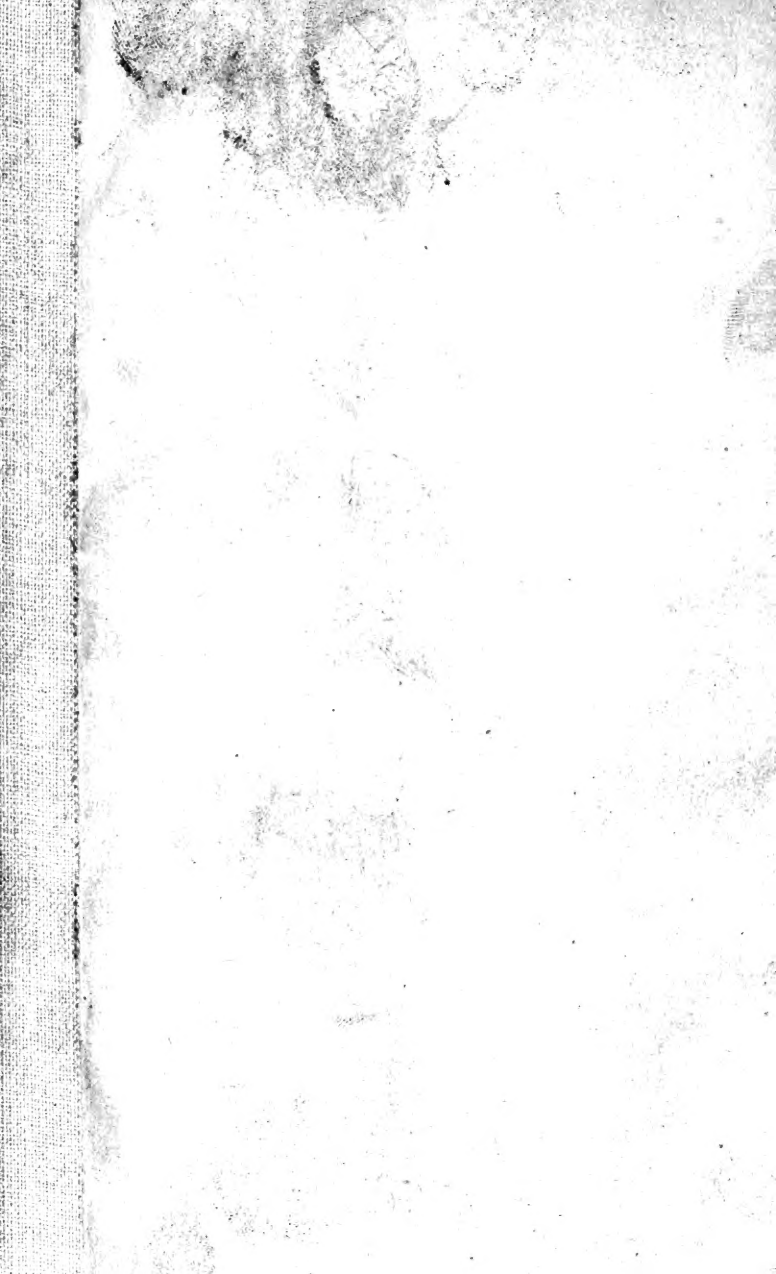


AN INTRODUCTION TO  
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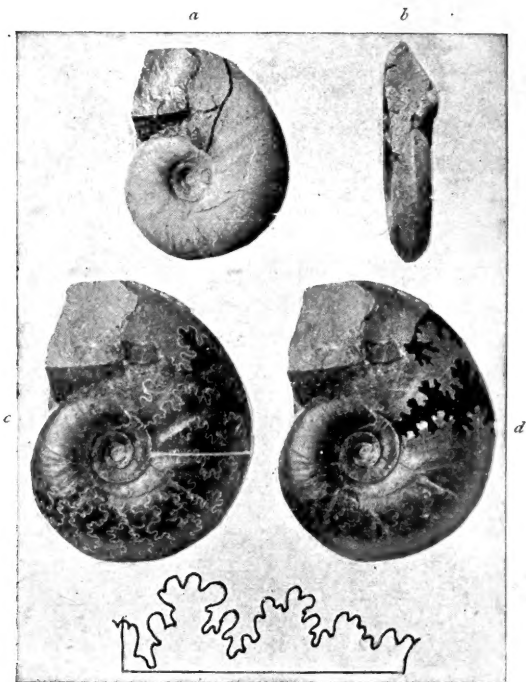




AN  
INTRODUCTION TO PALÆONTOLOGY



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AMAUROCERAS FERRUGINEUM (SIMPSON), AN AMALTHEID FROM  
THE DOMERIAN OF WHITBY.

Photographs by J. W. Tatcher of the holotype in Whitby Museum, reproduced from "Type Ammonites," by S. S. Buckman, vol. iii. (1919).

- a*, Side view. ( $\times \frac{1}{2}$ .) Radial line painted black. *b*, Peripheral (apertural) view. ( $\times \frac{1}{2}$ .) *c*, Side view. ( $\times 2$ .) Suture-lines strengthened on negative, guide-line in white. *d*, Side view. ( $\times 2$ .) Intervals between certain sutures painted on print. *e*, Right half of suture-line, straightened out. ( $\times 4$ .)

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D.

AN INTRODUCTION  
TO  
PALÆONTOLOGY

BY

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## PREFACE

My object in writing this book has been to introduce the principal facts, problems, and results of Palæontology to those who have to study it as a self-contained science, whether students of Geology or amateur fossil collectors. Though, from an academic point of view, Palæontology cannot claim the status even of a branch of Biology, being an aggregate of accidentally detached fragments of that science; yet, from the practical point of view, its special technique and applications give it an individuality as worthy of recognition as that, for instance, of Astrophysics. Valuable as a preliminary training in general Biology is to the student of Palæontology, I have tried to show that the latter, even when studied by itself, need not be reduced to a mere descriptive catalogue of fossils.

My ideal (not always attained) has been, in treating each great group of fossils, first to describe with some fulness a few common species from which an idea of the general characters and range of variation may be obtained; and then to give a brief systematic account of the group. The reader should not be satisfied unless he actually handles the selected species and compares them, point by point, with the description. When he cannot obtain the actual species described, he should take the nearest allied form accessible, and determine precisely how it differs from that described. Only by such definite practical work can he begin to qualify himself to become a palæontologist.

The writing of this book was begun in 1913, and interrupted for nearly four years by pressure of war-work. It was at first intended that it should be illustrated by original drawings of fossils, and a certain number of such drawings were made before the war from specimens in the collection of the Imperial College. I have to record my grateful thanks to the Governors of the Imperial College and Professor Watts, F.R.S., for permission for the use of these specimens, and to Mr. F. G. Percival, B.Sc., the artist. Subsequently it became evident that to continue this method of illustration would delay the work too much, and that for the purposes of the book diagrammatic copies of figures in standard monographs would be equally useful. I have to thank Miss L. Lyle, F.L.S., and my wife for these later figures, about four-fifths of the total.

Mr. S. S. Buckman has been so kind as to read the manuscript of the chapters on Brachiopoda and Cephalopoda, and I have profited by his criticisms and suggestions, and incorporated additional information to a much greater extent than it was practicable to acknowledge in the text. I cannot sufficiently express my gratitude to him for this help, as well as for the generous loan of the block which forms the frontispiece—a beautiful example of Mr. Tutchter's photographic skill, from the latest part of Mr. Buckman's "Type Ammonites."

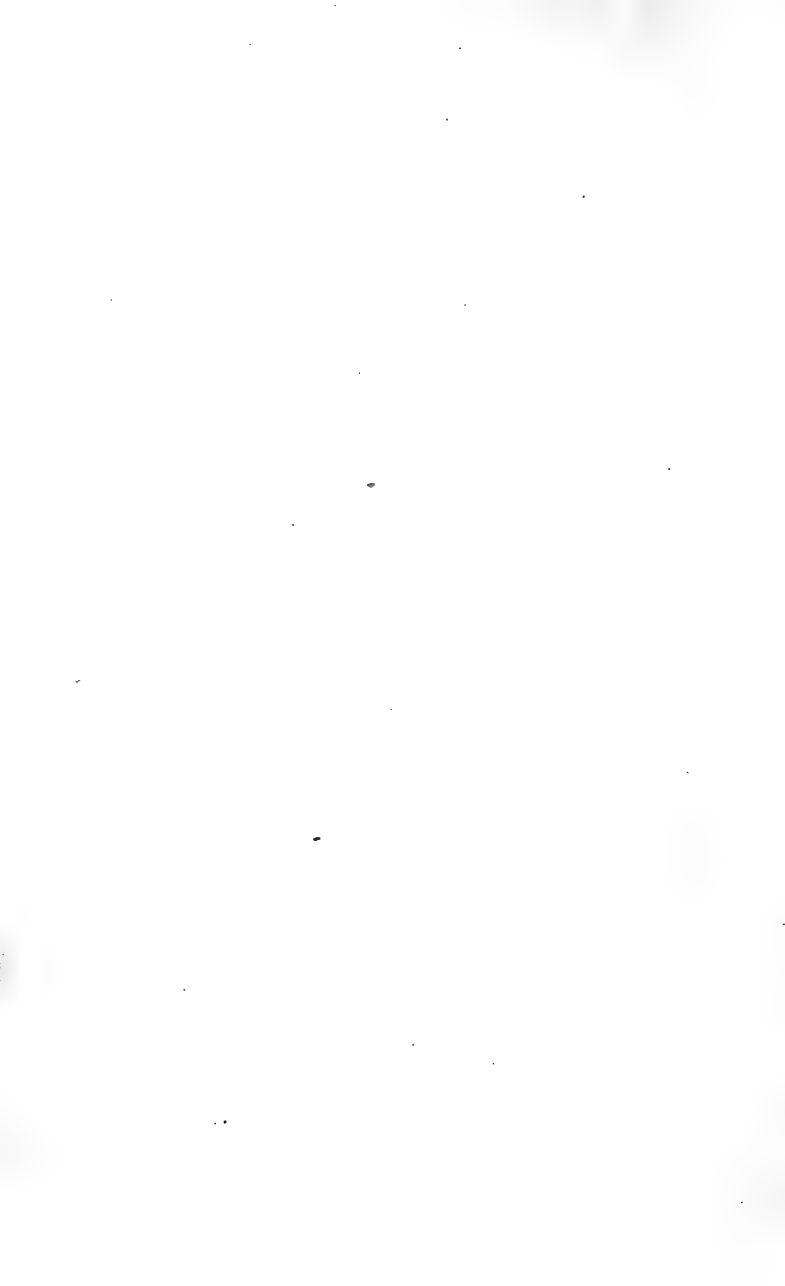
A. MORLEY DAVIES.

*February 2, 1920.*



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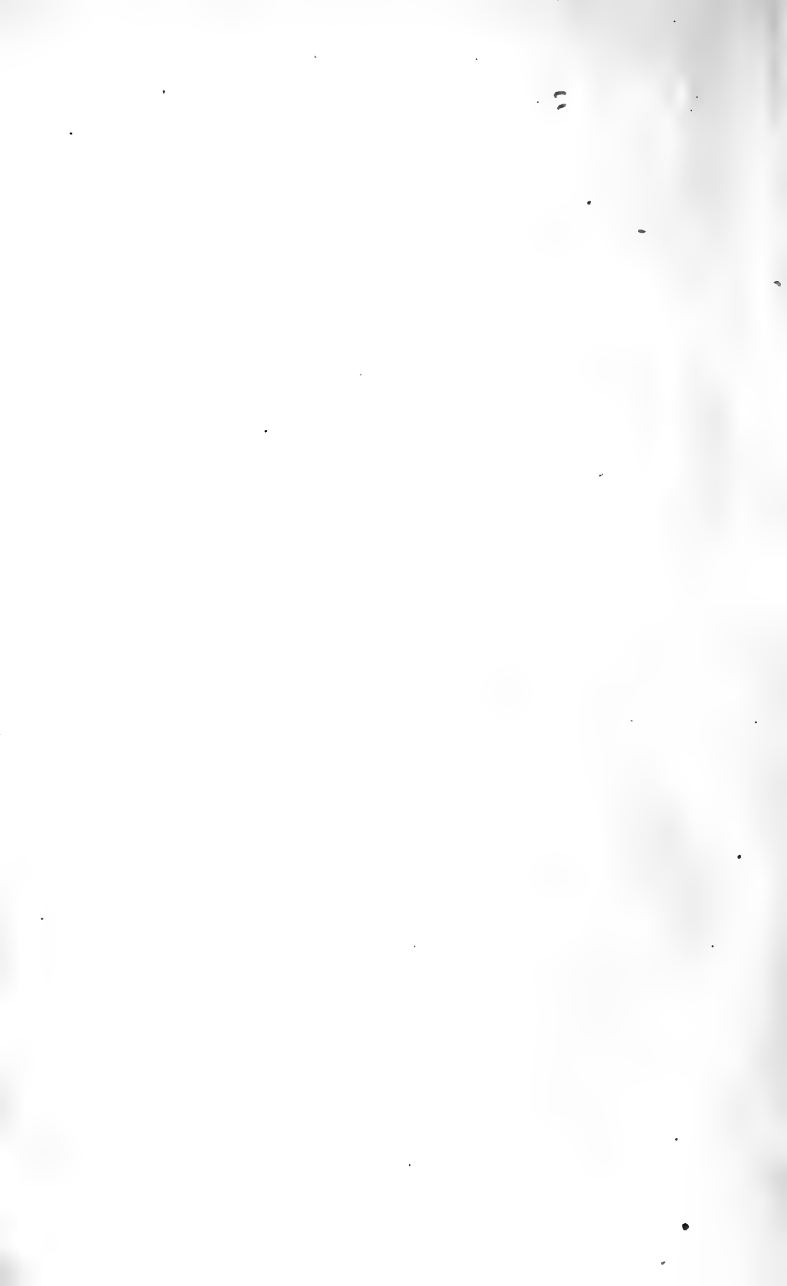
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# PALÆONTOLOGY

## I

### THE BRACHIOPODA

ON a large-scale geological map of England there is seen a narrow, sinuous band of colour traceable almost continuously from the Dorset coast to that of Yorkshire, explained on the index as "Cornbrash." This corresponds to the outcrop on the actual ground of beds of rubbly limestone, in which are many small pits very attractive to the fossil collector. Various kinds of fossils may be picked up, but among the most noticeable, and often the most beautifully preserved, are the forms represented in Figs. 1 and 2.

It is seen at once that these two forms, though differing in details, have many features in common which distinguish them from their companions in the Cornbrash. Each one shows perfect symmetry about a single plane; each has at one end a rounded projection perforated by a circular opening; and the surface of each, examined under a lens, shows, if in a good state of preservation, a regular pattern of minute dots (Fig. 1, *c*).

Although, as a rule, each specimen appears at first sight to be a single solid body, examination soon shows

that it is really a hollow shell (the *test*) composed of two main portions in contact along their edges. These are called the *valves* of the shell, and the valve which carries the circular opening is called (for reasons to be seen presently) either the *ventral valve* or the *pedicle valve*; the

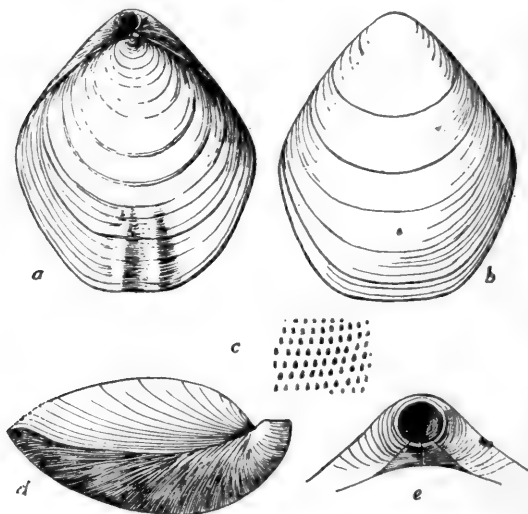


FIG. 1.—*TEREBRATULA INTERMEDIA* (J. SOWERBY).

