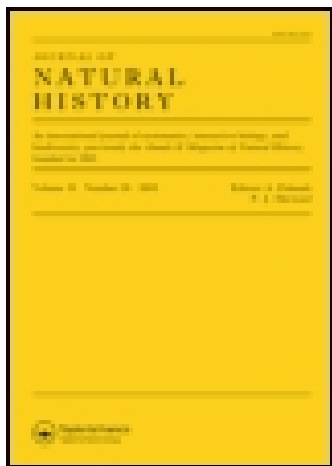


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### X.—A discussion of the general classification of the Pelecypoda

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X. — *A Discussion of the General Classification of the Pelecypoda.* By M. COLLEY MARCH, M.Sc., Geological Department, Manchester University.

[Plate III.]

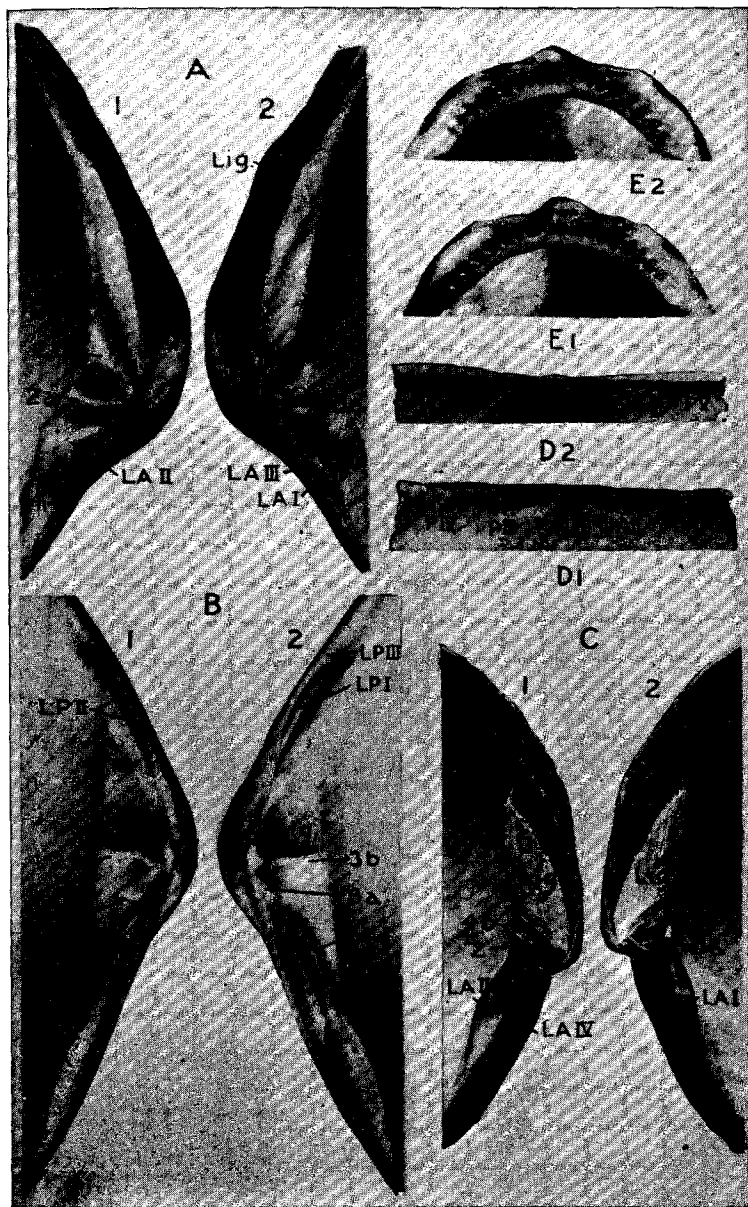
THE Pelecypoda, like all other animals possessing skeletons, can be classified from the standpoint of their hard or soft parts. The ideal method, where both are taken into consideration, is only available to the palæontologist when the soft parts leave some trace on the hard.

In the case of the Lamellibranchs, the modern classifications are based on the gills or the teeth. Dall, writing in support of a general hinge classification, said, that as the gills leave no impression on the shell, a gill classification must necessarily exclude all fossil forms, and so do away with the possibility of forming a phylogenetic classification.

It might also be argued that the evolution of gills is not of sufficient taxonomic importance for the division of orders and suborders. It is generally acceded that the pelecypod gill is homogenetic, being evolved from a type in which there was a main rachis giving off hollow and partially flattened leaflets. This type is held to have been developed in the earliest Pelecypoda. The object of specialization in gills and gill-chambers is twofold, to secure the maximum respiratory surface and a separation of the incoming and outgoing currents. These ends have been secured in the Pelecypoda by specialization along one line only, that is by elongation of the leaflets and the upgrowth of the free ends. The junction of these upturned ends has procured the division of the respiratory chamber. Ridewood has shown that in the connections between the opposite sides of the leaflets ciliary junctions preceded organic.

These stages in gill development, then, are of great interest as showing the evolution of the gill, but are useless taxonomically, for they were followed by all lines diverging from the common ancestral stock. They form only transverse divisions across the general classification and can no more be used to subdivide the group than can the articulation of the femur with two or three bones of the pelvis in the Ichthyosauria and Plesiosauria be taken as breaking those groups up into orders and suborders.

Moreover, in general evolution the gills are singularly unaffected by any change in environment or habit such as



leads to the development of new species or genera. Their broad changes must be looked upon as being purely intrinsic and as common to the whole group as such.

On the other hand, the primitive Pelecypod ancestor is conceived to have been hingeless. The evolution of the hinges must therefore have taken place entirely within the group. Its development was due to the necessity for securing rapid and accurate closing of the shell, as was pointed out by Dall. Such an end might be assured in many ways not of necessity related to each other, as the hinge has no ancestral form common to the whole group. So that the development of the hinge apparatus should be of taxonomic value, as similarity of development would show a close relationship between subdivisions, and not merely a common membership in the group. The fact that the variations are extrinsic leads to the occurrence of heterogeneric homœomorphy, but such cases should be distinguishable by the study of ontogeny and phylogeny.

### *Modern Classifications based on the Hinge.*

#### A. NEUMEYER.

Neumeyer was the first, after Martini, to classify the Pelecypoda on the characters of the hinge; he recognized six orders, founded on distinct teeth characters.

1. *Cryptodonta*. Including forms without teeth or with folds which involved the whole thickness of the valve and which were often continuous with the radial ribs.
2. *Taxodonta*. Including forms where, in the simplest cases, the teeth were perpendicular to the hinge-line, but which might become more or less oblique peripherally.
3. *Heterodonta*. Including the most highly specialized of the Lamelli-branches in which the teeth were distinguishable into cardinals and laterals.
4. *Schizodonta*. Including those forms which possess one bifurcated tooth in the left valve, fitting into two divergent lamellæ in the right valve.
5. *Desmodonta*. Including forms very similar to the Heterodonta in anatomy, but with an internal ligament, and teeth not homologous.
6. *Dysodonta*. Containing those Heteromyarians and Monomyarians that have partially or totally reduced teeth.

