each other. The sudden closing which danger incites leaves no time for clearing out obstructions and the gap is especially liable to the incursion of gravel, etc., in species which live with the plane of junction of the valves in a vertical direction. In certain brachiopods such as *Glottidia* and *Discina* such a semi-rotary motion of the valves exists, but is less dangerous to them since the plane of junction with them appears to be generally horizontal.

To avoid these dangers and to guide the motion of the valves in closing, and to prevent their sliding upon one another after closing, Nature, through natural selection and physical stresses, has developed these cardinal processes which are known as teeth.

Attention has already been called to the fact that there can be but three fundamental types of hinge, which may be called the anodont, prionodont and orthodont, the latter term being used to indicate the forms in which the cardinal margin has become longitudinally plicate. Actually the pure orthodont type hardly exists; in nearly all forms traces of the prionodont characters are mingled with it. For those forms in which the archaic anodontism still persists as the characteristic of chief importance, though frequently modified by special mechanical contrivances which to a certain extent mask the type, I have proposed the term *Anomalodesmacea.* The fossette, cuilleron or spoon-shaped process for the cartilage is a separate development serving a special purpose; though influencing the teeth, if any exist, in its vicinity, it must not be confounded with them. The weakness of the anodont type has left an opening for the specialization and perfection of this process which, to a considerable extent in this group, assumes the functions which in groups without a cartilage are the special office of the teeth.

For those forms in which transverse plication of the hinge is the chief characteristic, though rarely wholly exclusive of orthodont influence, I have used the term *Prionodesmacea.* In some cases what may seem to be the chief features of the hinge as regards size and strength are orthodont, yet these I believe to be comparatively modern specializations illustrating the general tendency of evolutionary processes toward a teleodont hinge. In cases of doubt the sum of the characters will enable us to decide on the proper place for a given genus. It must not be supposed that, because the *names* suggested by a single set of characters are used to denominate the proposed orders, that therefore that set of characters is to be our sole criterion. Such too hasty assumptions are a relic of the days when the immutability of species was an orthodox dogma in biology, and doom to failure any system founded upon them.

For those forms in which the various types of hinge have become harmoniously combined, though in varying proportion contributing to the final mechanism, I have selected the designation of *Teleodesmacea.* These may be regarded as the highest and evolutionally the most perfect in type of hinge, though this perfection shows itself in a variety of forms. Prionodont traces remain with most of them but are never characteristic of the type.

The three groups I propose to call Orders. It is difficult to say whether they can be compared in systematic value with orders in other classes. All that can be said is that these three divisions are discernible in the very compact and homogeneous class which includes them, and it contains no other groups of equal value or significance.

Each Order as it now exists contains archaic and modern specialized types. Each indicates a tendency toward an ideal of fitness to the environment, which results in a certain parallelism of minor characters common to minor groups in each of the three orders. In each (we are coming to regard it as inevitable), certain members show affiliations with members of the other orders. In each there are certain groups which represent a relatively modern specialization carried so far as to be quite peculiar.

Pearliness or a truly nacreous character of shell substance is a source of weakness. This kind of shell is more fully permeated with animal matter, is more liable to decay and exfoliation and is more readily drilled by enemies than the arragonitic type of shell substance which conchologists call porcellanous. The tendency of evolution is to promote the porcellanous type. The older groups (*Prionodesmacea* and *Anomalodesmacea*) contain all the pearly Pelecypods, among the *Teleodesmacea* there is not a single one. Furthermore, in the two former orders the most specialized and, developmentally, the most modern forms are preferably porcellanous; those which we may reasonably regard as of more ancient type tend to pearliness. For example in the *Anomalodesmacea* the most striking instances of specialization are the Pholads, *Tubicolæ* and certain *Myacea*, all are earthy or at least not pearly. The *Anatinacea* which paleontologically are very ancient, are largely pearly. The *Prionodesmacea* have few porcellanous groups, but those which show this character, such as *Ostrea* and *Pecten*, generally stand at the nearer end of the long line of progressive modification. There are exceptions to this, such as *Tindaria* in the *Nuculacea* which is obtrusively porcellanous, while *Leda* and *Solenomya*, which retain so many archaic features in their soft parts, have almost lost the pearly layer while still falling short of the porcellanous character conspicuous in most of the *Teleodesmacea*. The Arcas conspicuously earthy in their shells are modern in their total characters compared with the pearly Nuculas. Turning to Gastropoda for a moment we find that *Pleurotomaria*, one of the very earliest types of that class which can be recognized in the now existing fauna is extremely pearly. On the whole the relation between the two types of shell substance if not constant enough to be called a rule is sufficiently so to be extremely suggestive.