*a*, Dorsal view; *b*, ventral view; *c*, punctation; *d*, side view; *e*, umbo, foramen, and deltidial plates of ventral valve. *a*, *b*, *d*, Natural size; *e*,  $\times 2$ ; *c*, greatly enlarged. (Original.)

other is called the *dorsal* or *brachial* valve. The rounded protuberance of the ventral valve is called its *beak* or *umbo*. The dorsal valve has a similar, but much less prominent umbo, without any opening. The end of the shell at which lie these *umbones* is regarded as the hind or *posterior* end, the opposite end being the front or



*anterior*; the *length* of the shell is from one to the other. The *breadth* of the shell is measured at right angles to the length, in the plane separating the two valves, while the *thickness* is from the surface of one valve to that of the other where they are farthest apart.

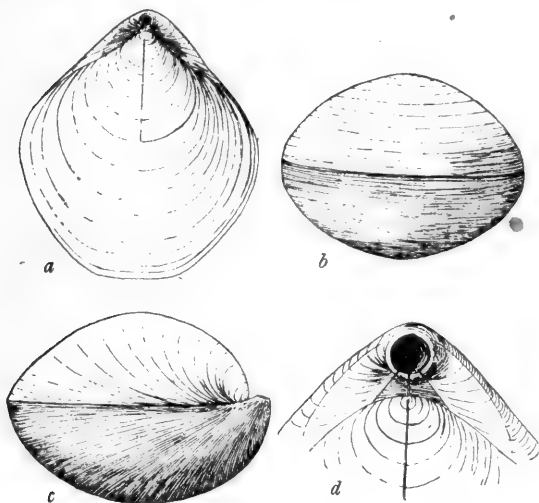


FIG. 2.—ORNITHELLA OBOVATA (J. SOWERBY).

*a*, Dorsal view; *b*, anterior view; *c*, side view, all natural size; *d*, umbonal region of both valves,  $\times \frac{2}{3}$ , showing cardinal area, foramen, and deltidial plates in ventral valve, umbo and dark streak indicating internal septum in dorsal valve. (Original.)

The surface is nearly smooth, but at irregular intervals it is marked by fine lines nearly parallel to the valve margins, but becoming crowded together as they approach the umbo. Evidently these lines, like the rings of a tree or those of a ram's horn, mark stages of growth (*growth-lines*); they must, in fact, represent the margins

of the valves at successive intervals, and it is evident that the earliest formed shell must be that in the region of the umbo.

The region of the umbones is usually obscured by rock substance, which it is a tedious matter to remove, but when this is done some interesting features are revealed. The anterior side of the circular opening (*foramen*) is seen to be differently bounded from the remaining three-quarters of its circumference. It is not bounded by the ventral valve proper, but by the oblique ends of two small plates of triangular shape: these are called the *deltidial plates*, and the complete gap in the shell (of which the foramen is only a part) which would be exposed by their removal is called the *delthyrium*. On either side of these plates the surface of the ventral valve shows a somewhat crescent-shaped, concave area, having the appearance of being cut out from the shell: this is the *cardinal area*. Along this area the margin of the ventral valve is seen to be pressed close against and slightly to overlap that of the dorsal valve: it is easy to see that here the valves are hinged together, while elsewhere they may have been free to gape apart, the gaping being greatest at the anterior end. Indeed, although the great majority of these fossils are found with the valves tightly closed, one is occasionally found in which they yawn more or less.

All the description so far given will apply equally well not only to the two forms from the Cornbrash, but to many others found in older or younger strata. All these were long united under the common name *Terebratula*,

and were said to constitute a *genus* of animals. At the present time the name *Terebratula* is used in a more restricted sense, but we can still speak of all these forms as *terebratuloids*. To distinguish these two *species* from one another James Sowerby, nearly a century ago, named one *Terebratula intermedia* and the other *Terebratula obovata*. Let us now see some of the differences that underlie their resemblances.

The two Cornbrash species obviously differ in proportions. The ratio of length, breadth, thickness is in *T. intermedia* roughly 12, 10, 6, in *T. obovata* 11, 10, 8, the latter being thus broader and thicker. In the latter also the boundary between the cardinal area and the general surface of the ventral valve is a very definite edge, while in the former it is rounded off so as to be somewhat indefinite. The foramen of *T. intermedia* is much larger in proportion to the size of the whole shell, and the outer edges of the deltidial plates, if continued, would form an obtuse angle; while in *T. obovata* the foramen is small, and the corresponding edges would form a right or slightly acute angle.

If we break open these two shells we shall often find them to be hollow, and projecting into the cavity from near the posterior end there is what looks like a looped ribbon covered with little crystals of calcite. In the case of *T. obovata* this loop extends forward nearly to the front end of the cavity; in *T. intermedia* it is less than half this length (Fig. 3). In the former also there runs along the middle line of the dorsal valve an internal ridge, forming an incomplete partition (*septum*). The presence of this can

be detected from the exterior by the appearance of a dark streak: little or no trace of such can be seen externally in *T. intermedia*. It has been found that the presence of such a dark streak, indicating a strong dorsal septum, is constantly associated with the presence of a long internal loop, and its absence with a short loop, in all terebratu-

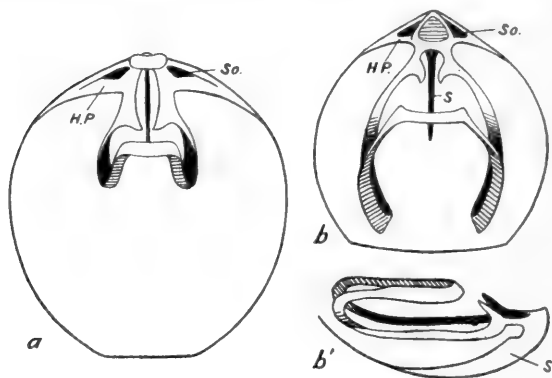


FIG. 3.—BRACHIAL LOOPS.

*a*, *T. intermedia*; *b*, *b'*, *O. obovata* (natural size); *a*, *b*, interior views of dorsal valve; *b'*, side view, test removed to expose the septum; *H.P.*, hinge-plate; *S.*, septum; *So.*, sockets. (After Davidson.)

loids. We may therefore divide these into a long-looped and a short-looped group.

This difference in the length of loop is regarded by palæontologists, for reasons that will appear later, as a more fundamental difference than any of the others that have been given. It is considered too important to be expressed by a mere difference of specific name: the generic (and even the family) names must also be

different. Thus it is that the species *obovata* is no longer called *Terebratula*, but *Ornithella*.\*

Shells such as these are not only found fossil in many different strata; they are also dredged, with the animal still living of which they form part, from the ocean in most parts of the world. Altogether 112 species of terebratuloids have been found in the exploration of the sea, as well as forty-six other species which, though not actual terebratuloids, are so near them in structure that they are united with them in zoological classification under the name *Brachiopoda* (or *brachiopods*). They are purely marine in habitat, no species having ever been found in any lake, river, or estuary; the largest number of species live on the bottom between the depths of 30 and 100 fathoms; many species (and perhaps the greatest number of individuals) live in shallower water than this, even in a few cases above low-water mark; only a few species live in water beyond the 100-fathom line. The coasts of Japan furnish the largest number of species for any one area: those on the east and west coasts being almost entirely different (20 species in eastern, 11 in western waters, of which only 2 species are common to both.) The geographical range of some species is very wide, that of others very restricted.

A living terebratuloid, such as *Magellania flavescens* of the Southern Seas, lives attached to the sea bottom (usually many individuals in a cluster) by a short muscular stalk (*pedicle*) which emerges through the

\* For further explanation of the terms *species*, *genus*, *family*, etc., see Chap. XII.

foramen in the ventral valve. It feeds entirely upon the microscopic organisms, both animals and plants (but probably in the main the minute plants known as diatoms) which drift about helpless in the currents in the water. So enormously abundant are such organisms in the ocean, and so quickly do they grow and reproduce themselves, that they form the food, at first, second, or third hand, of nearly all the animals in the sea. It has well been said that "all fish is diatom" in the sense that "all flesh is grass," for there is nothing in the ocean comparable to the vegetation of the land. The larger sea-weeds do not afford food to many of the marine animals.

An animal feeding upon such helpless microscopic prey can do without many of the organs that are essential to the familiar animals of the dry land—eyes and ears to see their prey, arms and jaws to seize them, swimming or running organs to pursue them, are all needless. Shut up within its shell a brachiopod is comparatively safe from enemies; fixed by its pedicle, only very violent storms can throw it up to die on the shore. All it needs in external organs are (1) some means of creating a constant current into and out of its shell-cavity, to bring in food and oxygen and carry out waste products; (2) a shell so arranged that it can be closed tightly when necessary for safety, and opened at will to allow ingress and egress of the water-currents. These necessities control and determine the structure both of the soft parts of the animal's body and of the shell which it secretes.

The actual "body" of the terebratuloid, containing

the digestive tube, central nervous system and other fundamental organs, occupies a surprisingly small portion of the interior of the shell. From it there arise a pair of muscular sheets which form a lining to the two valves, and by which the valves are in fact secreted: these are called the mantle-lobes, and the cavity enclosed by them is called the mantle-chamber. Hanging freely in this mantle-chamber are a pair of spiral ribbons, fringed with tentacles along their whole length and covered with microscopic vibratile hairs (*cilia*), the constant movement of which creates the water-current which is so vitally necessary, and also serve as gills (breathing organs for the exchange of gases between blood and sea-water). The shelly "loop" which we have seen in the fossil forms serves to support these spiral "arms" (or *brachia*) as they are misleadingly termed. In *M. flavescens* the loop is long and doubled back on itself, the two halves of this doubled-back portion being distinguished as "ascending lamellæ" from the longer "descending lamellæ" (Fig. 8).

If we examine the interior of the valves of a modern terebratuloid, we can make out certain details of structure more easily than on a fossil specimen; though afterwards we shall find we can recognize the same details in the fossils. The two valves are hinged together by means of a pair of projections from the ventral valve (*hinge-teeth*) which fit into two hollows (*dental sockets*) in a horizontal shelf in front of the umbo of the dorsal valve (*hinge-plate*). To give leverage for the opening of the valves there is a short knob-like projection (*cardinal*

*process*) from the dorsal valve into the umbonal cavity of the ventral valve. The line along which the margins of the two valves meet in the neighbourhood of the hinge-teeth is called the *hinge-line*. To effect the opening of the valves there are muscles fixed at one end to the cardinal process, at the other to the interior of the ventral valve (*divaricator* muscles); to close the valves there are other muscles running across from valve to valve (*adductor* muscles). All muscles act by contraction which pulls their two attachments towards one another. The dorsal attachments of these two sets of muscles being on opposite sides of the fulcrum (the *hinge-line*), they work against one another. The muscles of the pedicle are attached to the interior of the ventral valve.

When the muscles decay after death, the areas of the shell to which they were attached show as slight depressions devoid of the smoothness of the rest of the internal surface. Thus it is possible to tell in a fossil brachiopod the presence and arrangement of these muscles. Although the details differ greatly among the many forms of brachiopods, the adductor impressions in the ventral valve are always close together, and the divaricator impressions lie more or less to the right and left of them.

The body proper of a brachiopod being so small, it is not surprising that the reproductive organs should extend into the mantle which lines the two valves; impressions of the ovaries are in many forms to be seen on the inner surface of the shell; so also are the branching impressions of vessels belonging to a circulatory system (*vascular markings*). In forms like the terebratuloids



which have a punctate shell, each punctation contains a minute outgrowth of the mantle, and in at least one recent species this has been shown to have the structure of a simple sense-organ, though the nature of the sense is unknown.

From the egg the larval brachiopod escapes as a microscopic body covered with vibratile cilia, by means of which and the action of currents it gets the only chance of its life to migrate away from the fixed home of its parents. It is not likely that any one generation travels very far, yet some modern species are world-wide, thanks to the cumulative effect of small journeys through thousands of generations. The length of life of brachiopods in general is not known, but in one species there is evidence of five years' life.

Very soon the larva fixes itself by a rudimentary pedicle and begins to secrete two valves. In all observed cases this first shell, or *protegulum*, has the same general form, which is also the form of the most primitive brachiopod shells in the Lower Cambrian rocks (Fig. 6, *a*). This resemblance favours the view that the development of the individual (*ontogeny*) repeats, in an abbreviated and more or less imperfect manner, the ancestral history of the race (*phylogeny*). This principle of *recapitulation*, or *palingenesis*, is of the utmost importance in palæontology as a criterion of blood-relationship, and especially in the case of those animals whose shell-growth is of the kind found in brachiopods, where the early stages of the shell are preserved and added to, to form the later (growth by *accretion*).

The protegulum of a brachiopod forms the apex of each valve. Too often, owing to the exposed position of the umbo, especially of the ventral valve, it may be rubbed away in later life; in some forms it is absorbed in the enlargement of the pedicle-opening; but in many cases it persists through life. Growth consists in adding to it both on its inner surface and on its margins—to the greatest extent at the anterior margins. During this growth the shape of the shell may change, perhaps more than once; it may acquire surface-ornament, and this may alter or disappear; but (apart from wear and tear) every stage is preserved in the adult shell, and if the characters of an early stage are the same as those of the adult shell of a brachiopod of earlier date, there is a presumption that the latter may be ancestral to the one under consideration.

Growth by accretion is not possible, however, for all parts of the skeleton: the loop, once formed, could not grow so and remain a loop. As the valves increase in size, repeated resorption and fresh secretion of the shelly substance of the loop must take place. The difference in development between the valves and the loop is like the difference between that of a ram's horn and that of a stag's antler. Hence the adult loop affords no evidence of the stages through which it has passed. These can only be determined by actual observation of the development in living brachiopods, and by the fortunate preservation of immature as well as mature specimens among fossils. The former method has yielded results which afford striking confirmation of the principle of palin-

genesis, for it has been shown by Beecher and Thiele that the loops of the modern terebratuloids *Magellania* and *Macandrevia*, though much alike in the adult stage, pass through two quite different series of metamorphoses, and in each case the successive stages correspond to the adult loop in a number of other genera, some still living, others extinct (Fig. 9).

It will be convenient here, before returning to the

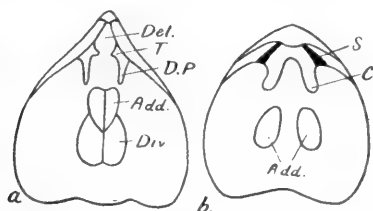


FIG. 4.—HEMITHYRIS PSITTACEA (CHEMNITZ).

Recent,  $\times \frac{5}{4}$ .

*a*, Ventral; *b*, dorsal valve; *Add.*, adductor muscle-impressions; *C*, crus; *Del.*, delthyrium, the deltidial plates removed; *Div.*, divaricator impressions; *D.P.*, dental plates; *S*, socket; *T*, hinge-tooth. (Original.)

fossil forms, to consider some of the other brachiopods found living in the sea.

*Hemithyris psittacea* (Fig. 4) is a form living in the cold northern waters: its shells are often cast up by storms on the coast of Labrador. It agrees with the terebratuloids in having dissimilar symmetrical valves, the larger being perforated for a pedicle, and in having the delthyrium partly closed in by a pair of deltidial plates. But these plates, instead of bounding the foramen on its anterior side only, bound it laterally and even tend to meet on the posterior side just under the umbo (as in Fig. 9). On

examining the surface with a lens we fail to find any trace of the pattern of punctations so characteristic of the terebratuloids; but we observe a silky, fibrous appearance. Internally, we find still more striking differences. It is true that the cardinal process, hinge-plate and sockets, hinge-teeth and the several pairs of muscle-impressions are all present with only slight differences of arrangement; but although spiral brachia exist there is no calcareous loop. From the hinge-plate two short processes project into the cavity, and correspond to the beginning of a loop: they are termed the *crura* (plural of *crus*). Again, in the umbonal cavity of the ventral valve there are a pair of vertical partitions which, as they extend into and strengthen the teeth, are called *dental plates*: these, however, are also found in some terebratuloids.

Forms more or less similar to *Hemithyris psittacea* are often found fossil, in the Cornbrash among other strata. In the works of Sowerby they were included under the broad name of *Terebratula*, but afterwards distinguished by the separate name *Rhynchonella* by Fischer von Waldheim. This name in turn has had to be restricted to a portion only of these forms, but we can still conveniently speak of them as *rhynchonellids*.