#### B. FISCHER.

Fischer added a seventh order to Neumeyer's six:—

*Isodonta*, included by Neumeyer in the Desmodonta, contains those forms which have their teeth symmetrically arranged about an internal ligament.

## C. GROBBEN.

Grobben used the hinge in conjunction with other anatomical characters as the basis of his classification. He recognized three sub-classes :—

1. *Protobranchia*, equivalent to the Protobranchia of Pelseeneer.
2. *Desmodonta*, equivalent to Neumeyer's order of that name.
3. *Ambonodonta* : (1) Eutaxodonta (Arcidæ).  
                           (2) Heterodonta (*sensu* Neumeyer).  
                           (3) Schizodonta (*sensu* Neumeyer).  
                           (4) Anisomyarians (*sensu* Lamarck).

## D. DALL.

Dall's orders are three in number: Prionodesmacea, Teleodesmacea, and Anomalodesmacea.

The *Prionodesmacea* are described as having hinges which "are the product of evolution applied to the development of (among other things) teeth to the hinge-margin, or of amorphous teeth" (14, p. 452). This, as an isolated quotation, might seem to show that he considered the transverse direction of the Prionodesmacean teeth to be secondary. Quotations from his earlier paper of 1889 will, however, show that in his conception this transverse direction of the teeth was primary.

1. (13, p. 452.) "Attention has been already called to the fact that there can be but three fundamental types of hinge; which may be called anodont, prionodont, and orthodont, the latter term being used to indicate the forms in which the cardinal margin *has become* longitudinally plicate."
2. (13, p. 447.) There are three fundamental types of hinge :—  
     (1) The simple edentulous margin. [Anodont.]  
     (2) The hinge in which the teeth are developed transverse to the cardinal margin. [Prionodont.]  
     (3) The hinge in which the direction of the teeth is parallel to the margin. [Orthodont.]

I am disposed to think that the time relations of the different hinges are those of the order in which I have cited them.

The *Teleodesmacea* include those forms in which the prionodont and orthodont types are combined, the latter being superimposed on the former either by a fusion of the transverse teeth or by the subsequent development of longitudinal teeth.

The *Anomalodesmacea* contain those Pelecypoda in which the dorsal margin is without a distinct hinge-plate, the armature of the hinge being "feeble, often obsolete, or absent."

Dall's three orders, therefore, were made for those Lamellibranchs which have teeth—

- (1) transverse to the hinge-margin;
- (2) parallel to the hinge-margin;
- (3) so degenerate as to show no definite affinity to the other two orders.

The last worker on the hinge from a taxonomic point of view was Bernard. His main work on the subject is found in four papers in the Bull. de la Soc. Géol. de France, two in the 'Comptes Rendus,' and one in the Ann. des Sci. Nat., Zool. This last paper was the first half of a synopsis of his work, and summed up his views on the Taxodonts and Anisomyarians [Dysodonta, Bernard], and included a sketch of the relationships of the modern and Palæozoic forms. He died the year of the publication of this first part, and the second part is not recorded as having been published, although he frequently refers to it in the first part. Consequently he was unable to publish a classification, although the bulk of the material for it was already published, and he never gave his final views on the relationships of the Taxodonts and Anisomyarians [Dysodonta, Bernard] to the Heterodonts. For this reason it is necessary to give a short summary of his work, which leads to the adoption of a classification which, although agreeing largely with Dall's in general grouping, yet differs from it fundamentally in the bases of the classes.

Bernard's main work was confirmed by Munier-Chalmas, and, with the exception of one minor point, by Fischer.

The most important points of Bernard's work are:—

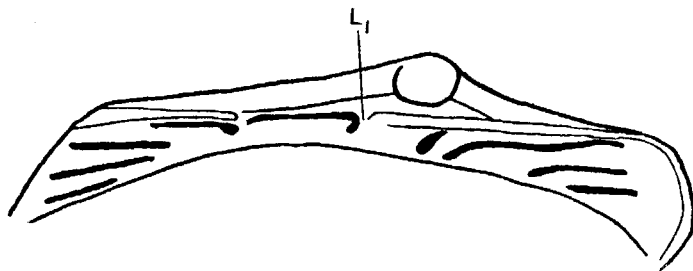
1. The tracing of the ontogenetic development of the taxodont teeth in the Taxodonta proper and also in the Anisomyarians.
2. The tracing of the origin of the taxodont dentition. (This was in part done also by Dall, though he did not grasp the bearing of his work.)
3. The discovery of the existence of an embryonic "dentition" in the Taxodonta equivalent to that found in some Heterodonts.
4. The tracing of the development of the heterodont hinge.

*The Development of Pleurodont [Taxodont and Dysodont]  
Teeth.*

The taxodont dentition was taken by workers previous to Bernard to differ essentially from the heterodont (Teleodesmecean, Dall) hinge, in having the teeth developed in a direction essentially *perpendicular* to the hinge-line instead of *parallel* to it. Bernard clearly demonstrated that in the prodissoconch stages, and sometimes continuing into dissoconch stages, there is an embryonic "dentition" consisting

of alternating ridges and folds, called by him "crenulations." This band is separated into anterior and posterior portions by the primary ligamental pit. In *Ostrea*, however, the anterior row is wanting, and the ligamental pit lies at the anterior edge of the shell. Subsequent to the development of the crenulations the true teeth make their appearance. These arise, not perpendicular to the hinge-line but as long ridges parallel to it. They may retain this position throughout life, as in *Cucullea crassatina*. Usually, however, the interior end becomes sharply curved and the external part atrophies, leaving the usual taxodont teeth (figs. 1, 2, and 3).

Fig. 1.



Young *Cucullea crassatina*, showing the recurving of the primitive lamellæ to form taxodont teeth. (After Bernard.)

L<sub>1</sub> = primary ligamental teeth.

The great importance of this is twofold :—

*Firstly.* It refutes the theory that the early embryonic dentition seen in certain Heterodonts, and which arises perpendicular to the hinge-line, represents an early taxodont condition, and for that reason necessitates the descent of the Heterodonts from Taxodonts as seen in modern forms.

*Secondly.* It does away with the radical difference between the heterodont and taxodont teeth.