I have already suggested the mechanism of the infolding which resulted in the cartilage and its supporting socket. It is a very difficult task to account for the initiation of all the types of teeth. A few suggestions may be ventured upon.

The radiating or transverse corrugations which we see in ribbed shells are not merely ornamental. They serve to add strength while they do not increase the weight as would a corresponding thickening of the shell. A familiar example of the same principle is afforded by the corrugated sheet metal so frequently used by builders. The ends of these ribs impinge on the margin of the shell and crenulate it when the shell is thin. *Crenella* is a notable example. Many *Mytilacea* exhibit a similar structure. These crenulations of the hinge line and margin are not to be distinguished from nascent teeth and have frequently been described as such by naturalists. *Nuculocardia* of Orbigny is a well known instance. The crenulations of the margin are useful in securing a close fit between the closed valves, whether at the cardinal or the basal margin. But they would be more useful at the cardinal margin because there they would prevent sliding of the valves upon one another before they were completely closed, as do the long teeth of the *Nuculacea*. Hence, it is probable that they would be perpetuated and specialized there even if the ribbing disappeared from the exterior of the valves. Greater stress arising from friction and pressure resisted, would tend towards the thickening, widening and even buttressing of the cardinal margin, until the hinge plate became developed and sufficiently strong to perform its functions with success. This is one of the ways in which a Prionodont hinge might be initiated.

The Anodont hinge, to reiterate, is a weak and unsatisfactory type. Its features could hardly continue to exist except in a burrowing and tubicolous generation. To some extent its features has been made up for by an asymmetry in the valves which permits a smaller valve to fit into a larger one. This is a very successful device as there can be, as long as the larger margin remains unbroken, no question of failure to close the valves. But the projecting margin of the larger valve is a weak feature, much more likely to get fractured than the convex combined edges of two. Once fractured the mollusk would be defenceless until he could mend the breach. Moreover, in moving about, a practice more common with Pelecypods than is generally realized, the asymmetry of the valves would be a nuisance, always tending to shift the traveler out of the line he might desire to take. We find, as we should expect, that the Anodont hinge is persistent with tribes which are borers, tube-dwellers, or burrowers; for the most part very sluggish creatures. In cases where the ventral margins of the valves do not meet, there is of course no especial call for a dentiferous hinge as the valves play the subordinate part of a dorsal shield. This is the case with *Solenomya* where the ventral hiatus is partly shielded by projecting epidermis. Most of these forms depend apparently quite as much on their activity and the protection of their burrow, as they do on that afforded by the valves of the shell. A reversion of the process is seen in the case of some groups like *Anodonta*, in which the edentulous hinge is the result of degeneration from a dentiferous type such as *Unio*. The dentiferous forms retain their teeth in the streams and rivers where they are subject to numerous casualties and much knocking about; while in the still water and soft mud of silent ponds the teeth vanish and the protective shell reaches its limit of practicable tenuity. One type of "cardinal" (as opposed to the so-called "lateral") teeth would arise through the modification of an Orthodont or a Prionodont hinge at one end (as in *Macrodon*) so that part of a row of teeth originally similar would come to differ from the rest. Many *Nuculacea* show stages of such a mode of change.

Another type would arise from the plications of the hinge parallel to and induced by the formation of a fossette or process for the internal cartilage. Such teeth or plications may be observed in most Pelecypods having an internal cartilage. All stages of development of this type may be observed, from the barely traceable parallel ridges of *Cuspidaria*, for instance, to the highly developed and specialized cardinal teeth in *Mactra.* Thus it will be observed the teeth called "cardinals" in Pelecypods are by no means all necessarily homologous; and it is even conceivable that cardinals of both types might come to be united in the hinge of a single species.