*Thecidea (Lacazella) mediterranea* is a small brachiopod with a very thick shell. It has no pedicle, but is found cemented to other shells by its ventral umbo. The long and narrow delthyrium occupies the middle of a large cardinal area, and is completely closed up, not by a pair of plates, but by a single one (*deltidium*). Internally there

are no crura even, but the thick dorsal valve has deep furrows with ridges between corresponding to the course of the spiral brachia. The other structures do not differ essentially from those of rhynchonellids and terebratuloids, but evidently this is something distinct from both. In particular, the single deltidium in place of two deltidial plates is a more important difference than might at first sight appear, because the study of the early development has shown that these structures appear as secretions by different parts of the body—the single plate, by the pedicle itself; the double plates, by the ventral mantle-lobe. Only two species of *Thecidea* are known to be living now, but many fossil species are known, though on account of their small size they are often overlooked. Among modern forms *Thecidea* is an isolated genus with no near allies; but there are many extinct forms more nearly related to it than to any other living genus.

*Discinisca lamellosa* (Fig. 7, *c*) is found in shallow water or between tide-marks on the coast of Peru. Its shell differs both in texture and in shape from those hitherto considered, for it is not calcareous but has a horny appearance and consists of organic matter with some calcium phosphate instead of carbonate; and each valve is nearly circular in outline, with the umbo near the centre. The ventral valve resembles a low cone of which one portion of the surface (on the posterior side) has been crushed in. In the middle of this depressed area is a narrow slit through which the pedicle passes obliquely. The dorsal valve is a still flatter cone. Internally, there are no hinge-teeth, no cardinal process

or hinge-plates, no crura or loop; in fact, the only internal features of the shell are the muscle-impressions and a small median septum in the ventral valve anterior to the delthyrium. Here is a brachiopod differing greatly from all the previous forms, especially in not having its valves hinged together, but only attached by muscles and other soft tissues. There are six species of *Discinisca* living and one species of the allied genus *Discina*: they may be spoken of as *discinids*. Many fossil discinids are known, but owing to the inarticulate (unhinged) character of the shell it is commoner to find isolated valves than complete shells—the reverse is the case in terebratuloids and rhynchonellids, and indeed most brachiopods.

*Lingula anatina* (Fig. 7, *b*) is a brachiopod which burrows in the sea-bottom in very shallow water; it has a very long pedicle which it uses to draw itself into its burrow when necessary. Like *Discinisca* it has a horny shell. In shape it is somewhat oblong, the two valves being very nearly alike, each having the umbo at the extreme posterior end. There is no delthyrium, the valves diverging at the posterior end for the passage of the pedicle. Internally the valves show no hinge-structures or brachial skeleton, though the spiral brachia are present as usual; but in the dorsal valve there is just below the umbo a reflected portion of the shell resembling a cardinal area. The muscular impressions are faint, but are more complex than in previous cases, the absence of articulation making it possible to have muscles for sliding the valves sideways as well as for opening and

closing the shell. Fifteen species of living lingulids are known, and a very great number of fossil species.

The resemblance of many fossil brachiopod shells to those of living forms compels us to believe that the former were also once parts of living organisms which lived in much the same manner. Where therefore we find brachiopod shells in a stratum we must conclude that it was originally a deposit on the sea-bottom, and we may even venture to estimate the depth below the surface at which it was deposited from a consideration of the abundance and generic identity of the brachiopods. But the fossils also serve another very important purpose.

As long ago as 1688, the famous Dr. Robert Hooke foresaw the possible utility of fossils as time-markers. "However trivial a thing a rotten shell may appear to some," he wrote, "yet these monuments of nature are more certain tokens of antiquity than coins or medals . . . and though it must be granted that it is very difficult to read them and to raise a chronology out of them . . . yet it is not impossible." It was William Smith who, at the end of the eighteenth century, was first able to "raise a chronology out of them," by showing that in the series of strata that lie one upon the other in the Bath district (and elsewhere) each division is distinguished by particular species of fossils.

Thus William Smith found that underneath the Cornbrash were a series of beds of hard flaggy limestone, which he termed the "Forest Marble"; below these again

the Bradford clay; below this the thick mass of oolitic limestone for which Bath is famous, and so on. In Fig. 5 are shown the species of brachiopods that are characteristic of two of these formations. The value of such fossils for arranging the stratified rocks of the earth in systematic order will be realized when we remember that though in a hilly district with many quarries and other openings into the rocks like that around Bath, or along a cliffy coast, it may be quite easy to prove clearly how one group of strata overlies another, yet when we try to follow the strata from place to place and especially into regions where exposures of the rocks are few and poor, there are many difficulties to be met. A stratum may change its character, for example the Forest Marble changes from limestone to clay in Northamptonshire; or it may "thin out" and disappear altogether; or a "fault" may suddenly shift its position greatly. Amid these difficulties, the finding of distinctive fossils will often save the geological surveyor from a mistake which might perhaps lead someone to sink a mine or bore for water in a wrong place.

The whole group of animal species found together in the same beds are spoken of as the *fauna* of those beds, just as the collection of species now living in any given area is the *fauna* of that area. In past times, as at present, a fauna had a definite *habitat* or distribution in space; so that the fact of a fossil fauna in Australia being different from one in England does not prove that they were not contemporaneous. This fact may at first sight seem to make it impossible to apply William Smith's



principle over great distances ; but how it can be done will be explained later. At present we must consider another point.

At least 6,000 species of fossil brachiopods have been described, and of these only 25 are identical with living species, while 133 living forms are unknown as fossils. These 6,000 species represent the members of a great number of successive faunas that have succeeded one another throughout geological time. If species followed one another without any guiding principle of succession, the human memory would be unable to grapple with the geological sequence. Fortunately this is not the case. While species are short-lived, geologically speaking, genera are longer lived, but yet most of them are restricted to a limited portion of geological time ; and the abundance of certain genera will characterize large groups of strata, just as the abundance of certain species marks a smaller group. The smallest thickness of rock that can be distinguished by means of its fossils over a wide geographical area is called a *zone* : its actual thickness may vary in different cases from an inch or even less to several hundred feet, according to the net rate at which sediment was accumulating. A zone can, if not very thin, be divided into a number of beds. The time during which the strata constituting a zone were deposited is called a *hemera*, and is defined as the time during which some one selected species was at the *acme* or height of its development. We are unable at present to bring this unit of geological time into relation with any of our astronomical time divisions.

A number of consecutive *hemera* (varying in different cases from three to ten) are grouped as an *age*, corresponding to the development of a genus or a family: the corresponding thickness of strata is called a *stage*. *Ages* are again grouped into *epochs*, these into *periods*, and these into *eras*, the bounds of these being determined by great and rapid changes of fauna. These terms and their equivalents may be tabulated thus:

TIME-DIVISIONS.	ROCK-DIVISIONS.
Era.	Group.
Period.	System.
Epoch.	Series.
Age.	Stage.
Hemera.	Zone.

Thus the Cornbrash is, approximately, the zone of *Terebratula intermedia*. Each of the brachiopods shown in Fig. 5 also gives its name to a zone, and all these zones with some others make up the Bathonian stage, which takes its name from Bath, around which city these zones are well displayed. This stage is part of the Upper Jurassic Series of the Jurassic System, so named from the Jura Mountains. This in turn is part of the Mesozoic Group.\*

The sequence of forms in division after division of geological time often appears casual and meaningless, but that is probably only owing to the imperfection of our knowledge. In a number of cases we can trace a

\* See Appendix I. for tabulated statements of time-divisions. Reference to these tables will frequently be necessary during the reading of what follows.

succession which has all the appearance of being an actual genealogical tree, and as we pass back into the earlier geological times we find a convergence of the lines of descent towards a few very simple forms. At the beginning of the palæontological record we seem to be very near the beginning of the Brachiopoda.

Classification must be based on structure and blood-relationship. We cannot at this stage give a full justification for the following classification (which is essentially that of Beecher, 1893), but it is given as the best of



FIG. 5.—BATHONIAN TEREBRATULACEA.

*a, a'*, *Epithyris bathonica* S. Buckman, Bath oolite,  $\times \frac{1}{2}$ ; *b*, *Ornithella digona* (J. Sowerby), Bradford clay,  $\times \frac{2}{3}$ . (After Davidson.)

many attempts to express the inter-relationships of Brachiopoda.

The Brachiopoda are so well defined and sharply marked off from all other animals that they may well be accorded the rank of a *phylum* or primary branch of the Animal Kingdom.\* Brachiopoda are marine animals fixed by a pedicle or otherwise, feeding on microscopic floating organisms by means of spiral "brachia,"

\* Many zoologists unite the Brachiopoda with the Bryozoa in a phylum Molluscoidea, of which they form two classes. The differences between them appear to the present writer too profound to be expressed as merely class differences.

secreting a shell with dorsal and ventral dissimilar symmetrical valves.

In the opinion of most students of the phylum, the most fundamental plane of cleavage is that between forms like *Lingula* and *Discinisca*, in which the valves are not articulated by teeth and sockets, and those like *Terebratula* in which they are. These two divisions constitute the **class** *Inarticulata* and the **class** *Articulata* respectively.\* The characters of the delthyrium afford the next means of subdivision. *Inarticulata* such as *Lingula* which have no delthyrium constitute the **order** *Atremata*; those with a delthyrium enclosed by the ventral valve (at least during early life), the *Neotremata*; *Articulata* with a median deltidium form the order *Protremata*; those with a pair of deltidial plates, *Telotremata*. Each of these orders is divided into **suborders** (or, as Prof. Schuchert prefers to call them, **superfamilies**) and these into **families**, made up in turn of one or more **genera**, each with one or more **species**.

The beginner in Palæontology is often troubled by the importance attached in classification to the internal characters of fossils or other features which are often invisible in ordinary specimens, and is puzzled to understand how identification is possible in such cases. It may be pointed out that if one single specimen shows all the characters that are necessary to determine its systematic position, many others can be recognized as

\* Professor Schuchert, of Yale University, dissents from this view, regarding articulation as a feature that has been evolved independently in the orders *Protremata* and *Telotremata*.

identical with it by their minor features. Hence the apparent paradox that it is often easier to determine the species of a fossil than its genus, which is quite contrary to the ordinary conception of classification. For the specific character is commonly some feature of external shape or ornament that is easily recognized but might be found in any one of a number of genera, while the generic character may be some feature which only an exceptionally well-preserved specimen will show. We must never forget that classifications are not framed as means for the easy naming of specimens, but are intended to indicate the real natural relationships of species.

In the particular case of the internal characters of brachiopods, however, these are not so inaccessible as a beginner may think. It often happens that the interior of a shell may be filled, after death, with foreign material such as mud or sand, and that afterwards the shell may be dissolved, leaving the consolidated mud or sand as in *internal cast* or mould of the shell. On such a cast all the structures on the inner surface can be recognized—hollows being represented by elevations, and projections by depressions. It is even advisable, when the infilling material is suitable and specimens are abundant, to make casts artificially by burning away or otherwise removing the shell.

#### ORDER I.: ATREMATA.

Inarticulate Brachiopoda with horny and phosphatic shells, the pedicle emerging between the divergent valves, which show little or no tendency to enclose it in a delthyrium.

This is the most primitive order, especially characteristic of the Older Palæozoic era, only a single family, the *Lingulidæ*, surviving through later eras down to the present day. It is divided into two sub-orders:

1. **Obolacea**.—Rounded and lenticular in form, with short pedicle and thick shell; probably fixed to floating seaweed. These are confined to the Older Palæozoic era, and range from the most primitive of all brachiopods, *Rustella* of the Cambrian, which may be near the ancestral form of all four orders, through the *Obolidæ* to the highly specialized *Trimevellidæ* of the Ordovician and Silurian. In these last, the muscle attachments are carried on platforms separated from the inner surface of the valves by long and narrow cavities: these give the internal casts a very complex form. In *Obolus*, each valve has a well-marked cardinal area, that of the ventral valve with a longitudinal pedicle-groove, and its umbo being more prominent.

2. **Lingulacea**.—Elongated in form, burrowing, with thin shell and long pedicle.

These begin in the Cambrian with *Lingulella*, which retains the obolid characters of a cardinal area, with pedicle-groove in the dorsal valve only, and of a more prominent ventral umbo. It is followed in the Ordovician by *Lingula*, in which the valves are almost equal, and the pedicle groove is wanting. This genus survives to the present time, and so is one of the longest-lived of all genera, not only of Brachiopoda, but of all but the lowliest phylum of animals.

## ORDER II.: NEOTREMATA.

Inarticulate Brachiopoda, in which the valves acquire a more conical form, and the pedicle becomes surrounded by the ventral valve and comes to emerge close to the

umbo and at a distance from the margin. In the more typical sub-orders the shell is horny and phosphatic.

SUB-ORDER 1. **Acrotretacea.**—Shells but little changed from obolids in shape, especially the dorsal valve. Older Palæozoic. Chief genera: *Acrotreta*, in which the ventral valve has a high cardinal area (Camb.–Ord.),\* and *Siphonotreta* in which the pedicle-opening leads into an internal tube, and the shell is perforated by pores which extend into hollow spines (Ord.–Sil.).

SUB-ORDER 2. **Discinacea.**—With each valve more or less conical in shape, umbo eccentric. In *Trematis* of the Ordovician the pedicle-aperture is a long slit extending from the posterior margin to the umbo; but in *Orbiculoides* (Ord.–Cret.) it becomes closed-in as growth proceeds by a plate called the *listrium*, and the short pedicle passes obliquely through the slit that remains. In existing seas this sub-order is represented by *Discinisca* and *Discina*.

SUB-ORDER 3. **Craniacea.**—Aberrant forms, in which the shell is calcareous and the pedicle and pedicle-opening are lost, fixation by cementation taking the place of fixation by pedicle. Ordovician to Recent. The principal genus *Crania* has the range of the sub-order.

### ORDER III.: PROTREMATA.

Articulate Brachiopoda, with delthyrium restricted by a deltidium. Shells calcareous. No brachial skeleton, except crura in some cases.

SUB-ORDER 1. **Strophomenacea.**—In the Cambrian, this is represented by the little *Kutorgina*, which, but for its more calcareous shell, broader shape and wide delthyrium, differs little from the contemporary Inarticulata, for

\* These are obvious abbreviations of the names of the geological systems, tabulated in Appendix I.

its deltidium and hinge-teeth are rudimentary. It shows, however, the long straight hinge-line and wide shell that characterize so many of the Palæozoic Articulata.

In the Ordovician, and still more in the Silurian, this sub-order attains very great importance, and some of its most familiar members deserve detailed treatment.

*Leptæna rhomboidalis* (Fig. 6) of the Wenlock Limestone

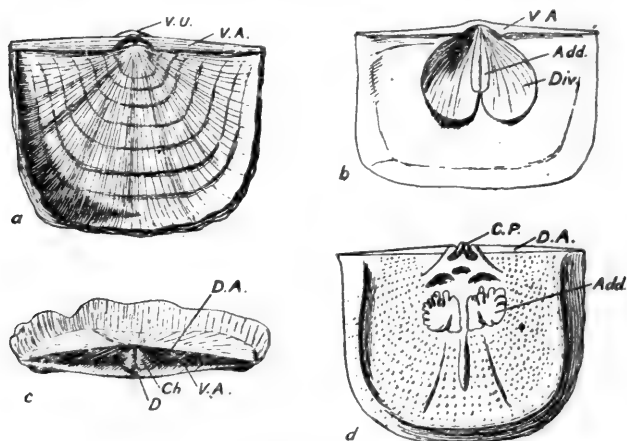


FIG. 6.—LEPTÆNA RHOMBOIDALIS, WILCKENS.  
(Natural size.)

*a*, Dorsal view; *b*, interior of ventral valve; *c*, posterior view; *d*, interior of dorsal valve; *Add.*, adductor impression; *Ch.*, chilidium (showing median pedicle-groove); *C.P.*, cardinal process; *D.*, delthyrium; *D.A.*, cardinal area of dorsal valve; *Div.*, divaricator impression; *V.A.*, cardinal area of ventral valve; *V.U.*, umbo of ventral valve. (Original.)

is a broad shell (length : breadth = about 2 : 3) with a semi-elliptical outline, the long straight hinge-line forming the greatest breadth of the shell. The early (posterior) part of the shell is flat, but after growing to a length of about two centimetres a sudden change takes place and the



surface of the ventral valve becomes bent on itself at about right angles, making that valve in the adult highly convex externally, while the ventral valve is correspondingly concave, so that the change does not result in great increase of thickness.\* Concavo-convex shells are common among Palæozoic brachiopods: when, as in *Leptæna*, the dorsal valve is concave, they are said to be *normally concavo-convex*; when the ventral is concave they are *reversed concavo-convex* (or convexi-concave).