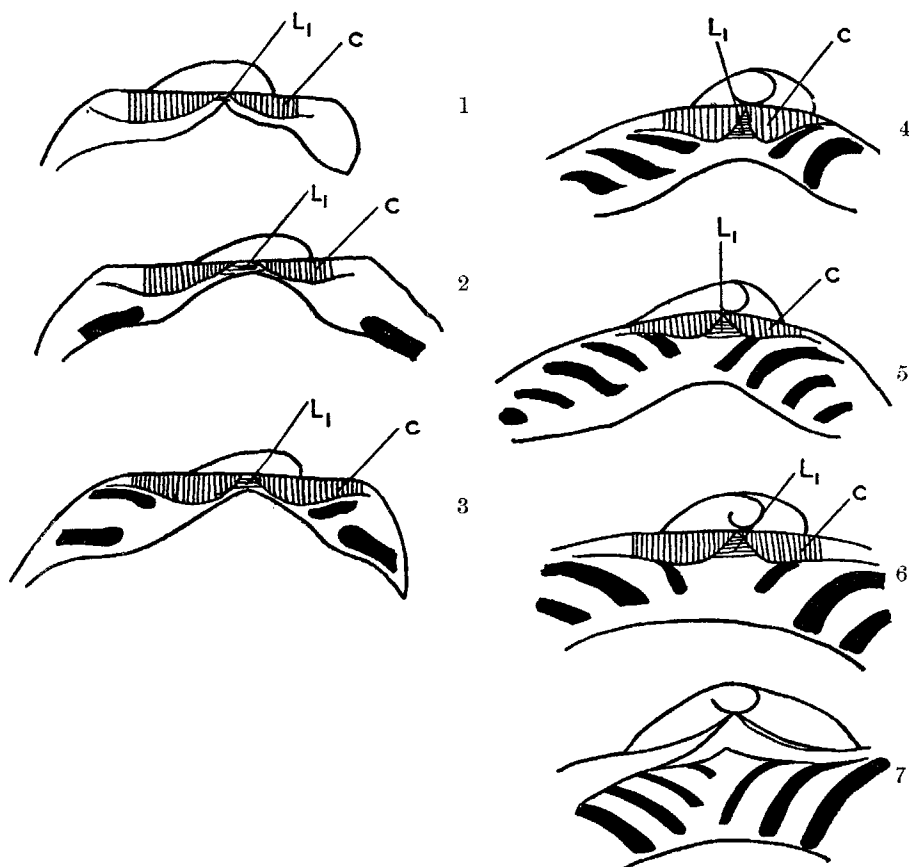
#### *The Origin of the Pleurodont Dentition.*

Amongst the Anisomyarians (figs. 4 & 5) the teeth show a still earlier stage than in the Nuculidæ and their allies. Here they rise before the development of the cardinal plateau as lateral folds alternating with the external ribs. These internal ribs may occur where the outer test is smooth. In forms where the test thickens greatly a transition can be



traced from a period when these internal ribs alternate with the external ribs, and a time when they are entirely independent of them. The cardinal plateau is a subsequent development to the first-formed teeth and arises on them.

Fig. 2.



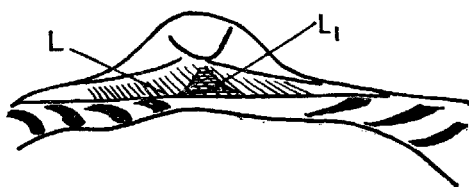
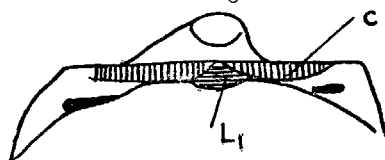
Development of *Pectunculus obovatus*. (After Bernard.)

1 & 2, right valve; 3-7, left valve.  $L_1$ =primary ligamental pit;  
C=band of crenulations.

Where these first-formed teeth remain as internal ribs they are called "dysodont," when they are developed on the plateau, or take their place on it, they become true taxodont teeth, and as such become capable of growth into the usual

taxodont form. Dall noticed the same origin for the Anisomyarian teeth; but he read it as excluding them from any connection with the Taxodonta, whose teeth he

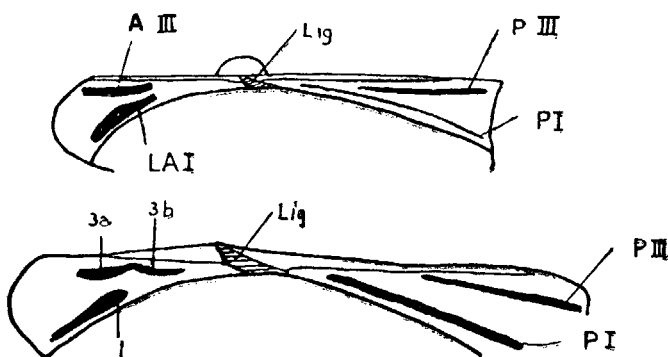
Fig. 3.



Young stages of *Arca*. (After Bernard.)

C=band of crenulations; L<sub>1</sub>=primary ligamental pit; L=ligament.

Fig. 4.



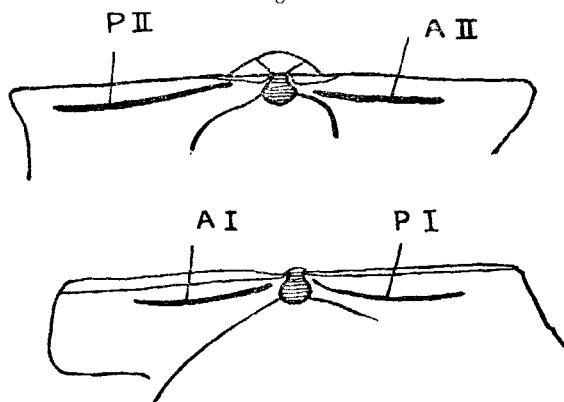
*Avicula microptera* (after Bernard), showing the dysodont teeth, which anteriorly show a tendency to produce cardinals,

conceived as arising perpendicular to the hinge-line. Confirming the fact that the dysodont stage precedes the taxodont, Bernard cites the case of the development of those young

*Ann. & Mag. N. Hist. Ser. 8, Vol. x.*

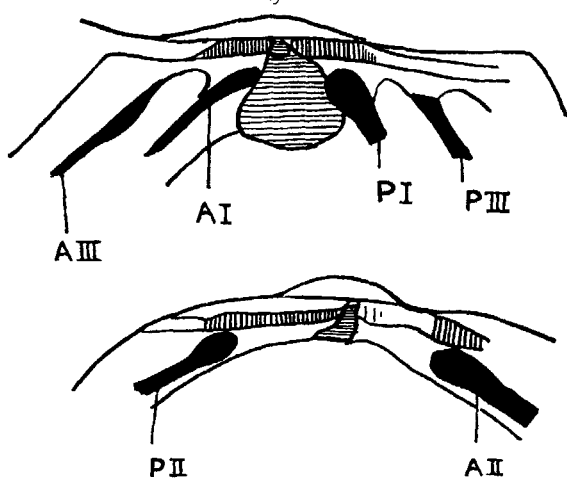
Arcidæ which grow slowly and have a thin test. Here the transition between dysodont and taxodont teeth is clearly seen. The Monomyarians develop rudimentary dysodont

Fig. 5.



*Pecten varius*, showing the first dysodont teeth. (After Bernard.)

Fig. 6.



*Plicatula ramosa*, showing the development of I, II, and III. (After Bernard.)

teeth, which show extraordinary variation. Bernard concludes from these facts that they are degenerate.