The development of lateral teeth from transverse teeth is a very easy process of which a full exhibit might be made by arranging in a continuous series the valves of selected *Arcacea* and *Nuculacea.* It is probable however, that not all Orthodont dentition originated in this way. The thickening of the cardinal margin rendered necessary by the stresses involved in the mechanical operation of cardinal teeth or strong external ligaments, would render parallel plication of the thickened area along the margin not only easy but almost inevitable in some cases. The infolding of the edge of the mantle necessarily accompanying the production of a strong specialized socket for an internal cartilage would lead incidentally to occasional deposition of shelly matter in ridges parallel with the longer edges of such sockets. The greater efficiency in guiding the valves to effective closure, in proportion to the increased distance from the umbonal region, of such interlocking plications would tend through natural selection to the perpetuation of favorable variations and to their gradual removal farther and farther from the beaks until the most useful distance was attained.

When we consider the remarkable uniformity in hinge characters attained by the species with more perfected forms of hinge, through long series of individuals, it seems almost incredible that these results should be brought about by the action of a thin soft film of secretive tissue, which, unaided, could not hold itself erect. It is only when we remember that the result, in the main, is brought about through the action and reaction of certain definite mechanical stresses, propagated through the hard valvular skeleton and constantly imposed upon the softer tissues, that any adequate reason for the marvellous uniformity presents itself. There are certain groups such as the *Isocardiidæ* in which the hinge seems still to be in what may be termed a transition state. With these no such strict uniformity prevails. While the differences are not excessive, yet the hinge of each individual specimen compared with others of the same age will show individual characteristics and the changes which the hinge undergoes in the same individual between adolescence and old age are greater than one would ordinarily find in the whole membership of a species, say of the *Veneridæ*, taking all ages, above the larval stage into account.

We may now proceed to consider the groups of which these orders should be made up.

To the *Anomalodesmacea* I refer the *Anatinacea*, the *Myacea*, the *Ensiphonacea* or *Tubicolæ*, the *Solenomyacea* and the *Adesmacea*.

In the first three groups or suborders we have forms whose relationship will hardly be questioned, embracing also some instances of the most remarkable specialization of characters. To refer to a few I may mention *Aspergillum*, *Clavagella*, *Cuspidaria* and *Poromya*, using these names in their widest sense.

From several characters of the gills and other soft parts paralleled in the *Nuculacea*, *Solenomya* was at first affiliated by me with the Prionodonts. On mature consideration, while admitting that the last word on this subject has not yet been put on record, I am inclined to believe that this genus is an Anodont which has retained certain archaic features of the soft parts and represents in the *Anomalodesmacea* a survival analogous to that of the *Nuculacea* among the Prionodonts.

From a very early period the *Solenacea* have been associated with the forms now gathered in this order. Prof. Verrill has called attention to the fact that *Tagelus caribæus* and its allies have the organization of *Tellinacea*, and I have removed them to the vicinity of *Psammobia*, in my Check-list of the Marine shell-bearing Mollusks of the Southeastern coast of the United States.* But are the *Solenidæ* to be left behind? After due consideration I can see no sufficient reason for such a course, and conclude that the united siphons and burrowing habit, with its resulting specialization, do not warrant it. I have therefore excluded them.

In the *Adesmacea* or *Pholadacea* we have the most remarkable specialization of the hinge known in the whole class. The relations of the parts are best understood by a study of the open-shelled forms like *Zirphæa crispata* or *Barnea costata* and the young of the closed Pholads. In the adult forms of the latter specialization has proceeded so far that the true relations of the parts are more or less masked.

In *Barnea costata* we have the anterior dorsal margin of the valves reflected dorsally until the anterior adductors following the shell pass the axis of motion of the hinge and pull at the short end of the lever, tending to open the valves instead of to close them. The posterior adductors pull in the normal way and balance the anterior ones. The ligament is reduced to an ineffective film. The cartilage remains as a survival, but reduced to such dimensions as to be practically of no use. Its elastic properties are lost and it merely serves to connect two

* Bull. U. S. Nat. Mus., No. 37, 1889.

little processes, the feeble remnants of the original fossettes. An appendage analogous to and possibly homologous with an original ossiculum has (that view being taken) revolved around the cartilage, taken its place outside of the axis of motion of the hinge, and instead of keeping the valves from crushing each other by checking the closing stress of the adductors as in *Verticordia* or *Bushia* and other *Anatinacea*, it accomplishes the same end by locking over the reflected edges of the shell on the dorsal surface acting, like the anterior adductors, on the short instead of the long arm of the lever, and as before in a sense opposed to the action of the adductors. Though greatly specialized and modified this appendage retains something of the butterfly shape of a broad ossiculum.