The surface of the shell is ornamented with radiating ridges, crossed by much finer concentric lines. In addition to these there appear at a little distance from the umbo coarser and irregular concentric corrugations, which rapidly increase in size up to the line of growth-change (reflection), beyond which they cease, as though they were premature attempts to make the change in growth-direction.

On each valve there is a wide and low cardinal area, extending all along the hinge-line. The delthyrium notches both areas equally so that it is rhomboidal in shape. In the ventral valve there is a small deltidium close to the umbo; in the dorsal a much larger convex plate (*chilidium*), with a median groove, covers the whole opening. The pedicle-opening is small, between umbo and deltidium (encroaching on the former in old age); the pedicle probably rested on the groove of the chilidium.

In the interior of the ventral valve, well-marked muscle-

\* In *Ornithella obovata* a somewhat similar growth-change takes place in old age, but that being a biconvex shell, both valves increase in external convexity, and so the shell becomes greatly thickened.

impressions and teeth are seen. The raised rims of the divaricator-areas join on to the teeth and delthyrial margin like rudimentary dental plates, and there is a slight median septum. In the dorsal valve, the cardinal process is short and bifid and fits closely under the chilidium. Dental sockets are conspicuous.

Allied genera to *Leptæna* are *Rafinesquina* (with fine radial striations alternately larger and smaller, and with ridged muscle-areas) and *Stropheodonta* (with fine denticulations along the hinge-line, and inconspicuous chilidium). Neither of these has the concentric corrugations of *Leptæna*. All three are represented by common species in the Ordovician and Silurian systems. *Davidsonia* of the Devonian fixed itself by cementation on to other shells, and shows internal spiral markings which are interesting as evidence that spiral brachia existed in this extinct family.

Of genera with reversed concavity, *Strophomena* might be described as a reversed *Rafinesquina*, and *Strophonella* as a reversed *Stropheodonta*.

The sub-family *Orthotetinae* (Fig. 7, *f-i*) is characterized, in general, by well-marked dental plates, which may extend far forward in the pedicle-valve — sometimes parallel to one another (*Meekella*), or diverging (*Schellwienella*) or converging to form a median septum (*Orthotetes*). In *Derbya*, however, the dental plates are greatly reduced, the septum extending to the apex of the umbo. These four genera are Carboniferous and Permian. Externally all the genera of this sub-family are radially ribbed. Certain species belonging to different genera are so closely similar externally, that it is impossible to discriminate between them without examining the interior, for which the grinding of sections may be necessary: such species are said to be *homœomorphs* of

one another. The failure to discriminate between homœomorphs has frequently led to mistakes in the correlation of strata.

*Productus productus* (commonly, but wrongly, termed *Productus martini*) is one of many species of *Productus* that abound in the Lower Carboniferous Limestones and Shales. In general form it is not unlike *Leptaena*, but the convex ventral valve shows a stronger and more uniform curvature, and its umbonal region is much larger and more rounded; there is no cardinal area and no delthyrium. The dorsal valve is for the first two centimetres from the umbo, almost flat, very slightly concave; it also has no cardinal area and its umbo does not project above the hinge-line. The hinge-line is long and straight, but less than the greatest breadth of the shell. The profile of the ventral valve first forms an arc which is almost a semicircle, of which the dorsal valve forms the chord, and at two centimetres from the umbo the valves meet as though the shell were complete. From this distance on, however, the ventral valve is continued with very slight curvature for a considerable length, while the dorsal valve bends abruptly and continues in close contact with the ventral, the two valves thus forming a sort of flange with no space between them when the shell is closed. This flange is very easily broken off during extraction of the fossil from the rock, and what remains has all the appearance of a perfect shell, two centimetres long and about 2.5 centimetres broad.

The surface is ornamented with close-set radiating ribs, rounded in section, with a few concentric corruga-

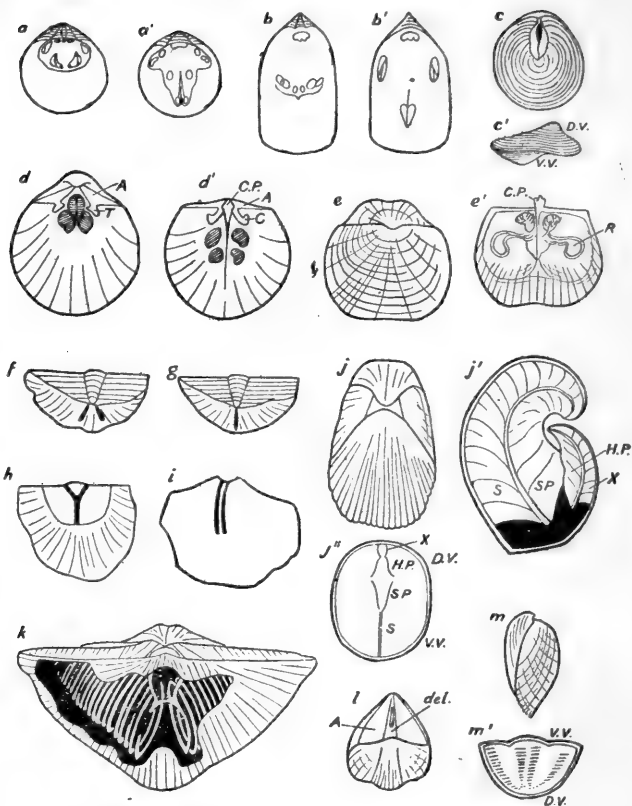


FIG. 7.—VARIOUS BRACHIOPODS.

- a, a'*, *Obolus appolinis* Eichwald, Cambrian, ventral, and dorsal valves: below the umbo in each is the cardinal area (shaded), that of the ventral valve having a median pedicle-groove; muscle-impressions in outline. (Natural size.) *b, b'*, *Lingula anatina* Bruguière, Recent, ventral, and dorsal valves: parts as in *a, a'*, ( $\times \frac{1}{3}$ .) *c, c'*, *Disciniscia lamellosa* Broderip, Recent, ventral, and side views. Foramen black. (Natural size.) *d, d'*, *Dalmanella* [*Orthis*] *elegantula* (Dalman), Silurian, ventral, and dorsal valves: muscle-impressions shaded. ( $\times \frac{1}{3}$ .) *e, e'*, *Productus semireticulatus* (Martin), Lower Carboniferous, dorsal view, and interior of dorsal valve. ( $\times \frac{1}{3}$ .) *f, g*, Umbonal views of ventral valves of *f*, *Schellwienella*; *g*, *Derbya*; areas shaded, dental plates (black) showing through the test. *h*, Um-

tions near the umbones. Here and there, especially near the sides, may be seen round spots, proved by comparison with better-preserved specimens to be the stumps of long curved spines. These spines are the special characteristics of the family *Productidæ*, and they served perhaps to anchor these brachiopods to the stems of crinoids or other suitable objects, or perhaps to support them like springs on the sea-bottom, thus enabling them to dispense with a pedicle.

Internally, *Productus* does not differ greatly from *Leptæna*: the divaricator-impressions in the ventral valve are more widely separated, and in front of each one there is a spiral thickening of the interior of the valve like that of *Davidsonia*; in the dorsal valve there is a pair of somewhat similar, *reniform* (kidney-shaped) elevations.

In the genus *Chonetes* (Ord.-Perm.) we seem to see a link with the *Leptænidæ*. It has similar spines to *Productus* on the cardinal margin of its ventral valve only, and it retains cardinal areas and delthyrium. On the other hand, *Etheridgina* (known only in the Carboniferous of Scotland) shows a further modification of the *Productus* method of fixation: the spines grip the crinoid stem tightly, and the ventral valve becomes cemented to it.

FIG. 7.—VARIOUS BRACHIOPODS (continued)

bonal region of *Orthotetes*, ground down to show dental plates and septum (black). *i*, Internal cast of ventral valve of *Meekella*, dental plates black. *j*, *Conchidium knighti* (J. Sowerby), Silurian, dorsal view. *j'*, Naturally split section; *j''*, cross-section. ( $\times \frac{1}{2}$ .) *k*, *Spirifer striatus* (Martin), Lower Carboniferous, dorsal view, with test partly removed, showing spiralia. ( $\times \frac{1}{2}$ .) *l*, *Cyrtia exporrecta* (Wahlenberg), Silurian, dorsal view. ( $\times \frac{1}{2}$ .) *m*, *m'*, *Atxya reticularis* (Linné), Silurian, side view and cross-section showing spiralia. ( $\times \frac{2}{3}$ .) *A*, Cardinal area; *C*, crus; *C.P.*, cardinal process; *del.*, deltidium; *D.V.*, dorsal valve; *H.P.*, crural plates (cruralium); *R*, reniform impression; *S*, septum; *SP*, spondylium (dental plates); *T*, hinge-tooth; *V.V.*, ventral valve; *X*, septal plate. *a*, *b*, After Walcott; *f-i*, after Thomas; the rest after Davidson.

In the Permian *Strophalosia* also, the ventral valve is cemented to foreign bodies.

The family *Orthidæ* may be illustrated by *Dalmanella elegantula* of the Wenlock Limestone, a small shell, nearly circular in outline, little over a centimetre long and about as broad (Fig. 7, *d*). The length of the hinge-line is less than the greatest breadth. The ventral valve is very convex, with a well-defined slightly concave cardinal area, a triangular delthyrium without any deltidium, and teeth supported by dental plates. The dorsal valve is very slightly convex, with a very narrow area, and a very small, bifid cardinal process occupying the centre of a small delthyrium and at the end of a slight median septum; the inner side of each dental socket is produced into what at first sight looks like a tooth, but as these do not fit into sockets in the ventral valve they cannot be teeth but must be crura like those of the rhynchonellids. The surface is marked by rather fine radial ribs, which here and there increase in number by bifurcation.

The absence of deltidium and presence of crura form two important differences from the Strophomenacea and appear to justify raising the orthids to the rank of a sub-order—Orthacea.

**SUB-ORDER 2. Pentameracea.**—The uppermost Ordovician and lowest Silurian beds in parts of England and Wales are much alike, both consisting of calcareous sandstones often crowded with fossils which are largely in the form of internal casts. Many of these fossils are common to the two systems, or differ by characters too slight to be detected in the field; but the geological surveyor

knows at once that he has Silurian and not Ordovician rocks before him when he sees casts of rounded outline cut almost in half by deep fissures. These fissures in the cast correspond to large internal plates in the shell, such as only occur in the pentamerids, a group of brachiopods which suddenly migrated into the British area at the opening of the Silurian period.

One of the most familiar pentamerids is *Conchidium* [*Pentamerus*] *knighti* (Fig. 7, *j*) of the Aymestry Limestone. This is a large shell, attaining a length of 7.5 c.m., and then about 4 c.m. broad and 5.5 c.m. thick. Both valves are highly convex, with the umbo of each greatly curved over; there is no cardinal area; the delthyrium is broad and bears a concave deltidium (often wanting); the hinge-line is short and curved. The surface is marked by coarse rounded ribs which increase in number sometimes by bifurcation, sometimes by intercalation of a new rib. There are no regular concentric markings, but occasional stoppages in growth are indicated by growth-lines.

It is not easy to extract a perfect specimen, because the fossil splits so readily along the large internal plates; and it is not difficult to get an almost median section. By combining what we see in such a section with the evidence of a transverse section (Fig. 7, *j'*, *j''*) we can realize that the mantle-cavity in the umbonal region and for some distance forwards was divided into three chambers, the middle one containing the body proper, the lateral chambers probably containing the spiral brachia. Towards the anterior end the three chambers united. In the ventral valve there is first a large median plate, a

great development of the little septum seen in *Leptaena*. At its inner edge this is continuous with a pair of diverging plates which on being traced to the hinge can be recognized as greatly-developed dental plates. We have already seen that in *Leptaena* the rims of the muscle-areas are continuous with the dental plates, and it is evident that in *Conchidium* the development of these plates must lift the muscles right off the inner surface of the shell into the median chamber. Such a pair of muscle-bearing dental plates is called a *spondylium*.

In the dorsal valve instead of a median septum there is a pair of *septal plates* a little on either side of the middle line; from these diverge at a low angle another pair of *crural plates* the free edges of which are in contact with those of the dental plates for some distance from the hinge, thus bounding the central chamber.

Although *Conchidium knighti* is commonly referred to the genus *Pentamerus*, that should only contain smooth species (e.g., *P. oblongus* of the Upper Valentian or Llandovery stage). Other genera closely allied are *Stricklandinia* (e.g., *S. lens*, of the Lower Valentian or Llandovery), with straight hinge-line and without the greatly-curved umbones, and *Gypidula* (e.g., *G. galeata*, Wenlock Limestone) in which there is a median elevation (*fold*) on the ventral valve, and corresponding depression (*sinus*) on the dorsal, an arrangement found in many brachiopods, and serving to separate the lateral areas of the mantle, where the inhalent current enters, from the central exhalent area. Less close is *Camarophoria* (Dev.-Perm.) with the closest external resemblance to a rhynchonellid, from which it may readily be distinguished by the internal plates (seen through the



translucent shell or, better, on an internal cast), and by the absence of the small foramen and deltidial plates of the rhynchonellids. In this genus there is a dorsal as well as a ventral median septum.

The Pentameracea appear to spring from the Cambrian *Syntrophia*. Other primitive genera (*Clitambonites*, *Poram-bonites*) occur in the Ordovician of Russia; the typical pentamerids abound in the Silurian and Devonian; *Camarophoria* endures to the Permian, after which the whole sub-order is extinct.

#### ORDER IV.: TELOTREMATA.

Articulate Brachiopoda in which the delthyrium is restricted by a pair of deltidial plates; the brachia are supported by calcareous crura, loops or spirals.

SUB-ORDER I. **Rhynchonellacea.** — Crura-bearing Telotremata. Shell fibrous, not punctate. Deltidial plates more or less embracing foramen, which is small, often elliptical, and does not encroach on the umbo (*hypothyrid*). Typical form short and stout (length, breadth, and thickness not very unequal) with short curved hinge-line, usually with a fold on the dorsal valve and sinus on the ventral; smooth or ornamented by fine radial lines or strong radial ribs, sometimes by spines. Teeth supported by dental plates. Cardinal process usually wanting.

The rhynchonellids can generally be recognized by their form, though *Triplexia* among strophomenids and *Camarophoria* among pentamerids are similar. The presence of a sinus in the ventral valve and fold in the dorsal, with consequent **V** or **W** shaped plication of the valve margin, is very generally characteristic of this sub-order; it is one method of separating the inflowing and outflowing water-currents.

In some cases they approach terebratulids in shape,

but from them they can be distinguished by the impunctate shell, the surface of which, under a lens, commonly shows a silky fibrous appearance. At one time all the species of the sub-order were included in the one genus *Rhynchonella*, and although the Palæozoic and Triassic forms have been separated off into separate

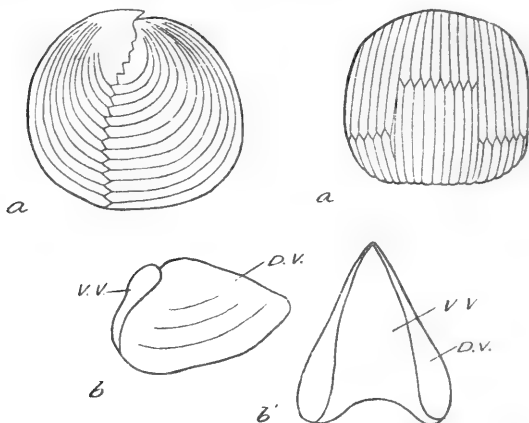


FIG. 8.—PALÆOZOIC RHYNCHONELLIDS.

*a, a'*, *Wilsonia wilsoni* (J. Sowerby),  $\times \frac{3}{4}$ ; *b, b'*, *Pugnax acuminatus* (Martin),  $\times \frac{1}{2}$ ; *a, b*, side-views; *a', b'*, anterior view.

genera, the sorting of the Jurassic and Cretaceous species is only begun.