An important fact brought out by Bernard is the order of

development of teeth in the Taxodonta. The later teeth in the Taxodonta appear ventrally except :—

- (a) In the case of the Pectunculidæ, where the third tooth in the left valve appears dorsally to the first and second teeth. This may possibly be a case of degeneration, Bernard, however, does not suggest this (3, p. 61). (Fig. 6.)
- (b) In *Nucula* (3, p. 166) two teeth appear dorsally, which Bernard takes as being developed in their normal order. He comments, however, on their irregularity. In the case of the Monomyarians the irregularity in the development of the dysodont teeth is taken by him as postulating degeneration, so that these dorsal teeth might possibly be degenerate. In both these cases the other teeth develop ventrally,
- (c) In the Pectinidæ and Spondylidæ, and also in *Mytilus*, the teeth develop dorsally,

So far the points established by Bernard are :—

- (1) That the Taxodonta (*i. e.* Prionodesmacea—Naiadacea) have an embryonic dentition which is also seen in some Heterodonta (*i. e.* Teleodesmacea + Anomalodesmacea + Naiadacea).
- (2) That the true taxodont dentition develops parallel to the hinge and that its position perpendicular to the cardinal line is due to rotation.
- (3) That the dysodont dentition of the Anisomyarians is an early stage in the development of the taxodont and is originally formed from internal ribs, alternating with external ribs when these are present.

#### *The Development of the Heterodont Dentition.*

The last great point brought out by Bernard is the development of the heterodont teeth. These may or may not show the embryonic crenulations. In either case the true teeth are developed on a common plan.

The teeth, lateral or cardinal, are developed from laminae running parallel to the edge of the cardinal plateau. Those of the right valve lie ventral to those of the left valve. They are numbered I, II, III, IV, V, VI, from ventral to dorsal, those of the left valve being denoted by the even numbers, and those of the right valve by the odd numbers. As before, there are two sets of these teeth, one lying anterior, and the other posterior, to the ligament-pit,

Anterior to the ligament :—

LA I, LA III, LA V, for the right valve.

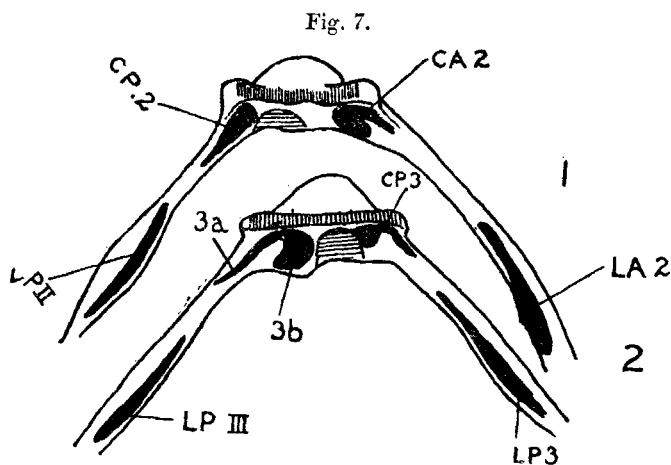
LA II, LA IV, LA VI, for the left valve.

Posterior to the ligament :—

LP I, LP III, LP V, for the right valve.

LP II, LP IV, LP VI, for the left valve.

The posterior ends of these lamellæ bend round so as to lie more or less perpendicular to the hinge-line, and may become differentiated from the anterior part. The posterior portions form the cardinals, the anterior portions form the lateral teeth or remain as undifferentiated lamellæ. The posterior lamellæ are unaltered except in the case of *Condylocardia* (fig. 7). The anterior cardinals may become bifurcated forming anterior portions.



*Condylocardia crassicosta* (after Bernard), showing the occurrence of posterior cardinals.

1. Left valve. 2. Right valve.

The reduction of the heterodont hinge to a scheme, and the cursory comparison of that scheme with the actual adult heterodont hinge, makes the conception seem too simple to be really possible. It is only by carefully following out Bernard's papers, and by the comparison of his descriptions of the adult shells with the actual specimens that it becomes clear that the hinges do develop on that plan. In actual practice V appears rarely, and VI very rarely.

LP=lateral posterior lamella.  
 LA=lateral anterior lamella.  
 CA=anterior cardinal.  
*a*=anterior portion of an anterior cardinal.  
*b*=posterior portion of an anterior cardinal.

*Left valve.**Right valve.*

	<u>LP VI</u> lig. <u>LA VI</u>		<u>LA V</u> lig. <u>LP V</u>
<b>A.</b>	<u>LP IV</u> lig. <u>LA IV</u>		<u>LA III</u> lig. <u>LP III</u>
	<u>LP II</u> lig. <u>LA II</u>		<u>LA I</u> lig. <u>LP I</u>
	<u>LP VI</u> lig. <u>CA 6</u> <u>LA VI</u>		<u>LA V</u> <u>CA 5</u> lig. <u>LP V</u>
<b>B.</b>	<u>LP IV</u> lig. <u>CA 4</u> <u>LA IV</u>		<u>LA III</u> <u>CA 3</u> lig. <u>LP III</u>
	<u>LP II</u> lig. <u>CA 2</u> <u>LA II</u>		<u>LA I</u> <u>CA 1</u> lig. <u>LP I</u>
	<u>LP VI</u> lig. <u>6 b</u> <u>6 a</u> <u>LA VI</u>		<u>LA V</u> <u>5 a</u> <u>5 b</u> lig. <u>LP V</u>
<b>C.</b>	<u>LP IV</u> lig. <u>4 b</u> <u>4 a</u> <u>LA IV</u>		<u>LA III</u> <u>3 a</u> <u>3 b</u> lig. <u>LP III</u>
	<u>LP II</u> lig. <u>2 b</u> <u>2 a</u> <u>LA II</u>		<u>LA I</u> <u>CA 1</u> lig. <u>LP I</u>

Diagrams showing the relation of the teeth  
 according to Bernard.

- A.** Stage showing primary lamellæ only.  
**B.** Stage showing development of anterior cardinals and laterals.  
**C.** Stage showing bifurcation of the anterior cardinals.

Bernard provisionally divided the Heterodonta into two classes. He did not hold these classes to be strictly natural ones, but he made them for the sake of convenience.

*Subdivisions of the Heterodonta.*

- A.** The *Cyrina* type, where the CA I is present, and CA II is divided into 2 *a* and 2 *b*.  
**B.** The *Lucina* type, where the first cardinal is undeveloped and the second cardinal is consequently simple.

*Families in Bernard's Orders and Suborders.***Heterodonta.****PLIODONTA.**

*Mactridæ*: Mactra, Schizodesma, Lutraria, Merope,  
 Schizothærus, Eastonia, Raëta.  
*Scrobicularidæ*: Cumingia, Semele, Scrobicularia.

- Mesodesmatidæ* : Paphia (= Mesodesma), Anapa.  
*Cardiliidæ* : Cardilia.  
*Anatinidæ* : Anatina, Thracia.  
*Cuspidariidæ* : Cuspidaria.  
*Cyrenidæ* : Corbicula, Iphigenia, Cyrena, Sphærium,  
                     Cyrenoida, Velonta.  
*Rangidæ* : Rangia.  
*Veneridæ* : Cytherea, Venus, Tapes, Circe, Macrocallista,  
                     Dosina, Glaucomya.  
*Cyprinidæ* : Cyprina, Pygocardia, Cypricardia, Corallio-  
                     phaga.  
*Isocardiidæ* : Isocardia, Modiolaria.  
*Petricolidæ* : Petricola.  
*Erycinidæ* : Lascea, Kellya, Bornea, Scacchia, Montacuta.  
*Kelliellidæ* : Lutetia, Kelliella.  
*Chamidæ* : Chama, Echinochama, Gyropleura, Monopleura,  
                     Capratina.  
*Rudistæ* : Valletia, Radiolites.  
*Diceratidæ* : Dicerias, Heterodicerias.