An appendage, sometimes called the styliform process or apophysis, with its proximal end attached in the hollow of the beaks, has been homologized by Deshayes with the cardinal teeth. In *Pholas costata* it supports the posterior oral palpus which is very massive, and some of the internal viscera. If one of the umbonal laminæ of *Callocardia* were detached from its connection with the cardinal margin and allowed to project into the cavity of the valve, it would somewhat resemble the apophysis of *Pholas.* But on this view I am at a loss to explain the present connections of this process about the development of which little or nothing is known. How a cardinal tooth should come to be situated inside the mass of the body would seem to be hard to explain. The environment of the Pholads is of a very special character and the modifications of the organization march with the peculiar circumstances under which it exists. To enter into their mutual reactions would take much space and obscure the more general questions to which this paper is addressed.

It may be added that in this order as well as the others the particular constituency of each of the suborders, even the number and scope of the families, must be regarded as tinged with uncertainty from the magnitude of our ignorance. To properly ascertain and correlate the data in regard to the different genera and the families of which they are the members is a labor worthy of devotion, but which will yet require a large amount of original research.

In the *Prionodesmacea* the *Nuculacea* represent an archaic type in many of their features. So far as the hinge is concerned *Arca* (*Noæ* and related species) is perhaps the most fully and typically developed instance of Prionodont dentition. The Naiades declare in *Spatha* and *Iridina* their Prionodont origin, traces of which are to be seen in the transverse striation of the teeth of many species of *Unio*, even when lateral teeth have become well developed and preëminent. The same is true of *Trigonia* which has many points in common with Naiades. To the latter immediately *Mülleria* bears such a relation in its adult state as do the Monomyarian *Pecten* and *Ostrea* to the rest of the *Prionodesmacea* as a whole. The Prionodont character of the *Mytilacea* will not be questioned. Through them we pass to the *Pectinacea*, in which in *Spondylus* we have the finest instance of a Prionodont hinge with few teeth, as *Arca* is of one with many teeth. The original transverse grooving of the hinge is visible on the very young valves of many species of *Pecten*, *Janira*, etc. The *Ostracea* are the last term of specialization in this line; the *Anomiacea* are brought in by the total of their characters, though so far modified as to indicate little, by the hinge, of what I suppose to be their origin. Above all it must be admitted that the *Monomyaria* and *Heteromyaria* represent not fundamental types of structure but special modifications though geologically ancient. The presence of a prismatic layer of cretaceous otell substance, outside of the pearly layer, is also characteristic of most of the forms of this order.

The remaining forms representing the march of progress toward a mechanical perfection in hinge characters, though retaining traces (as in the striated teeth of some Mactras) of Prionodont ancestry which once dominated the dentition, constitute the order *Teleodesmacea*.

In the main, in the combination of hinge characters which they represent, the most striking features are the effective manner in which the orthodont laterals and prionodont cardinal teeth are subordinated to and supplement each others action, the occasional introduction of the internal cartilage in happy combination with the others and the general absence of nacre in the shell structure and archaic characters in the soft parts.

It is a question whether the *Rudistes* are to be considered a group apart, or, like the *Pholadacea* among the *Anomalodesmacea*, merely an erratic special development, of forms related to the *Chamacea*. Leaving the question to be settled by the special studies its difficulties call for, I conclude this paper with a tabular view of the orders and suborders into which the class is divided. One group, the *Leptonacea*, stands much in need of thorough study without which its component families and even its permanent standing must remain doubtful. With our present knowledge it is yet impossible to determine the number of families of which each suborder should be composed, or even how many groups are entitled to rank as families. But in the major groups I feel a certain amount of confidence that the present arrangement is in most respects more harmonious and in accord with the balance of characters than any of the systematic arrangements of the class which have been hitherto proposed.

CLASS PELECYPODA.

I. ORDER ANOMALODESMACEA.

Suborders.

1. Solenomyacea.
2. Anatinacea.
3. Myacea.
4. Ensiphonacea.
5. Adesmacea.

II. ORDER PRIONODESMACEA.

Suborders.

1. Nuculacea.
2. Arcacea.
3. Naiadacea.
4. Trigoniacea.
5. Mytilacea.
6. Pectinacea.
7. Anomiacea.
8. Ostracea.

III. ORDER TELEODESMACEA.

Suborders.