Among Palæozoic genera are *Camarotoechia* (Sil.—Carb.) with a small spondylium and septum in the ventral valve; *Wilsonia* (Fig. 8, *a*; Sil.) similar, but of more globose shape and finer ribbing; *Rhynchotreta* (Sil.) with acuminate beak on which the foramen encroaches, and conspicuous deltidial plates; *Pugnax* (Dev.—Carb.) with very strong fold and sinus, and few strong ribs or even smooth as in the familiar Carboniferous Limestone species, *P. acuminatus* (Fig. 8, *b*).

Among Mesozoic genera the true *Rhynchonella* (*R. loxia*) is rare, being only known from the Upper Jurassic of Russia: it is not unlike *Pugnax acuminatus* in form. Very similar in form, but differing in being smooth instead of finely striate, are the Middle Lias species *acuta* (now named *Homæorhynchia*) and the Inferior Oolite *cynocephala*.

Somewhat similar, but with more numerous ribs, originating rather suddenly after a long smooth stage, is *Tetrarhynchia* (*R. tetraëdra*) of the Middle Lias.

Another very characteristic species-group, not yet given a generic name, is that of "*Rhynchonella*" *concinna* of the Bathonian, in which the fold and sinus are very slight, the ribs close-set and rather fine, and the beak

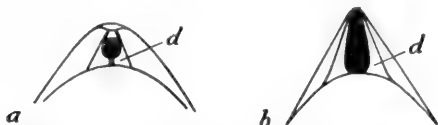


FIG. 9.—DELTIDIAL PLATES OF RHYNCHONELLIDS.

*a*, *Rhynchonella obsoleta*, Davidson (non Sowerby),  $\times 2$ ; *b*, *R. concinna* (J. Sowerby), young,  $\times 2$ ; *d*, deltidial plate. (Original.)

very acute and prominent: Young specimens of this group are the best on which to study the deltidial plates (Fig. 4, *c*), which in so many rhynchonellids become obscured by the curvature of the beaks. *Acanthothyris* has numerous fine ribs ornamented with spines: it is a Jurassic genus, but a similar spiny rhynchonellid lives off the east coast of Japan.

The commonest Cretaceous species belong to the genus *Cyclothyris*: they are rather broad forms, with very fine and close-set ribs, distinct fold and sinus, and deltidial plates protruding more or less as a tube around the pedicle. Such are *C. latissima* of the Lower Greensand, *C. grasiana* of the Upper Greensand, and *C. plicatilis* of the Chalk.

SUB-ORDER 2. **Terebratulacea**.—Loop-bearing Telo-tremata, with punctate shell, foramen encroaching on the umbo (*epithyrid*), and deltidial plates not bounding the foramen laterally. Common form, ovoid and smooth; sometimes with a few coarse plications, consisting of a radial elevation (*fold*) on one valve, and a corresponding depression (*sulcus* or *sinus*) on the other; very rarely with numerous ribs. Ventral umbo and foramen usually much larger than in rhynchonellids.

The terebratulids first appear at the opening of the Devonian period. One of the Devonian genera has so many peculiarities that it is best described apart from the bulk of the sub-order.

*Stringocephalus burtini* of the Middle Devonian is a large shell, nearly circular but for its straight hinge-line and high and pointed (rostrate) ventral umbo. Unlike other terebratulids it is hypothyrid, and the deltidial plates arch over and meet above the foramen. The shell does not show the typical terebratulid pattern of punctation. The loop is long and wide, parallel to the margin of the dorsal valve; and there is a median septum in each valve. The cardinal process is so long that it has to bifurcate to avoid the ventral septum.

The remainder of the terebratulids are divided into *short-looped* forms with obsolete dorsal septum and rarely with dental plates, and *long-looped* forms with strong dorsal septum, and in most cases dental plates.

The short-looped forms begin with the Devonian *Centronella*, smooth, with a very simple loop, not doubled back like that of later genera. *Dielasma* (Dev.—Carb.) has a doubled-back loop, large crural lamellæ running towards one another from the top of the descending lamellæ, and strong dental plates. Similar forms without dental plates are common in the Jurassic and Cretaceous, and are usually placed in the genus

*Terebratula*, but that genus in the strict sense is Cainozoic only. A few well-marked Mesozoic forms have been given separate generic names. Thus *Terebratulina* has a ring-like (annular) loop, and is finely ribbed; *Glossothyris* has a very small loop and an anterior dorsal sulcus; *Epithyris* (Fig. 5, *a*) has a small dorsal septum, a rather large loop, a rather unusual beak, and more or less of a quadriplicate margin; *Pygope* and some other genera pass through a *Glossothyris*-like stage, and the lateral outgrowths meet and unite again around a central perforation (these are found in the transition beds from Jurassic to Cretaceous in the Alpine region); *Liothyris* (Cret.-Rec.) has a number of radial grooves in the inner surface of the ventral valve (well seen in internal casts).

Although long-looped forms are known at least from the Trias, it is in the Lias that the simplest form first appears. This is the minute *Zellania*, in which the loop is incomplete and the dorsal septum anterior in position. This is followed by *Megathyris*, a broad form with a loop not unlike that of *Stringocephalus*, but supported by two lateral septa as well as the median septum. Several allied genera are known in the sea today, survivors of this primitive group. The higher recent genera fall into two families, one in northern, the other in southern seas, and the highest in each case (*Dallina*, northern; *Magellania*, southern) has a very similar adult loop, but they attain it respectively through two quite distinct series of metamorphoses, and the temporary loop-forms of these genera correspond to adult loop-forms of other genera, mostly extinct. These facts are illustrated in Fig. 9. It will be noticed that some of the intermediate stages are represented by recent, not fossil, genera. This can be accounted for by the imperfection of the geological record, for the genera in question are small forms, not easily preserved as

**MAGELLANINÆ**  
(Austral)



**Magellania**  
(Cainozoic-Recent)



**Terebratella**  
(Jurassic-Recent)



**Magasella**  
(Recent)



**Magas**  
(Cretaceous)



**Megerlina**  
(Recent)

**DALLININÆ**  
(Boreal)



**Dallina**  
(Cainozoic-Recent)



**Trigonosemus**  
(Cretaceous)



**Mühlfeldtia**  
(Jurassic-Recent)



**Ismenia**  
(Jurassic)



**Platidia**  
(Recent)

**MEGATHYRINÆ**



**Megathyris [Argiope]**  
(Jurassic-Recent)



**Cistella**  
(Cretaceous-Recent)



**Zellania**  
(Jurassic)



FIG. 10.—EVOLUTION OF THE LOOP IN LONG-LOOPED TEREBRATULACEA.

Loop in outline, septum black. (After Becher.)

fossils, and not easily found by collectors when they are preserved.

In addition to the genera illustrated in Fig. 10, the following are noteworthy:

*Ornithella* (Figs. 2, 5, b) of the Jurassic, smooth, with straight anterior margin; *Aulacothyris*, Jurassic, smooth, with ventral fold and dorsal sinus; *Lyra* and *Trigonosemus*, Cretaceous, plicate forms, with high cardinal areas.

**SUB-ORDER 3. Spiriferacea.**—Telotremata with calcareous spirals; deltidial plates in some cases fused into a single plate.

*Spirifer striatus* (Fig. 7, k) of the Carboniferous Limestone is a very broad shell, being just about twice as broad as long. The greatest breadth is at the hinge-line, which is straight. Both valves are strongly convex, but the ventral has a deep median sinus, the dorsal a corresponding fold. The surface is ornamented with numerous radiating costæ. The umbo of the ventral valve is prominent, but not large, and below it is a large cardinal area showing growth-striations at right-angles to the hinge-line; it includes a triangular delthyrium, in which a large pseudo-deltidium arches over the pedicle-foramen. In the dorsal valve there is a much narrower area.

The internal structure can only exceptionally be made out. The chief feature is the pair of spirals. Starting from the crura the ribbons first approach one another, and then, as the coiling begins, diverge from one another, so that the apices of the spiral cones are near the outer ends of the hinge-line. From this it would seem that, unlike most other brachiopods, *Spirifer* had a median inhalent current and a pair of lateral exhalent currents. The first turn of one spiral is joined to that of the other, on the dorsal side, by a simple bar, the *jugum*. In the ventral valve there are short dental plates.

Various other species of *Spirifer* will answer this same

description very closely, e.g., *S. bisulcatus* of the Carboniferous Limestone, or *S. verneuili* of the Devonian. The genus in the strictest sense ranges from Devonian to Permian, but there is an allied form, *Delthyris*, small and coarsely plicate in the Silurian, e.g., *D. crispus* of the Wenlock Limestone.

Other genera closely allied to *Spirifer* are—*Martinia* (Carb.—Perm., without dental plates and with tendency to smoothness of surface), *Syringothyris* (Upper Dev.—Lower Carb., with very large ventral cardinal area, facing in a direction at right-angles to the plane separating the valves, instead of parallel to it as usual, and a peculiar “split-tube” or syrinx between the dental plates), and *Cyrtia* (Fig. 7, *l*, Sil.—Dev., with high ventral area, and narrow delthyrium with pseudodeltidium perforated centrally for the pedicle). Not quite so near are *Cyrtina* (Sil.—Carb.) and *Spiriferina* (Carb.—Jur.) with punctate shell and ventral median septum supporting dental plates: they resemble in form the previous genera which they respectively resemble in name. All these, and various other genera, are usually united into one family *Spiriferidæ*.

In the family *Atrypidæ* we find the only Ordovician spire-bearers, such as *Zygospira*, in which not only are the spirals short and simple, but their apices are directed towards one another, so that they must have had a median exhalent current as in normal brachiopods. Thus in every respect they are the most primitive spire-bearers. The later (Sil.—Dev.) and more familiar *Atrypa* (Fig. 7, *m*) has the spiral cones parallel with dorsalward apices.

Lastly, the family *Athyridæ* includes the forms with most complex brachial skeleton. The spirals point away from one another as in *Spirifer*, but they start by a sharp bend back from the crura, and the jugum is never a



simple bar, as in the two other families: its least complex form is a Y, but it may be scissors-shaped or have still more elaborate forms. Genera in this family usually have a rounded form and short hinge-line. *Meristina* is a Silurian genus, with a median dorsal septum, and paired ventral septa (the converse of the contemporary pentamerids); *Athyris* and *Seminula* are Carboniferous forms, the latter mimicking the contemporary *Dielasma*, but distinguishable from it not only by its internal spirals, but also by its non-punctate shell.

The Spiriferacea appear in the Ordovician, where only primitive atrypids are found; all families are represented from the Silurian to the Carboniferous, when the atrypids die out. The other two families survive to the earlier part of the Jurassic period, some species of *Spiriferina* being quite common in certain zones of the Lias. The Whitbian age (time of lower part of Upper Lias) seems the date of the final extinction of all Palæozoic types of brachiopods—not only spiriferids (*Spiriferina*) and athyrids (*Koninckella*), but also leptænidids (*Cadomella*) making their last appearance. Certain minute forms in the Inferior Oolite that have been ascribed to the spiriferids really belong to other groups (Megathyrinæ and Rhynchonellids).

### Short Bibliography.

This and succeeding short bibliographies are intended to give the student some idea of the original works from which he may obtain more detailed information than can be given in any textbook, and of which he must study those which are relevant if he is engaged in research—even the simple research involved in naming accurately the fossils he collects. In selecting works for these lists, regard has been had to accessibility (to English

students) as well as to importance. Reference should also be made to Chapter XII. and the bibliography there given.

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## II

### THE LAMELLIBRANCHIA

ASSOCIATED with the terebratuloids in the Cornbrash, though for the most part less well preserved, are other bivalve shells obviously different from brachiopods. In many of them the two valves are obviously right and left, not dorsal and ventral, since they are like mirror-images of one another; and though in some the two valves are unequal, they do not show the perfect symmetry of brachiopod-valves. There is never a pedicle-perforation, and though there is a hinge-line and often a cardinal area not unlike those of brachiopods, the internal muscle-impressions are very differently arranged, and there is never a brachial skeleton.

These bivalves belong to a distinct phylum from the Brachiopoda—the great phylum Mollusca, of which they constitute a class, the Lamellibranchia. The resemblances between them and brachiopods is due to their leading a similar life and having the same needs; the differences are due to the fact that they had a different ancestry, so that a different initial structure had to be adapted to the same needs.

As in brachiopods, each valve has an umbo and near it the hinge-line, but the anatomy of the animal shows that

these structures mark the *dorsal* region, not the posterior, as in brachiopods. The region where the valves separate most widely when the shell opens is therefore *ventral* (instead of anterior). The measurement from the dorsal to the ventral edge is the *height* of the shell, the measurement at right angles to this (in the plane separating the valves) is the *length*, being from the anterior end to the posterior; and the measurement across both valves, at right angles to both height and length, is the *thickness*.

Lamellibranchia are very rare in the oldest strata; they were rarer than Brachiopoda throughout the Palæozoic era; as the latter diminished in numbers, they increased, until in the Cainozoic era and at the present time they far outnumber the Brachiopoda. They are less restricted in their distribution, a few genera being found in fresh waters, though the great majority are marine.

Though the mode of life is similar to that of brachiopods, they are more free to move about. A few fix themselves after the larval stage by cementation (as the oysters) or by silky threads (*byssus*), as the mussels, never by a muscular pedicle; many burrow in sand or mud, a few bore into harder materials, the majority move sluggishly about the bottom, and a very few (as the scallops) swim by a series of jumps.

In the majority of cases, the animal is bilaterally symmetrical, and the right and left valves are as nearly counterparts as is possible, seeing that the hinge-teeth of the one must come opposite the sockets of the other (*equivalve* shells). But in some families, especially those with a fixed habit, the valve on which the animal lies is

the larger. This may be the left valve, as in the oyster, or the right (*inequivalve* shells).

1. **Pectunculus.** As a first example of a lamellibranch we will take this genus, one very common at the present day and in the Cainozoic era. Familiar species are *P. glycimeris* of the Red Crag, and *P. deletus* of the Barton beds. The shell is circular in outline and is lenticular in shape, the valves are symmetrical to one another and very nearly symmetrical in themselves, the distinction between anterior and posterior ends being very slight. In fact the only external distinction in most species is that the umbo is very slightly nearer to the anterior end and faces towards the posterior end, and these facts would not help us much in deciding which end was which, for although in most lamellibranchs the umbo is nearer the anterior end, yet there are exceptions; and on the other hand the umbo usually points towards the anterior end.

The external surface is marked by radial and concentric lines: the latter are always very slightly marked, the former vary in different species from very faint striæ to coarse ribs.

Beneath the umbo and above the hinge-line there is an obtusely triangular cardinal area, which in a fossil shell is seen to be bounded above by a slightly raised margin, and to bear a number of ridges arranged like a set of inverted 'Vs,' one within the other. In a living animal this area is concealed by a brown leathery mass uniting the two valves, known as the *elastic ligament*. (Occasionally this is preserved in fossils.) This elastic ligament is something unknown in Brachiopoda, and

connected with a fundamental difference in the method of opening the shell in the two groups. The lamellibranch has no divaricator muscles: when its adductors contract so as to close the shell tightly, the elastic ligament is subjected to tension; when they relax, the elasticity of the ligament draws the two cardinal areas towards one another and the valves open. Throughout life, however, the adductors are never completely relaxed, and the ligament is always more or less stretched, so that it is



FIG. II.—PECTUNCULUS GLYCIMERIS (LINNÉ), PLIOCENE.  
Exterior of right valve. (Natural size, not full grown.) (Original.)

not until after death that the ligament has full play and the valves then yawn apart more than ever during life.

Fossil lamellibranch shells are most commonly found in one of three conditions, according to the rapidity of their burial after death. (1) When quickly buried (or when the animal lived and died in a burrow), the valves remain tightly closed, the weight of the sediment counteracting the tendency of the ligament to open them: in this case the interior is filled with calcite or other

material deposited from solution (except in those genera whose valve-margins do not meet for their whole length). (2) If the muscles decay away before burial, the valves yawn open, and sediment drifting in prevents their closing, but they remain united. This case is well illustrated by the specimens of *Pectunculus brevis* that

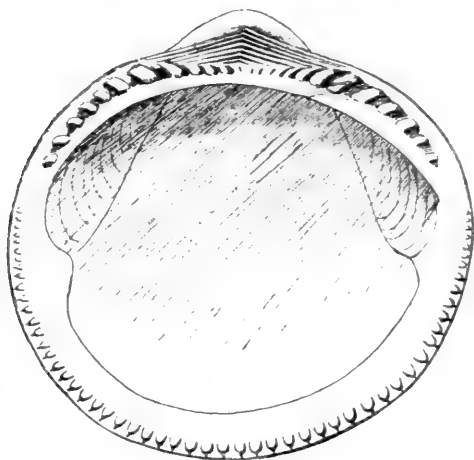


FIG. 12.—PECTUNCULUS GLYCIMERIS (LINNÉ), PLIOCENE.