## OLIGODONTA.

- Lucinidæ* : Lucina, Fimbria, Diplodonta, Axinus, Felania,  
                     Ungulina.  
*Astartidæ* : Astarte.  
*Condylocardiidæ* : Condylocardia.  
*Cardiidæ* : Cardium, Hemicardium, Pterocardium, Pro-  
                     sodacna.  
*Donacidæ* : Donax.  
*Corbulidæ* : Corbula, Mya, Sphenia, Tugonia.  
*Tellinidæ* : Tellina.  
*Solemidæ*.  
*Panopeidæ*.  
*Pholadidæ* : Pholas.  
*Dreissensidæ* : Dreissensia.  
 \* *Trigoniidæ* ; Trigonina.

## Pleurodonta.

## TAXODONTA.

- Nuculidæ* : Nucula.  
*Arcidæ* : Arca, Cucullea.  
*Pectunculidæ* : Pectunculus.  
*Ledidæ* : Leda, Yoldia, Malletia.

## DYSODONTA.

- Mytilidæ* : Mytilus, Modiola, Modiolaria, Crenella, Litho-  
                     domus, Hochstetteria.  
*Aviculidæ* : Avicula.  
*Pectinidæ* : Pecten, Lima.  
*Spondylidæ* : Spondylus, Plicatula.  
*Anoniidæ* : Placunanomia.  
*Ostreidæ* : Ostrea.

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\* Possibly may belong to the Pliodonta.

*Bernard's Classification.*

Bernard's discovery of the discontinuity of the embryonic and adult dentitions of the Taxodonta, and his working out of the development of the definitive teeth, overthrew the hypothesis that the crenulations observable in certain Heterodonta postulated the descent of the latter from the former. On the other hand, he regarded the Heterodonta as being derived from an early taxodont (*i. e.* dysodont) ancestry by the specialization of the lateral lamellæ—that is to say, he considered these lamellæ to be homologous in both groups, for he says:—

“Pour comparer la charnière des Hétérodontes à celle des Taxodontes, il sera nécessaire de s'adresser, non pas aux formes adultes mais aux formes embryoniques . . . Une dent des Taxodontes sera homologue non pas à l'une quelconque des dents Hétérodontes adultes mais à l'une de leurs lamelles primitives qui se recourbent . . . pourra donner naissance, suivant les cas à 1, 2, ou 3 dents définitives.”

In his work Bernard clearly states that the Taxodonta and Anisomyaria form one group, the latter showing clearly the evolution of taxodont teeth from internal ribs. This is also shown by the *Arcas* in the former group. The Anisomyaria show the beginning of the taxodont dentition, but not its full development. The Monomyarian dentition he shows to be degenerate—indeed, *Ostrea* never passes through a taxodont stage. The absence of a well-developed taxodont stage may of course be due either to want of phylogenetic development or to a similar degeneration. Into this point Bernard does not go. The evidence of the Monomyaria and the specialized habit of the Anisomyaria generally point to its non-development being due to degeneration. That this loss of later specialization threw more and more work on to earlier stages is shown by *Ostrea*, which, never passing through a taxodont stage, has embryonic crenulations persisting late.

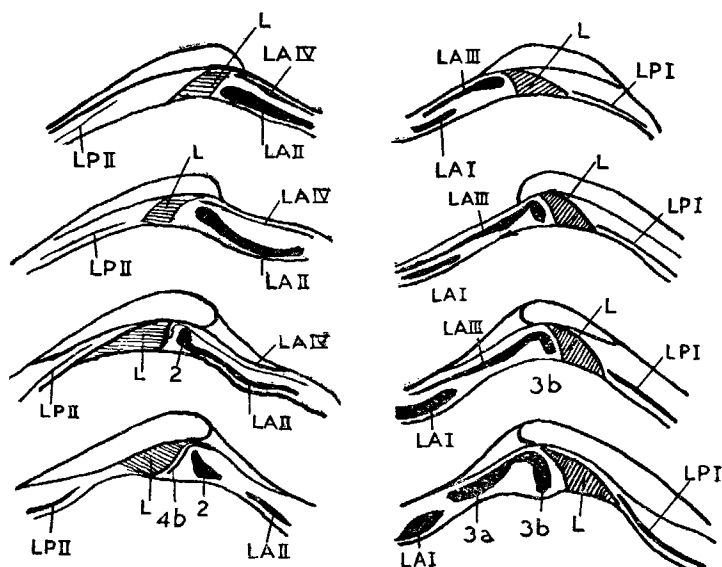
As the Taxodonta and Anisomyaria are included in one order, that order cannot very well be called Taxodonta. A name which seems suitable is Pleurodonta, as it refers to the definite proof of the evolution of the taxodont teeth from internal ribs. As to the names of the two suborders, Taxodonta is perfectly suitable; but the name Anisomyaria cannot very well stand, as it seems to show an order in a general classification based on the considerations of the hinge, divided off because of its muscular characters. For the



teeth of this suborder Bernard retains the name dysodont, therefore it might be called the Dysodonta.

The second order Bernard called Heterodonta. Its two main subdivisions he based on the fact that in one type cardinal 1 is not differentiated from lamella 1, and therefore

Fig. 8.

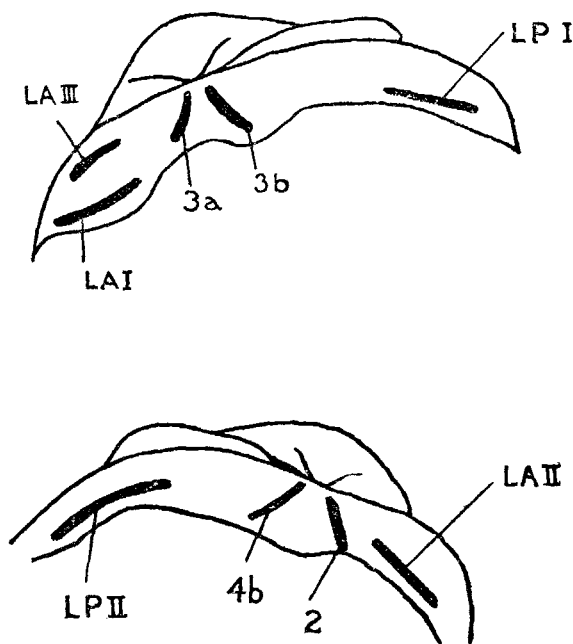
Development of *Lucina neglecta*. (After Bernard.)

cardinal 2 is undivided. In the other type cardinal 1 is present and cardinal 2 is divided. These two suborders might perhaps be called Pliodonta and Oligodonta (figs. 8 & 9), in reference to their diagnostic characters. The former suborder is again divided into four classes :—

1. Containing those forms which are typical of the suborder (figs. 10 & 11).
2. Containing those forms in which CA 1 is either quite undeveloped or not strongly developed (fig. 12).
3. Containing those forms in which the ligament is either entirely or nearly internal and where CA 1 is undeveloped (figs. 13 & 14).
4. Containing *Chama* and its allies (fig. 15).