1. Tellinacea.
2. Solenacea.
3. Mactracea.
4. Carditacea.
5. Cardiacea.
6. Chamacea.
7. Tridacnacea.
8. Leptonacea ?
9. Lucinacea.
10. Isocardiacea ?
11. Veneracea.

* *

? Rudista.

Supplementary Note.—When I first began to consider the relations of the teeth and other parts of the hinge, I naturally remembered the brief abstract of the important paper on the hinge of Bivalves by M. Neumayr which I had seen in the Zoological Record for 1883. I intentionally deferred a careful perusal of Neumayr's essay until I had entirely completed my own. Then a careful examination of his original afforded me great pleasure. It showed that in the matter of the influence of ribbing in promoting the nascence of teeth; in the discrimination of lateral plications, arising in connection with the fossette of the cartilage, from the true cardinal teeth; in the influence of the environment on the degeneration of hinge characters: in the estimate of the characters of the primitive bivalves; and some minor points we had arrived independently at the same conclusions and even illustrated them by identical or nearly identical examples. This is certainly strong presumptive evidence of the correctness of those inferences. In the points in which we differ, it seems to me that the differences arise from the fact that Neumayr has approached the subject more from the paleontological standpoint and has less considered, or has given less weight to biological considerations not imprinted on the shell; while in my own case from the nature of my previous studies I have been led to attack the problem from the other side. Recent investigations, available only since the date of Neumayr's paper, have thrown much light on the inosculation of characters not before known to interlace. Neumayr also, from my standpoint has insufficiently grasped the importance of the different processes involved in the production of the internal cartilage and its shelly coefficients on the one hand and the denticulation of the hinge margin on the other. These two processes, though they must often have proceeded simultaneously in the same genus, were not necessarily connected except in so far as by resulting stresses each might react on the hinge-product of the other. So instead of having a Desmodont type of hinge as opposed to a Prionodont, and, as Neumayr would say, a Heterodont (Teleodont) type, we may have either an Anodont (Paleoconch), a Prionodont (Taxodont), or a Teleodont (Heterodont) type of hinge, either with or without an internal cartilage and its accessories.

By the elaboration of this view, as attempted in the foregoing discussion, it seems to me the discrepancies so evident in Neumayr's system have been avoided; the types of hinge assigned their proper weight in the system; while those biological relations which are not fully reflected in the shelly parts, have not been slighted; though inevitably numerous improvements in detail will suggest themselves to students, or be effected by a future expansion of our knowledge.

As regards the Rudistes, if, as claimed by Woodward and others, they possessed an internal cartilage, it is probable that they must form a specially modified and extraordinary ramification of the *Chamacea.* If, however, as is claimed by some authors, there was no internal cartilage or external ligament and the smaller valve simply rose and fell under the control of adductor muscles guided by interlocking processes, it is evident, that this would establish an interrelation between the valves unlike anything among the Pelecypods, and only comparable, perhaps, with that of certain operculated corals. In the latter case the Rudistes would have to be regarded as ranking at least among the subclasses, if mollusca at all. My own impressions are that the first mentioned view is the more probably correct one.

The opinion is occasionally expressed in scientific literature that the shell is a "mere secretion of the mantle." This usually proceeds from some person who has not thoroughly studied the molluscan shell, or appreciated its relations to the animal. Such a statement is one of those half-truths which are more dangerous than pure error since the ballast of truth they contain will enable the error to navigate some distance, while the unfreighted error would capsize at once.

The shell is in one sense the product of secretion from the mantle, as the mammalian tooth is derived from the ectoderm of the jaw or the skeleton from the periosteum and cartilages. Both are that and much more. It would be as reasonable to say that a steam boiler in process of construction is the product of the boy inside who holds the rivet-heads, as to claim that the shell has no more significance than is implied in the term "secretion of the mantle."

The original theoretic protoconch may have been so, but, as soon as it came into being, its development was governed by the physical forces impinging upon it from all sides and through it influencing the growth and structure of the soft parts beneath. The Gastropod shell is the result of the action and reaction between the physical forces of the environment and the evolutionary tendencies of the organic individual. In the Pelecypod we have the mechanical stresses and reactions of one valve upon the other added to the category of influences. To some extent it is doubtless as true that the animal is moulded by its shell as it is that the shell is shaped by the soft parts of the animal. This results in that correlation of structure which has enabled students to, in the main, correctly judge of the relations of mollusks by their shell-characters, when the latter were intelligently studied and properly appreciated.