Interior of left valve. (Natural size.) From above down are seen in order—umbo, cardinal area, curved row of teeth, edge of hinge-plate, adductor impressions, pallial line, crenulate ventral margin. (Original.)

abound in the Bognor rock, a band of hard sandstone in the London Clay of the Sussex coast. (3) If burial is long delayed, the valves are drifted about until not only the muscles but the ligament also is decayed; then the valves become completely separated. This is the case with the abundant valves of *P. glycimeris* in the Red Crag of Suffolk. Each of these three conditions may be

represented by internal and external casts, the material of the internal cast in the two latter cases being rock-matrix, in the first case usually calcite or calcium phosphate, etc.

On examining the interior of a valve of *Pectunculus*, we see below the cardinal area a curved hinge-plate bearing a row of teeth, all practically alike, usually slightly **V**-shaped and about twenty or more in number. Comparison of young and old shells of the same species shows that as growth proceeds new teeth are added at each end of the row, while the cardinal area as it increases in size encroaches on the central teeth until they become obliterated.

Around the margin of the ventral half of the valve is a series of radial grooves and ridges, by which one valve locks into the other when tightly closed. These look very much like a continuation of the row of hinge-teeth, but are separated from it at either end by a short smooth area. Margins provided with such ridges and furrows are said to be *crenulate*.

The *adductor* muscle-impressions are two in number, anterior and posterior in position. They differ slightly in shape and size, more in some species than in others. From the inner margin a very distinct line runs up to the umbo, marking off the *path of shifting* of each muscle as the growth of the shell proceeded.

From one adductor to the other there runs, parallel to the ventral margin, a very distinct line, the *pallial line*. This takes its name from the mantle or pallium, the two halves of which line the interior of the two valves, much



as in brachiopods. The edges of these mantle-folds are thickened, both because this is the region by which new shell is secreted, and because there is here an important muscle (*orbicular* muscle) by which the lips of the mantle can be pressed together even when the valves are not closed. The pallial line marks the inner margin of this thickening of the mantle. The mantle-edges separate only at certain points—(1) antero-ventrally, where the foot may be protruded; (2) posteriorly, where they enclose two openings like a figure 8: the lower opening being that by which water is sucked in (*inhalent aperture*), the upper that by which it is expelled (*exhalent*). These two apertures are in some lamellibranchs extended into long projecting siphons, and in that case the necessary local increase in the orbicular muscle, to form a *retractor* for the siphons, causes the pallial line to be more or less indented as it approaches the posterior adductor. Such an indentation is termed a *pallial sinus*: it is not present in *Pectunculus*.

It is necessary now to point out which of the characters seen in the shell of *Pectunculus* are not characteristic of all lamellibranchs, and for these technical terms must be given.

The shell of *Pectunculus*, having the umbo directed towards the hind end, is *opisthogyral*. The elastic ligament, as it lies entirely dorsal to the hinge-line, is an *external ligament* or *tension-ligament*. As it extends without interruption fore and aft of the umbo, it is *amphidetic*. The same adjective may be applied to the cardinal area. The hinge, being set with numerous undifferentiated teeth, is

*taxodont*. As there are two adductor muscles, the shell is *dimyarian*; and, as these two are approximately equal in size, it is *isomyarian*. As there is no pallial sinus, it is *integripalliate*.

2. **Nucula** is a genus represented by several hundred species ranging from Silurian to Recent, and varying very little in that long period. The following description applies specially to the Pliocene and Recent species, *N. nucleus*, but in all essentials it will apply to any other. (Fig. 13).

The shell is oval tending to triangular, equivalve, the surface (as preserved in the fossil state) nearly smooth with very delicate concentric striæ. The umbones are opisthogyral, and situated much nearer the posterior end, so that without a knowledge of the living animal the posterior end would be taken for anterior. There is nothing like the large dorsal area of *Pectunculus*, but the region just behind the umbo is slightly flattened or concave, and in some species forms a large depressed area called an *escutcheon*. Internally, the hinge is *taxodont*, there being a narrow hinge-plate bearing a long row of simple, slightly curved teeth. Just below the umbo this row is bent and almost interrupted, and the hinge-plate extends downwards in a projection that bears a deep hollow facing its fellow in the other valve. These hollows are *ligament-pits*, the representative of the elastic ligament running across the median plane from one to the other. Such a ligament, lying below the hinge-line, is described as an *internal ligament*, or better as a *resilium*, for when the valves are closed it is under compression, not under

tension like the external ligament of *Pectunculus*, and it is its resiliency (or tendency to recover its shape when the pressure is removed) that causes the valves to open. *Nucula* is isomyarian and integripalliate; its valve-margins are slightly crenulate. An important difference from *Pectunculus* is that the inner shell-layer is *nacreous* (pearly), that is to say it is composed of thin oblique laminæ of calcite bound together by organic matter

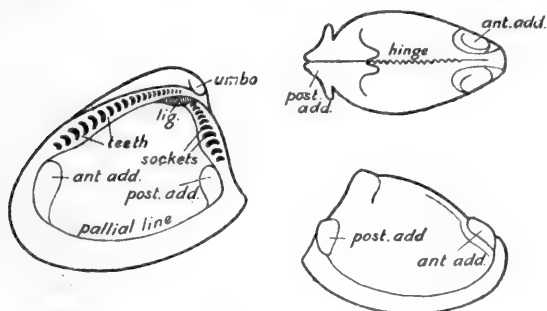


FIG. 13.—NUCULA.

Left-hand figure, internal view of right valve of *N. margaritacea*, Lamarch, Eocene. ( $\times 2$ .) (After Deshayes.) Right-hand figures, dorsal view (above) and right side view of internal cast of *N. pectinata*, J. Sowerby, Albian (Gault). (Natural size.) (After Woods.)

(conchiolin), and the reflection of light from the surfaces of such thin laminæ results in interference and consequent iridescent colours.

3. **Trigonia** is a genus very abundantly represented by well-preserved specimens in the Jurassic system, to a less extent in the Cretaceous, and very rare in later formations, though still surviving in Australian seas. We will choose the Upper Jurassic species *Trigonia bronni* (Fig. 14) for

description, though most that is said, apart from details of shape and ornament, will apply equally to other species.

The shell is equivalve, the shape between oblong and triangular, the posterior end truncated, the height about two-thirds the length; the umbo is near the anterior end and opisthogyral. The greater part of the surface is ornamented with tubercles, arranged in curved rows oblique to the margin and tending to run together anteriorly; fine growth-lines can be traced over the surface of the tubercles where these are not too worn; but from the umbo to the truncated posterior end there extends an area in which the ornament is different, the concentric striæ being more marked, the tubercles much smaller and in three radial rows. As it is the edge of the mantle which secretes the shell, this difference in ornament depends on a difference in the secreting activity of the siphonal part of the mantle from that of the rest of the mantle. Enclosed between this siphonal area and the dorsal margin is a narrow segmental escutcheon, not extending to the posterior end, and bearing only striæ whose obliquity to the margin shows that the shape of this area has remained the same during growth. In its extreme anterior portion, close to the umbo, is the short but thick external ligament. This may be preserved in the fossil; if not, the position it occupied can easily be recognized, when the two valves are in position, by the gap between their margins. Being entirely behind the umbo, the ligament is described as *opisthodetic* (in contrast to the *amphidetic* ligament of *Pectunculus*.) Although external, it does not act quite in the same way as that of

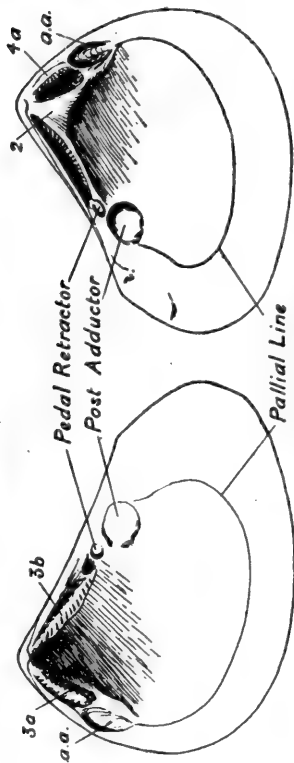


FIG. 14.—TRIGONIA BRONNI, L. AGASSIZ, UPPER JURASSIC (CORALLIAN), NORMANDY.  
 Upper figure, left valve, exterior; left lower figure, right valve, interior; right lower figure, left valve, interior. *a.a.*, Anterior adductor. Numbers denote hinge-teeth. (Natural size.) (Original.)

*Pectunculus*. It is shaped like a cylinder slit open along one radius, and yawning at the slit. The closing of the valves tends to close this fissure, and the outer layers are under tension while the centre is compressed.

The interior of the shell is nacreous; the wear and tear of the outer layer in the region of the umbo often leads to the exposure of the nacreous layer on the exterior.

The hinge-teeth are quite different from those of *Pectunculus*: they are very large and few in number, two in each valve (the left posterior one bifid). Their surfaces of contact are deeply grooved, as is also the posterior surface of the left posterior socket (this is sometimes taken as a third tooth, but it does not project beyond the median plane as a tooth must do). The right anterior and the left anterior and part of the bifid tooth are carried on a kind of buttress (*myophoric lamina*) which also supports the anterior adductor muscle. This muscle-impression is partly crossed by a series of ridges (which probably give greater "key" or grip to the muscle). The posterior adductor is rather larger, and is placed nearly half-way between the posterior end and the umbo, just behind the posterior hinge-teeth. The pallial line has no sinus. The margins are not crenulate.

Thus *Trigonia*, *Pectunculus*, and *Nucula* are all three equivalve, opisthogyral, and integripalliate, and *Trigonia* and *Nucula* agree further in having a nacreous interior, and in being very *inequilateral* (though in *Trigonia* it is the anterior region, in *Nucula* the posterior, which is the shorter). The opisthodetic ligament and hinge-teeth are features in which *Trigonia* differs strikingly from both the

other genera. This type of hinge is described as *schizodont*. According to the method of notation to be explained immediately, its formula is  $\frac{3a, b}{2, 4a}$ .

4. *Cyrena semistriata* is an abundant fossil in the Oligocene beds of the Isle of Wight. The shape is sub-trigonal, the umbo being about one-third the total length back from the anterior end; the anterior border is rounded, the posterior part of the dorsal border sloping obliquely back to a narrow rounded posterior end. (Apart from

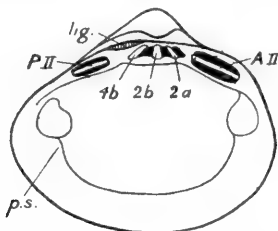


FIG. 15.—CYRENA SP. RECENT.

Interior of left valve. (Natural size.) Teeth white, sockets black.  
p.s., Pallial sinus; lig., ligament. (Original.)

this shape, the remainder of the description will apply in general to any other species of *Cyrena*, such as that shown in Fig. 15.) The shell is equivalve. The outer surface is smooth, with concentric growth-striations. The ligament is opisthodetic and short. Internally, the shell is isomyarian, and there is a very slight pallial sinus, so that it may be described as feebly *sinu-palliate*. The hinge-teeth are carried on a well-defined hinge-plate and fall into three distinct sets (**heterodont**): just under the umbo are a series of short, more or less vertical

teeth, radiating from the umbo—the **cardinal** teeth; in the anterior and posterior regions of the hinge-plates there are long teeth, more or less horizontal, parallel to the shell-margin—these are called (inaccurately) the **lateral** teeth. The anterior-lateral teeth come close up to the cardinals, but the posterior-laterals are separated from them by a space. The posterior-laterals are always posterior to the ligament—this fact is the essential distinction between them and the cardinals, the posterior of which may in many heterodont shells be long and nearly horizontal, so that it might be mistaken for a posterior-lateral if its position relative to the ligament is not noticed. To come to details—in the right valve there are two laterals, the inner of which is on the inner margin of the hinge-plate, while the outer one is not quite on its outer margin; there are three cardinals, of which the middle one is bifid; and two posterior-laterals, occupying similar positions on the hinge-plate to the two anterior-laterals. In the left valve, there is a well-marked anterior-lateral tooth, not quite on the inner margin of the hinge-plate (since it has to interlock between the two anterior-laterals of the right valve); the outer margin of the hinge-plate is very slightly raised into a vestigial tooth. There are three cardinal teeth, each fitting in *behind* the corresponding tooth of the right valve. The posterior-laterals are similar to the anterior-laterals.

The general arrangement of the teeth is always the same in all Heterodonts: the lateral teeth of the left valve are always on the outer side of (*i.e.*, above) the corresponding teeth of the right valve. This



makes possible a very convenient system of symbols, for which we are indebted to the French palæontologists Munier-Chalmas and Bernard. The lateral teeth are numbered from within outwards, so that those of the right valves have odd numbers, those of the left even: thus the right anterior cardinals are AI. and AIII., the

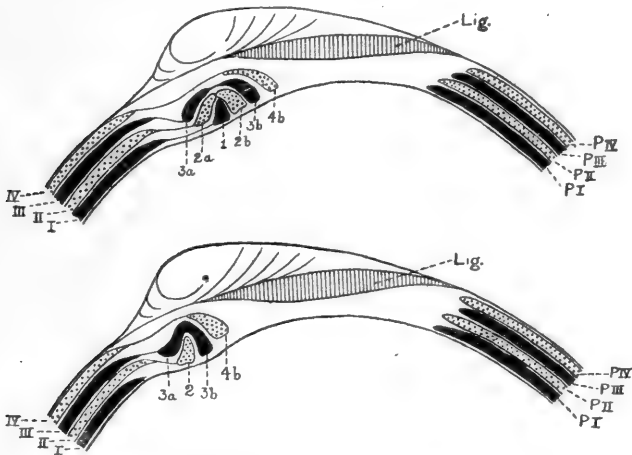


FIG. 16.—HETERODONT HINGES.

Diagrammatic representation of Cyrenoid type (above) and Lucinoid type (below). Interior views of right valves, all possible teeth represented, and those originating from the same lamina shown as connected. Teeth of right valve, *black*; sockets corresponding to teeth of left valve, *dotted*.

left AII. and AIV.; the posterior-laterals PI. and PIII., PII., and PIV. The symbols for the cardinals are based upon the facts of early development, which show them to be the detached hook-like ends of laminae of which the main portion forms the anterior-laterals: thus the right middle cardinal is derived from lamina I., and so is

symbolized by the arabic numeral 1; the other two are derived from lamina III., and are called  $3a$  (the anterior) and  $3b$  (the posterior). Similarly in the left valve the anterior and middle cardinals are both derived from lamina II., so they are called  $2a$  (anterior) and  $2b$  (middle), while the posterior comes from lamina IV., and so is called  $4b$ . These facts are expressed diagrammatically in Fig. 16. It will be noticed that the alternation of the cardinal teeth follows that of the anterior-laterals from which they are derived—those numbered 2 fit in between those numbered 1 and 3; those numbered 3 between those numbered 2 and 4.

Heterodont hinges like the one described are known as the Cyrenoid type; there is another type with fewer teeth, the Lucinoid type, shown diagrammatically in Fig. 16. In this, the central tooth of the hinge is in the left valve—it is 2, instead of 1. The complete dental formula for each may be written thus:

$$\text{Lucinoid type} \quad \dots \left\{ \begin{array}{l} \text{Al.}, \text{III.}, 3a, 3b, \text{PI.}, \text{III.} \\ \text{A II.}, \text{IV.}, 2, 4b, \text{PII.}, \text{IV.} \end{array} \right.$$

$$\text{Cyrenoid type} \quad \dots \left\{ \begin{array}{l} \text{Al.}, \text{III.}, 3a, 1, 3b, \text{PI.}, \text{III.} \\ \text{A II.}, \text{IV.}, 2a, 2b, 4b, \text{PII.}, \text{IV.} \end{array} \right.$$

A shorter formula, omitting the laterals, gives  $\frac{3a, b}{2, 4b}$  for the Lucinoid and  $\frac{1, 3a, b}{2a, b, 4b}$  for the Cyrenoid type.