There are two apparent objections to Bernard's conclusions. The first is Noettling's (17, p. 87), who, in criticizing Bernard's statement that the dorsal primary lamellæ of the Heterodonta appear later than the ventral ones, says:—"The view that the dorsal primary lamellæ are older than the ventral ones is . . . supported by the fact that the Bivalves grow in a ventral direction—in other words, the ventral portions of a bivalve shell are younger than the

Fig. 9.

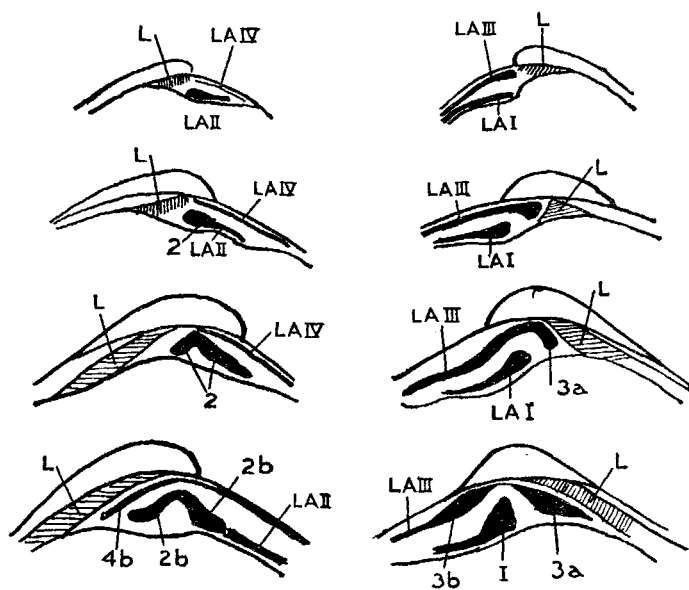
*Cardium.*

dorsal ones; it would be certainly strange if the opposite took place with regard to the hinge, where the ventral parts would be the older and the dorsal parts the younger ones—that is to say, the hinge would grow just in the opposite direction to the remainder of the shell." This certainly would be strange, but Dr. Noettling overlooks three facts:—

*Firstly.* That, as is shown by the growth-lines, the teeth are formed entirely by secondary thickening which may take place at any point.

*Secondly.* The growth-lines in the umbonal region of the shell show that the earliest formed part of the plateau is due to internal thickening. The first growth-line bends down, then up, cutting the edge of the young shell. If the plateau were formed by downgrowth of the external part the growth-lines would run towards the umbonal region as they do in the underpart of the plateau. If, then, as seems probable from the structure of the shell, the plateau is due to secondary thickening, it cannot be possible to speak of teeth as being dorsal or ventral with regard to each other

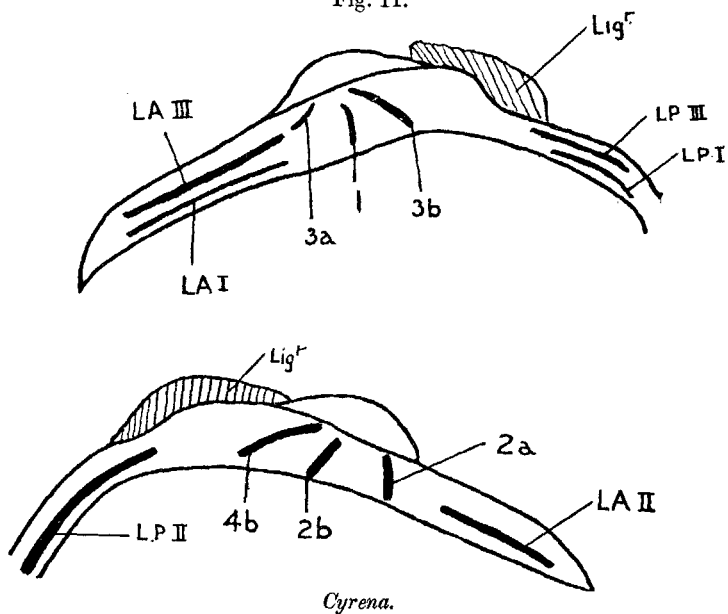
Fig. 10.

Development of *Cytherea deshayesiana*. (After Bernard.)

when they are formed by thickenings on its upper surface. They can only be more or less internal or external with regard to each other.

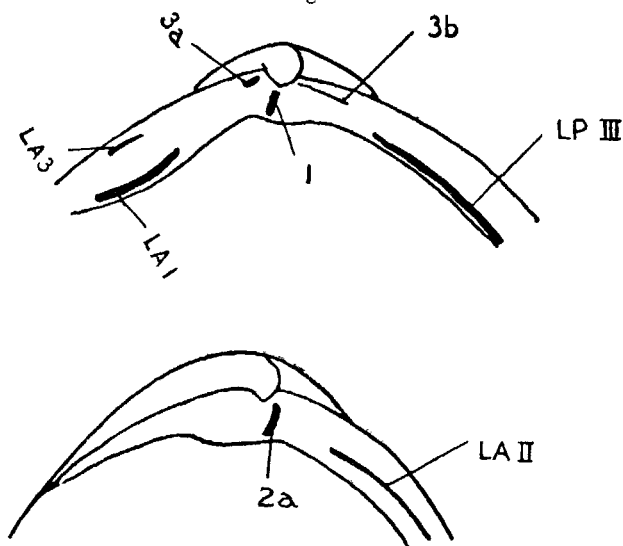
*Thirdly.* According to Bernard's hypothesis, the lamellæ are derived from radial internal ribs, which, except for intercalation (which only occurs in later shell-development), remain constant in number and normally develop simultaneously. Such ribs cannot be regarded as dorsal or ventral with regard to each other.

Fig. 11.



*Cyrena.*

Fig. 12.



*A Lævicardium with reduced teeth.*

Fig. 13.

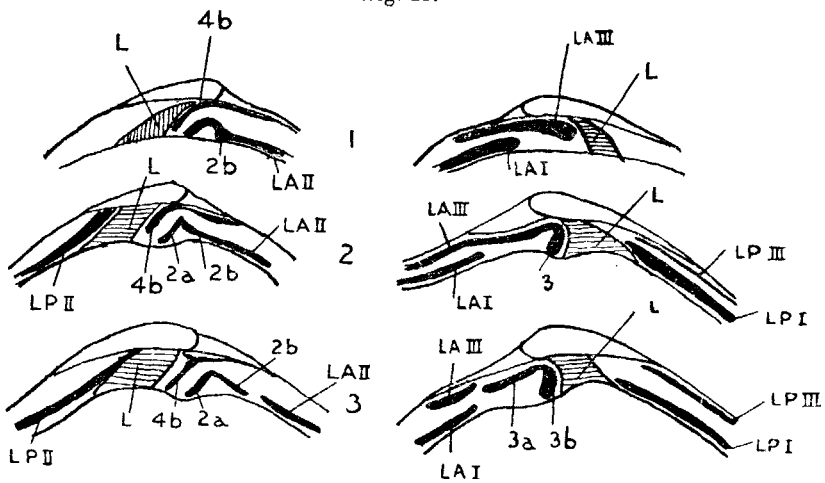
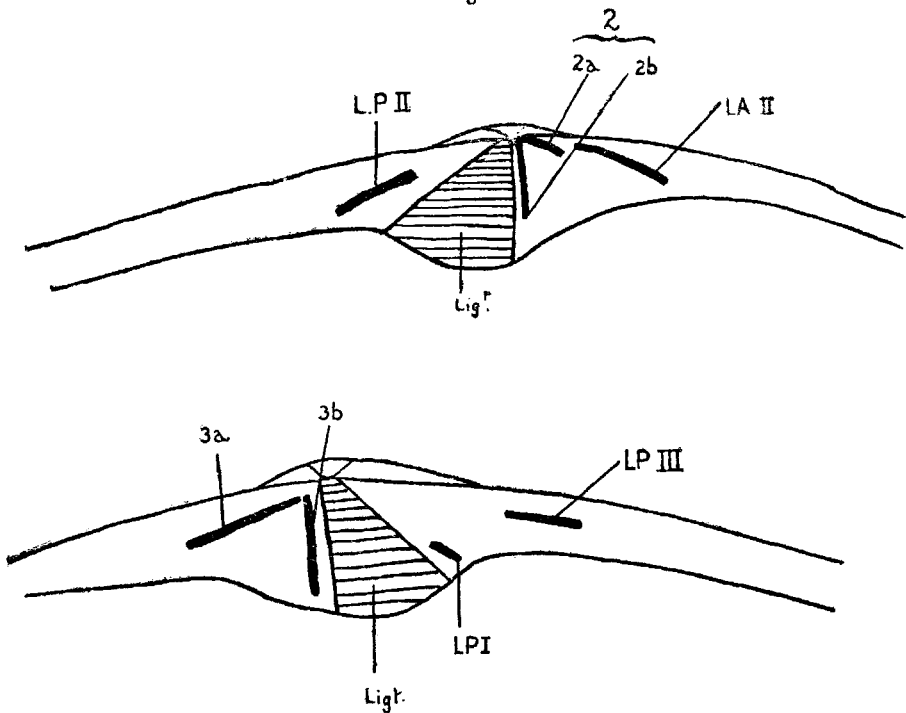
Development of *Mactra solida*. (After Bernard.)

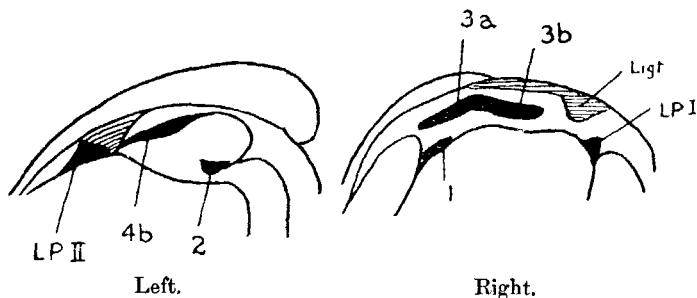
Fig. 14.

*Intraria*.

Those ribs would then be developed which were of greatest importance to the shell—they might be those nearest to the hinge-line or those furthest from it.

The second apparent objection is the alteration of a ventral succession in the Taxodonta and some Dysodonta to a dorsal one in the remaining Dysodonta and all the Heterodonta if, as seems probable, they have a common origin. This objection has already been partially answered, where it was stated that those ribs which were most important would develop first. The change in order of development, then, may merely mean a change in the relative importance of the upper and lower ribs. This may reasonably be accounted for on the

Fig. 15.

*Chama lazarus.* (After Bernard.)

firmly established principle that those parts of an organism most highly developed in the adult tend to appear first in ontogeny. In the early shells, the Palæoconchs, the shells were thin and would be likely to break under the strain of the ligament. The most external, that is the uppermost ribs, which are more than mere valleys between the external ribs, and, moreover, need not be associated with external ribs, would be extremely likely to be useful as helping to strengthen that part of the shell. Being more developed they would appear sooner than the less important ventral ones. After the appearance of the cardinal plateau, or even after the general thickening of the shell, this use would be subordinated to the use of guiding the shell to ensure rapid and accurate closing. This would be better accomplished by ventral ribs, which would then develop first.

Noettling reasons from diagrams 12, numbers 2 and 3 (see text-fig. 10), of Bernard's work on Heterodonts, that lamella III, which is shown as curved round, is more differentiated

<i>Bernard.</i>	<i>Family.</i>	<i>Dall.</i>	<i>Ridewood.</i>
Order I. <b>Pleurodonta.</b> Suborder A. <b>Dysodonta.</b>	Mytilidæ. Aviculidæ. Pernidæ. Pectinidæ. Spondylidæ. Anomidæ. Ostreidæ.	Prionodesmacea Dysodonta. Schizodonta. " Isodonta. " " Isodonta. Dysodonta. " Isodonta.	Eleutherorhabda Mytilacea. Pectinacea. " " " " Synaptorhabda Ostracea.
Suborder B. <b>Taxodonta.</b>	Pectunculidæ. Arcidæ. Nuculidæ. Lediæ.	Prionodesmacea Taxodonta. " " "	Eleutherorhabda Mytilacea. " Protobranchia. "
Order II. <b>Heterodonta.</b> Division A. <b>Platodonta.</b>	Mactridæ. Scrobiculidæ. Mesodesmatidæ. Cuspidariidæ. Cardiliidæ. Anatenedæ.	Teleodontesmacea Teleodonta. " included in the Se- melidæ. " Teleodonta. " " " " Anomalodesmacea Adelosiphonia.	Synaptorhabda Tellinacea. " " " " Poromyacea. " " Anatinacea.

Cyrenidæ.		Teleodesmacea Diogenodonta.	"	Submytilacea.
Cypricardiidæ.		"	"	"
Ptericolidæ.		"	Teleodonta.	"
Erycinidæ.		"	Diogenodonta Leptonidæ.	Synaptorhabda Cardiacea.
Kelliellidæ.		"	Diogenodonta.	"
Sphæridæ.		"	"	"
Chamidæ.		"	Teleodonta.	"
Rudistæ.		"	"	"
Diceratidæ.		"	Diogenodonta.	"
Astartidæ.		Teleodonta Diogenodonta.		Synaptorhabda Submytilacea.
Lucinidæ.		"	"	"
Carditidæ.		"	"	"
Condylocardiidæ.		"	"	"
Cardiæ.		"	Cyclodonta.	"
Crassatellidæ.		"	Diogenodonta.	"
Solenidæ.		"	Teleodonta.	Myacea.
Pholadidæ.		"	Asthenodonta.	Pholadacea.
Tellimidæ.		"	Teleodonta.	Tellinacea.
Corbulidæ.		"	Asthenodonta.	"
Donacidæ.		"	Teleodonta.	"
Dreissensiidæ.		Prionodesmacea Schizodonta.		"
Cardiniidæ.		"	"	Submytilacea.
Trigoniidæ.		"	"	Eleutherorhabda Mytilacea.



than lamella I, which is merely a straight ridge. Surely here he is confusing the appearance of teeth and lamellæ. The curving of III is the first stage in the development of 3 *a* and 3 *b*. Lamella I might appear before lamella III, and yet CA 3 be developed before I. Indeed, CA 1 may never develop. Also the early appearance of I causes II in the left valve to appear more or less curved, and this enjoins the same fate on III in the right valve. As a matter of fact, this reading of these diagrams supports the assumed change in order of development by showing that, although the first lamella to develop is the most internal, yet the earliest formed teeth appear more externally.