A dentition rarely contains the full set of teeth, but it can still be classed as Lucinoid or Cyrenoid; the laterals in particular are often reduced in numbers, and when the umbo is far forward the anterior-laterals may be

crowded out altogether. The posterior-laterals, again, are a late development, resulting from the shortening-up of the opisthodontic ligament: in early forms with a long ligament they are wanting.

*Cyrena* is a freshwater lamellibranch, ranging from Jurassic to Recent. Modern species live only in sub-tropical and tropical streams and mangrove-swamps, but the genus (including the sub-genus *Corbicula*, in which the lateral teeth are cross-striated) survived in Britain until well on in Pleistocene time.

5. ***Crassatella sulcata*** is a common fossil in the Barton Clay (Upper Eocene) of the Hampshire Basin. In shape it is much like *Trigonia*, but the umbones are forwardly directed (*prosogyral*). The surface is ornamented with strong concentric ridges, but many other species of the genus are nearly smooth (*e.g.*, the large *C. plumbea* of the Paris Basin, Fig. 17). There is an escutcheon, and in front of the umbo there is a very similar, but smaller, depressed semicircular area, the *lunule*. Internally the shell is not nacreous; it is isomyarian and integripalliate; the valve-margins are crenulate (though not in all species of the genus). The hinge-plate is very narrow in front and behind, but very deep in the umbonal region, where it bears a ligament-pit, much larger in proportion than that of *Nucula*. In front of this are two nearly-vertical cardinal teeth: those of the left valve (*2a*, *2b*) are both large, those of the right valve fit in front of those of the left, and the anterior tooth (*3a*) is very small. The articulating surfaces of the teeth are slightly cross-grooved like those of *Trigonia*.

Both anterior and posterior laterals are present, one of each in each valve. (In *C. plumbea* both 3a and the laterals are *obsolete*—i.e., so reduced as to be scarcely recognizable.) As the right anterior-lateral fits under the

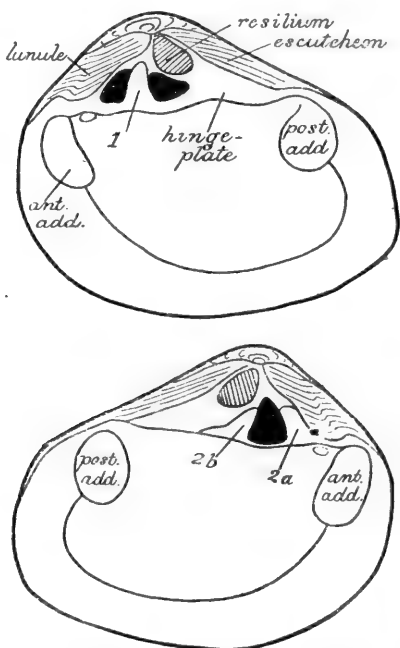


FIG. 17.—*CRASSATELLA PONDEROSA* (LINNÉ). ( $\times \frac{1}{2}$ .)

Right valve above, left valve below. Teeth white, sockets black.  
(Alter Deshayes.)

left, while the right posterior fits over the left, the teeth are probably AI. and AII., PIII. and PII.

*Crassatella*, at the present day, is confined to the Indo-Pacific province and the tropical parts of the

Atlantic. It is known fossil from the Lower Cretaceous onwards, and was less restricted in its geographical range until after the Eocene, as is shown by its presence in the Barton Clay and (much more abundantly) in the Eocene of the Paris Basin.

6. *Meretrix (Sinodia) incrassata* (Fig. 18) is an abundant fossil in the "Venus-bed" of the Lower Oligocene of the Isle of Wight and Hampshire—that bed taking its name from the genus in which this species was at one time included.

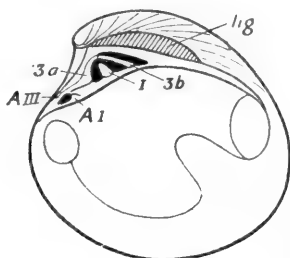


FIG. 18.—*MERETRIX (SINODIA) INCRASSATA* (J. SOWERBY),  
OLIGOCENE.

Interior of right valve. (Natural size.) (Original.)

The shell is rounded and sub-triangular, prosogyral, with fairly well marked lunule, without escutcheon, but with a fairly long opisthodontic ligament. The surface is ornamented with concentric striæ. The hinge-plate is large and thick, and bears three cardinal teeth in each valve, with two unequal anterior-lateral teeth (AI., AIII.) in the right valve, and one (AII.) in the left, the hinge being of Cyrenoid type. The absence of posterior-laterals is correlated with the length of the

opisthodontic ligament : only in genera in which the ligament becomes shorter do posterior-laterals appear, to strengthen the hinder region, which no longer has a ligamentary connexion. The shell is isomyarian and *sinu-palliate*, there being a well-marked pallial sinus caused by the large size of the retractor muscles of the long siphons. The valve-margins are sharp and not crenulate.

Thus *Meretrix* is heterodont and sinu-palliate, and therefore representative of what is regarded as the highest type of lamellibranch—certainly one of the most modern types. The genus has a world-wide distribution to-day, and species attributed to it are known as far back as the Jurassic.

7. ***Pseudomonotis echinata*** (Fig. 19) is the best preserved lamellibranch found in the Cornbrash. It is small (length about 14 mm., height 16 mm., thickness 7 mm.), rounded, and strongly inequivalve : the left valve being convex, with prominent umbo, and ornamented with spiny radial ribs ; the right valve being nearly flat, with inconspicuous umbo, and nearly smooth, with only slight radial striæ. The outline of each valve is somewhat gibbous—oval with the axis curved in a posterior direction ventrally ; but as the outline is traced round to the umbo posteriorly it is seen to be deflected out, giving rise to a flat triangular projection which has the effect of lengthening the hinge-line. Such projections are termed *ears* (or *wings*), and a shell possessing them is said to be *auriculate* (or *alate*). The posterior ears of *Pseudomonotis* are fairly large, the left anterior ear is barely

recognizable, but the right anterior ear, though small, is quite distinct and has a well-marked notch below it. Such a notch, as we know from recent forms, served for the passage from the interior of the shell of the *byssus* (a bunch of silky threads of conchiolin, secreted by the foot) by which the mollusc could attach itself, temporarily or permanently. The inequivalve character is here, as in other lamellibranchs, associated with a fixed habit of life.

Between the umbo and the long hinge-line there is in

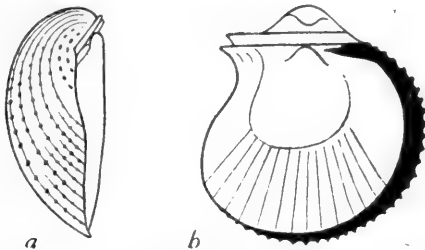


FIG. 19.—*PSEUDOMONOTIS ECHINATA* (J. DE C. SOWERBY),  
BATHONIAN. ( $\times 2$ .)

*a*, Posterior view; *b*, right side view: the black portion is the interior of the left valve where it overlaps the right. At the upper end of this is seen the very small right anterior ear, with the byssal notch below it; between it and the elevated umbo of the left valve is the amphidetic area of the left valve. (Original.)

each valve a long and low cardinal area, not separated into lunule and escutcheon. As in *Pectunculus*, this is occupied by an amphidetic ligament.

It is not easy to clear the interior of specimens of *P. echinata*, but from allied forms we may infer that hinge-teeth are feebly developed or obsolete, and that the shell is *aniso-* or *heteromyarian*, there being a large posterior

adductor from which a pallial line extends indistinctly forward and ends in a very small anterior adductor impression. The edge of the left valve overlaps that of the right, and the small portion of the interior thus exposed is seen to be nacreous.

The genus *Pseudomonotis* is found principally in the Triassic and Jurassic rocks, but allied genera range from the Ordovician to the Recent period. Among its Recent allies is the pearl "oyster" of the Pacific Ocean, *Meleagrina margaritifera*, pearls being pathological secretions of nacre around parasites or other irritating bodies, and mother-of-pearl being the normal nacreous layer of the shell.

8. The genus **Ostrea**, the true oyster, ranges from perhaps the Carboniferous period to the Recent. *O. ventilabrum* of the Oligocene (Fig. 20) is a convenient species to describe, but (except for shape and ornament) many other species will answer to the description. The oysters are fixed (sessile) forms, and consequently very inequivalve. The left valve is fixed by cementation to some solid object—often some other shell—and becomes thick and convex; the right valve is nearly flat and forms a lid to the left. The outline (of *O. ventilabrum*) is nearly semi-circular, the posterior margin from the umbo back being nearly straight. The height (in the morphological sense) is greater than the length (length 6 cm., height 7 cm., thickness 3 cm.) The shell is opisthogyral. In the left valve, a variable area of the umbonal region is adherent to some foreign body and shows only the impress of that instead of its own ornamentation. Beyond this area the



ornament consists of coarse diverging ribs, sub-angular to rounded in section, increasing in number by bifurcation or by intercalation of new ribs. The whole surface has a scaly look, due to the highly laminated structure of the shell. The right valve is nearly smooth, except for concentric corrugations due to growth irregularities, but also shows this laminated texture. In the umbonal region there is an area of more irregular character corresponding exactly to the area of attachment of the left valve. That

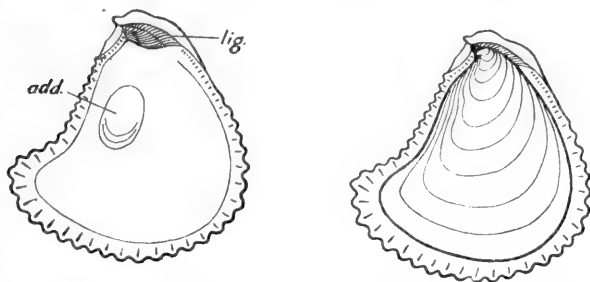


FIG. 20.—*OSTREA VENTILABRUM*, GOLDFUSS, OLIGOCENE. ( $\times \frac{1}{2}$ .)  
Right-hand figure shows both valves seen from the right side; in the left-hand figure the right valve is removed. *add.*, Adductor impression; *lig.*, ligament. (Original.)

the surface of the foreign body should thus “show through” a thick pair of valves is at first sight puzzling, especially as no trace of it is seen on the interior of either valve. The explanation is that the oyster fixed itself when very young, both valves of the very thin shell, as well as the animal’s body between, being moulded up and down over the irregularities of the surface to which it was attached. As growth proceeded the shell not only extended beyond the area of attachment, but also increased

in thickness by the addition of internal layers, which gradually smoothed over the irregularities of the inner surfaces but left those of the outer surfaces unchanged.

Internally, there are no hinge-teeth ; there is a large triangular elastic ligament, extending from the umbo to the hinge-line. When the valves are closed, the outer part of the ligament is probably under tension and the inner part under compression. The central part is thicker than the anterior and posterior, so that in the left valve the ligament-area appears divided into three parts, the central concave, the others flat : the whole ligament area is marked by fine horizontal striations.

There is only one adductor muscle-impression, posterior in position, the anterior adductor being entirely aborted in the adult : the shell is therefore *mono-myarian*. The interior is *sub-nacreous*, the iridescence being faint.

The external ribs give the valve-margin of the left valve, which projects beyond that of the right, a coarse crenulation. As this is traced towards the hinge it becomes supplanted by a slightly deeper-set series of crenulations, counterparts to which appear in the right valve, together forming an approach to a taxodont dentition. These "teeth" do not interlock tightly, however ; they are only found in a few species of *Ostrea* ; they are certainly not the relics of the hinge-teeth of the ancestors of the *Ostreidæ*.

The oysters (including allied genera as well as *Ostrea* itself) have the strongest shells of any lamellibranchs, in the sense of standing wear and tear best : they may be washed out of their original deposit, rolled about by

waves or streams, and retain a recognizable form while most of their associated fossils are pulverized. Hence they are often found as *derived fossils* in strata much younger than those to which they belong; Jurassic oysters, for instance, are very commonly found in the glacial gravels of the Pleistocene period.

9. **Corbula** is a genus represented by various small species in the Jurassic, Eocene and Oligocene strata of Britain, such as *C. pisum* and *C. revoluta* of the Barton Clay. The shell is inequivalve, the right valve being in every way larger than the left though the two scarcely differ in form; both being oval and rostrate posteriorly, with no ornament but lines of growth. The umbones are nearly central in position and opisthogyral. The hinge-structure is best made out on large species such as *Corbula gallica* of the Eocene of the Paris Basin (Fig. 21). In the right valve there is a sharp anterior-cardinal tooth projecting to an unusual extent towards the left valve and slightly upwards. Behind this is a space with a resilium-pit which instead of being vertical is horizontal, facing downwards, and placed within the umbo; behind this there is a long vestigial posterior-lateral tooth. In the left valve, a deep conical socket corresponds to the right cardinal tooth; behind this is a conspicuously-projecting horizontal plate (*resiliophore*), which carried the resilium and underlies the resilium-pit of the right valve. The interiors are not nacreous; the shell is isomyarian and has a short pallial sinus with vertical front edge.

Modern species of *Corbula* are marine, living in moderately shallow water, but an allied genus *Erodona*

lives in the great rivers of South America beyond the tidal limit, and is found in British freshwater Oligocene strata.

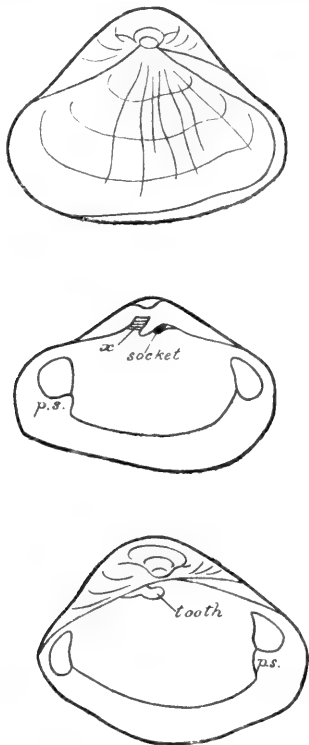


FIG. 21. --CORBULA GALLICA, LAMARCK, EOCENE, PARIS BASIN.  
(Natural Size.)

Upper figure, complete shell from left side; middle figure, interior of left valve; lower figure, interior of right valve. *p.s.*, Pallial sinus; *x*, resiliophore. (After Deshayes.)

10. **Pholadomya** is a genus which made its first appearance in the Lower Lias, was abundantly represented

by species throughout the Jurassic, became less common in the Cretaceous, is still represented by several species in the British Eocene beds and one in the Pliocene, but only survives to-day in deep waters in the Atlantic Ocean and West Indies, although many of the fossil species (even up to the Pliocene) must have lived in shallow waters. We may take *P. fidicula* of the Inferior Oolite as an example (Fig. 22).

The shell is extremely thin, so much so that when found as an internal cast, it requires careful examination to determine whether any of the shell is still adherent or

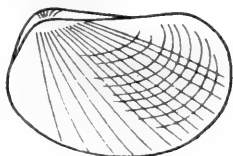


FIG. 22.—PHOLADOMYA SP. RESEMBLING BUT SHORTER THAN  
*P. FIDICULA* (J. DE C. SOWERBY), AALENIAN. ( $\times \frac{1}{2}$ .)  
Left side view. (After Goldfuss.)

not. Internally it is nacreous. The shell is equivalve, and strongly inequilateral, the umbones being far forward and prosogyral. The valves gape at the posterior end, the long siphons not being fully retractile; consequently the interior is always filled with rock-matrix and the posterior end has a rough, broken appearance where the matrix within joined that without. The surface is ornamented with numerous oblique, slightly curved, radiating ribs, dying away in the postero-dorsal area. (In some species the ornament is more elaborate, with fewer and coarser ribs and tubercles, and differing in

different areas.) The ornament is shown by the internal cast as well as by the outer shell. There is a short, opisthodontic external ligament. In the fossil it is difficult to determine whether teeth are present or not; but in the recent species there is only a vestigial tooth. The shell is isomyarian and sinupalliate, though the impressions are too feeble for this to be determined in many cases.