### Order I. PLEURODONTA.

Pelecypoda in which the prodissoconch stage always shows an embryonic dentition in the form of crenulations, which may or may not continue into the dissoconch stage. The true teeth normally develop as lateral folds at the periphery. The cases in which they do not may be taken as due to acceleration in development. The succession of teeth is normally from external (dorsal) to internal (ventral). The cardinal plateau develops after the first-formed teeth, which may or may not be traceable from internal ribs. The teeth when developing before the plateau are dysodont, when developing on the plateau they are taxodont. The teeth tend to become curved, so as to lie perpendicular to the hinge-line internally. Peripherally they tend to atrophy.

#### Suborder A. DYSODONTA.

Pleurodonta in which the teeth definitely arise as continuations of internal ribs. They are reduced in number and may become taxodont in nature or degenerate. The succession may be external (dorsal).

#### Suborder B. TAXODONTA.

Pleurodonta in which the origin of teeth from internal ribs is normally not evident. The teeth are numerous and become perpendicular to the hinge-line. The succession is internal (ventral), except where not more than two teeth arise externally (dorsally).

## Order II. HETERODONTA.

Pelecypoda in which the prodissoconch normally shows no embryonic crenulations. The teeth develop from lateral lamellæ. The succession is external (dorsal). The first-formed lamella is in the right valve. Each valve contains lamellæ in front of and behind the ligament. The anterior lamellæ may develop posteriorly into cardinal teeth and anteriorly into lateral teeth. Posterior cardinals are developed in one case only.

## Division A. PLIODONTA.

Heterodonta in which CA 1 is developed and CA 2 is subdivided into anterior and posterior portions.

## Division B. OLIGODONTA.

Heterodonta in which CA 1 does not develop and CA 2 remains undivided.

*Conclusion.*

The comparison and contrasts between these three classifications stand out clearly. To Neumeyer, the first to really tackle the problem of the hinge as a basis for classification, is due the honour of having divided the hinges into types. Three only of these divisions survive, two of these only as of subordinal value (Taxodonta and Dysodonta), the third (Heterodonta) as an order; but to him is due the general basis for such a classification. Dall kept these types of Neumeyer's, but reduced them to the rank of divisions in his orders. He created three new orders, founding them, as did Neumeyer, on the characters of the adult shell, and, as was shown by Bernard's later work, erroneously. Bernard's work was essentially that of an embryologist. His two orders and their suborders were founded on the study of individual development. Having worked out the main lines of his classification in this way, he compared it with Neumeyer's work on the Palæoconchs of the Palæozoic period, and found that the results of his work were borne out by these earlier researches.

Neither of these workers claimed that his work was ideal phylogenetically; each fully realized the importance of the consideration of other organs in tracing out the relationships of members of the group.

Neumeyer's seven orders bear no distinct relationship to the orders established by those who followed the differentiation of the gills. Dall's first order, *Prionodesmacea*, corresponds to the *Protobranchia* and *Eleutherobranchia* of Ridewood, except that *Ostrea* and *Pinna* are removed by the latter, on account of their gills, into the *Synaptorhabda*, which is equivalent to the *Anomalodesmacea* and *Teleodesmacea* of Dall, with the exception of the above-mentioned families.

Bernard's *Pleurodonta* includes the members of the *Protobranchia* and *Eleutherobranchia*, together with the *Ostreidae* and the *Pinnidae* placed in it, and without the *Cardiniidae* and *Trigoniidae*. His *Heterodonta* agrees with the *Synaptorhabda* with these two families removed and the *Trigoniidae* and *Cardiniidae* added.

Grobben's classification appears to be untenable for three reasons :—

- A. He separates the *Desmodonta* from the *Heterodonta*, placing them in a different order, although they are essentially similar in both the gills and the hinge.
- B. He separates the *Arcidae* from the other *Taxodonta*, placing them in the same order as the *Heterodonta*, although they differ in development and history.
- C. In spite of the same difficulty, he places the *Anisomyaria*s with the *Heterodonta*.

As Dall's orders have been shown to have been founded on a misconception of the value of the teeth, the only important comparisons are between Bernard's and Ridewood's classifications.

One of the differences between these classifications is the inclusion in the first of Bernard's orders of the first two of Ridewood's orders. Bernard's reasons for putting the *Taxodonta* and *Dysodonta* together are :—

1. They have a similar prodissoconch with embryonic crenulations.
2. The early dissoconch stages are similar in regard to the development of the teeth and cardinal plateau.

The differences in their later development justifies their separation into suborders.

Ridewood's reason for separating them is that the gills in one case are simple protobranchs and in the other they are recurved. Ridewood himself derives the filibranch type

from the protobranch, so that the difference is merely one of degree of development, while Bernard's comparisons imply a relationship of origin and development for the prodissoconch and early dissoconch stages. The reasons for the association of these two sections of the Pelecypoda seem to be stronger than the reason for their separation.

Of course it can be urged against Bernard's order that in the Pectinidæ, Spondylidæ, and Plicatulidæ the order of development of the teeth is towards the exterior (*i. e.* the dorsal side), but a foreshadowing of this may be seen in the Nuculidæ and Pectunculidæ.

The separation of *Ostrea* and *Pinna* from *Avicula* on account of the gills is opposed to the results of the researches of Jackson on the Aviculidæ and their allies, and of Bernard on the development of the hinge and the general characters of the shell.

The inclusion of the Trigonacea in the Heterodonta, which is another difference, as the Heterodonta are practically equivalent to the Synaptorhabda, is another point of difference. This position of this family resolves itself into the question of whether the teeth or the gills are taken as being the more important for classification. The arguments on this point were given at the beginning of this paper.

A third and more important point of difference is the inclusion by Ridewood of the Arcidæ with the Trigoniidæ and Mytilidæ in the subgroup Mytilacea. This arrangement is opposed to the results of both phylogeny and ontogeny. The types of hinge which these families possess were distinct at any rate in Ordovician times.

In general basis Bernard's classification is sounder than Ridewood's, because it is possible to include in it fossil forms and also because it is not based on the degree of development of a common character. Where the two disagree in detail Bernard's views are supported by other workers and by phylogeny and ontogeny. Moreover, Bernard's conclusions are the result of the detailed study of ontogeny.

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## EXPLANATION OF PLATE III.

- A. 1. Left valve of *Meretrix*.  
2. Right "
- B. 1. Left valve of *Macra*.  
2. Right "
- C. 1. Left valve of *Lucina*.  
2. Right "
- D. 1. Left valve of *Pecten*.  
2. Right "
- E. 1. Left valve of *Pectunculus*.  
2. Right "

LA=anterior lamella.

LP=posterior lamella.

1, 2 a, 2 b, &amp;c.=cardinal teeth.

A=anterior dysodont tooth.

P=posterior dysodont tooth.