The ten genera of Lamellibranchia here described form a very inadequate sample of a very extensive class, for which various methods of classification have been from time to time proposed. Classifications are of two kinds—morphological and phyletic. All early classifications necessarily belong to the former type, in which one proceeds to sort out the members of a class first into larger groups defined as precisely as possible by certain differences of structure, then into smaller groups defined by other differences, and so on. The important question to be settled in framing a morphological classification is—What characters shall we choose to define our larger groups, and what to define each successive grade in our subdivision? According as the characters are well or ill-chosen, the classification comes to be recognized as more or less “natural” or “artificial.” The characters to be considered fall into several categories:

(1) The most external or superficial characters, such as the shape and ornament of a shell. These are found often to differ greatly in a number of species which have most other characters alike, hence they are recognized as principally of value as specific distinctions; and only when they are constantly associated with other characters

can they be taken as part of the definition of larger groups.

(2) Characters which are evidently directly connected with the animal's particular mode of life—*adaptive characters*. These have to be taken very cautiously, since sometimes two animals from widely different groups may come to resemble one another very closely (especially when we have only the hard parts to deal with) on account of their adaptation to similar conditions (*convergence*). We have already seen how many features lamellibranchs and brachiopods have in common owing to general similarities of habit, and cases of homœomorphy among brachiopods have been mentioned. Among lamellibranchs themselves there are cases of similarity of external form (*e.g.* *Trigonia* and *Crassatella*), accompanied by great differences in internal structure. Nevertheless in many cases adaptation to different lives does form the basis of such fundamental divergence as to determine essential boundaries in classification, as for instance between the fishes and air-breathing Vertebrates.

(3) There are certain characters which are found to run, with but slight modifications, through forms of varied life-modes and varied external appearance. Such, for instance, are the various types of hinge-teeth in lamellibranchs. Such characters are found to provide the safest bases for classification.

The history of taxonomy (*i.e.*, the laws of classification) shows that morphological classification tends more and more away from what is regarded as "artificial" towards what is "natural," and this tendency has meant,

at first unconsciously, and later consciously, a tendency towards *phyletic* classification—that is to say, a classification expressing the *phylogeny* or evolutionary genealogical tree of the group to be classified. All morphological classifications must, in fact, be more or less artificial, since they proceed by definitions of structure, not of derivation: only by becoming phyletic do they become completely “natural.” Conversely, the more natural a classification, the more difficult is it to express it by morphological definitions, since the most important distinctions between two diverging lineages are not fully developed in the earlier members of the lineages, and also they may be lost in aberrant members whose connexion with a lineage is clearly shown by secondary features not characteristic of the whole of the lineage. Hence modern taxonomic definitions are full of such qualifications as “usually,” “in typical genera,” “in all but the earliest members,” etc.

An early classification of Lamellibranchia was into Monomyaria and Dimyaria, the latter being divided into Heteromyaria and Isomyaria, and these last into Integripalliata and Sinupalliata. If the definitions are not applied too rigidly, this forms a fairly natural classification, and has the advantage to palæontologists of being based on shell-characters. But Heteromyaria are more nearly allied to Monomyaria than to Isomyaria, and the sinupalliate condition has been arrived at independently along so many different (at least five) lines of descent, that it cannot be used to define a single group. Another classification by shell-characters was that of Neumayr, based



upon the hinge-teeth : the class was divided into orders Taxodonta, Heterodonta, etc. This is in large measure a natural scheme, but not entirely, as it brings together *Nucula* and *Pectunculus* as taxodonts, although they differ very greatly in other respects, and associates *Trigonia* and *Unio* as schizodonts more closely than seems really justified.

Zoologists, however, dealing with recent lamelli-branches, and not having only the shell to examine, have proposed as the soundest basis of classification the structure of the gills. Thus a few genera such as *Nucula* have plume-like gills like those of the other classes of Mollusca : these evidently form a primitive order (*Proto-branchia*). Others, as *Pectunculus*, *Trigonia*, *Pteria* (*Fili-branchia*), have gills transitional in character between the last and the typical sack-like gills which give the name to the whole class. Many others, including the remainder of those so far described, have the typical lamellate gill (*Eulamellibranchia*). Lastly, a few genera have the gills modified into a simple septum across the mantle chamber (*Septibranchia*).

This plan is unsatisfactory to palæontologists. Not only is it based on morphological characters that cannot be discovered in an extinct genus, but it separates genera (like *Pecten* and *Lima*) which shell-characters show to be nearly related, and unites them with others with which they have no near relation (*Pecten* with *Trigonia*, *Lima* with the Heterodonts and Desmodonts). The development of the typical lamellibranch gill is a process which must have gone on independently in different lineages,

and the different types of gill give us *grades* of development only, not lineages.

The latest proposal for classification (here adopted) is that of Professor Henri Douvillé, of Paris, according to whom the main lines of divergence of the lamellibranchs were determined by original differences in habits of life. There are three branches—active, fixed, and burrowing—so that we have here what has been termed by Vertebrate palæontologists an *adaptative radiation*. But the members of any lineage are not rigidly tied down to one groove; in each lineage there are cases of re-adaptation to one of the other modes of life, re-adaptations which lead sometimes to a close imitation of one type by another (convergence), but which can never obliterate or reverse the effects of ancestral history.

### I. Active Branch.

#### I. NUCULACEA.

Equivalve; isomyarian; internally nacreous; hinge-line primitively taxodont; without distinct cardinal area; surface rarely ornamented otherwise than by concentric striæ. Ligament external (*Ctenodonta*) or internal (*Nucula*, *Leda*). Integripalliate (except *Leda* and *Yoldia*). Ordovician to Recent.

*Leda* (Ord.-Rec., Fig. 23, *a*) and *Yoldia* differ from *Nucula* in having the mantle drawn out into distinct though small siphons. This greater development of the posterior region results in a more central umbo, while there is a slight pallial sinus, and in *Leda* a tendency to more or less rostration (drawing out of the posterior end): species which show this in an extreme degree are sometimes separated under the name *Dacryomya*. *Nucula* and *Leda*

share with the brachiopod *Lingula* the honour of being among the longest-lived genera of animals.

*Ctenodonta* has some resemblance in form to *Pectunculus*, but is far earlier in time (Ord.-Sil.).

Probably allied to the Nuculacea are two Silurian-Devonian groups—(1) *Actinodonta* (Fig. 23, *b*), *Lyrodesma*, etc., which show a change of the hinge-teeth from the parallel series of *Nucula* to a radiating series; and (2) *Cardiola* and *Buchiola*, with strong radial ornament and apparently toothless hinge.

## II. NAIADACEA.

Equivalve, strongly inequilateral; isomyarian; integripalliate; internally nacreous. Ligament external, opisthodontic. Hinge-teeth lamellar. Rarely ornamented otherwise than by concentric striæ. Freshwater habitat. Devonian-Recent.

The "freshwater mussels" are probably derived from forms like *Actinodonta* by the restriction of the ligament, various forms from the Permian of Russia showing hinge-teeth of taxodont to radial type. On the other hand, as early as the Devonian, there is found an apparently toothless form, *Archanodon*; and the hinge-structure of the common *Carbonicola* of the Coal Measures (Fig. 23, *c*) is imperfectly known. From Mesozoic time down to the present day the genus *Unio* shows a hinge which is transitional between the actinodont and heterodont types: its formula may be given as  $\frac{3a, b, 5}{2a, b, 4a, b}$  ( $3a$ ,  $4a$ , and  $5$  are usually described as "anterior-laterals,"  $2a$  as a "cardinal," and the other three as "posterior-laterals"—an incorrect term, since they extend below the ligament).

## III. PRÆ-HETERODONTA.

Equivalve, inequilateral, isomyarian, integripalliate; internally nacreous or porcellanous. Hinge-teeth con-

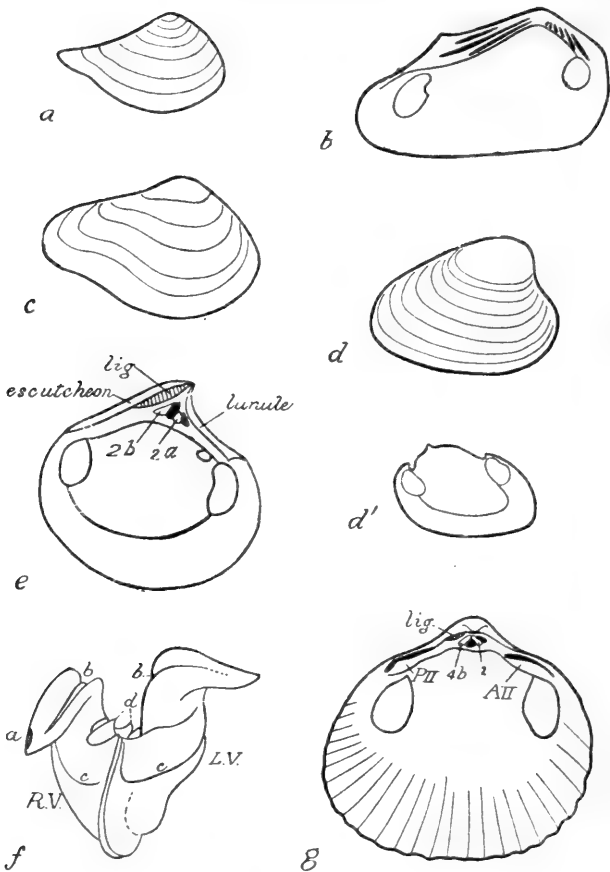


FIG. 23.—LAMELLIBRANCHS.

- a*, *Leda* (*Dacryomya*) *lacryma* (J. de C. Sowerby), Inferior Oolite. Right side. ( $\times 3$ .) (After Goldfuss.) *b*, *Actinodonta cuneata* Phillips, Ordovician. Interior of left valve. Teeth white, sockets black. ( $\times \frac{3}{2}$ .) (After Phillips.) *c*, *Carbonicola robusta* (J. de C. Sowerby). Coal Measures, Upper Carboniferous. Right side. ( $\times \frac{1}{2}$ .) (After Hind.) *d*, *Cardinia listeri* (J. Sowerby). Right side. ( $\times \frac{1}{2}$ .) *d'*, *C. ovalis* (Stutchbury), internal cast. ( $\times \frac{1}{2}$ .) (After Quenstedt.) *e*, *Astarte borealis* (Chemnitz),

sisting of cardinals without anterior or posterior laterals. Ligament opisthodontic. Ornament variable. Devonian-Recent.

Under this name, Prof. Douvillé includes two groups—(a) **Trigoniacea**, with nacreous interior and dental formula  $\frac{3a, b}{2, 4a}$  (Carb.-Recent); and (b) **Præ-astartacea**, with porcellanous interior and dental formula  $\frac{3a, b}{2, 4b}$  (Dev.-Jur.)

The *Trigoniacea* are a small but important group. *Schizodus* (Carb.-Perm.) and *Myophoria* (Trias) show a gradual change from smooth and prosogyrous, with tooth 2 simple, to the highly-ornamented and opisthogyral *Trigonia* with tooth 2 bifid. The geological and geographical distribution of this genus have already been mentioned.

The *Præ-astartacea* form a less compact and less familiar group. It includes *Cardinia* (Fig. 23, *d, d'*) of the Lias (frequently placed in the Naiadacea from its external resemblance to *Unio*, but non-nacreous and marine), with its old-age (senile, or gerontic) modification *Hippopodium* in which the growth in the direction of thickness leads to a most extraordinary shape. Other genera are *Megalodon* (Devonian and Rhætic) and *Pachyrisma* (Jurassic), large forms in which the hinge is short and high, with big coarse teeth; and the little *Tancredia* of the Jurassic.

FIG. 23.—LAMELLIBRANCHS (*continued*).

Pliocene. Interior of left valve. Teeth white, sockets black. ( $\times \frac{5}{8}$ ) (After S. V. Wood.) *f*, *Diceras minor* Deshayes, Upper Jurassic. Anterior view of internal cast. (Natural size.) *a*, Attachment; *b, c*, grooves on cast corresponding to myophoric laminae; *d*, casts of tooth-sockets; *L.V.*, left, and *R.V.*, right valve. (After S. P. Woodward.) *g*, *Cardium parkinsoni* J. Sowerby, Pliocene. Interior of valve. ( $\times \frac{1}{2}$ ) (After S. V. Wood.)

## IV. HETERODONTA.

Equi- or inequi-valve; isomyarian; integri- or sinu-palliate; internally porcellanous. Hinge-lamellæ differentiated into anterior-lateral and cardinal teeth, with frequent development of posterior-laterals behind the shortened ligament. Ligament opisthodontic, usually external, sometimes internal (resilium). Ornamentation varied. Jurassic to Recent.

This very large and important order falls into two series, in each of which a number of sub-orders may be recognized.

A. WITH TEETH OF LUCINOID TYPE:  $\frac{3a, b}{2, 4b}$ .

1. **Cardiacea**.—With radial ornament, at first (*Protocardia*) in siphonal region only, later on whole surface. Umbones fairly central. Anterior and posterior laterals well developed.

The common cockle, *Cardium* (Fig. 23, *g*), has a rounded outline, a central umbo, with well-defined and separated anterior-lateral, cardinal and posterior-lateral teeth; the whole surface is ornamented by strong radial costæ. In the Mesozoic *Protocardia* radial ornament is confined to the posterior end (*i.e.*, to the part secreted by the siphonal part of the mantle) the rest being concentrically marked. (Compare the case of *Trigonia*.) In the Aralo-Caspian region, from Miocene to Recent, are found *Adacna* and *Limnocardium*, cockles adapted to a freshwater or brackish habitat, with long siphons and a pallial sinus. Doubtfully referred to this sub-order is *Thetivonia*, common in the Lower Greensand of the Isle of Wight, with a myophoric ridge that has been mistaken for a peculiar pallial sinus.

2. **Rudistes**.—Highly aberrant fixed forms, probably derived from Cardiacea. Inequivalve. Fixed either by left valve (normal) or right (inverse); both valves spiral

in early forms, the fixed valve later becoming conical or cylindrical, the free valve flattened and lid-like. Teeth of normal forms  $\frac{A_{I.}, 3b}{A_{II.-2}}$ ; of inverse forms  $\frac{3b}{A_{II.-2}, P_{II.}}$ , according to Prof. Douvillé,  $A_{II.}$  and 2 being united into one tooth in each case. The ligament becomes deeply internal and finally disappears, the valves being no longer hinged but the free valve sliding up and down. The whole shell gradually loses all resemblance to ordinary lamellibranchs. Upper Jurassic and Cretaceous.

In the Upper Jurassic of North-East France is found *Diceras* (Fig. 23, *f*), having both valves twisted into a loose spiral, and fixing itself indifferently by either valve. This is the forerunner of a great series of the most remarkably modified of all lamellibranchs. In the Lower Cretaceous there are genera fixed some by the left valve, the majority by the right: in either case the fixed valve tends to become conical or cylindrical in shape, while the free valve takes on the character of a lid or operculum. The genus *Requienia* still has both valves spirally coiled, but the right valve is quite flat, so that the whole shell has a strange resemblance to a gastropod with a spiral operculum. In the Upper Cretaceous the forms fixed by the right valve develop into still more extraordinary forms, mimicking the rugose corals of the Palæozoic. Such is *Hippurites*, the right valve of which forms a cylinder a foot or more in height, of which the animal only occupies the uppermost portion, the lower part of the cavity having been cut off, as growth proceeded, by a series of calcareous partitions (like the tabulæ of a coral or the septa of a cephalopod). The left valve fits on as a lid, and the hinge-teeth and adductor muscles are strangely modified. These hippurites grew in reefs, like corals, and they (as well as their Lower Cretaceous predecessors) are almost restricted to tropical and sub-tropical

latitudes, only a few stragglers being found in British strata (*Toucasia lonsdalei* in the Lower Greensand of Wiltshire only; *Durania mortoni* and a few others in the Chalk). In the Mediterranean region they serve as zonal indices, particular species having a narrow range in time, contrary to the general rule among lamellibranchs. At the end of the Cretaceous period the Rudistes died out.

3. **Lucinacea.**—Ornament concentric, sometimes combined with radial. Trias. to Recent. Forms closely resembling *Lucina* (but hinge unknown) occur in Silurian and Devonian. The chief genera are the nearly circular, usually thin *Lucina* (Fig. 24, *a*), with a long and narrow anterior adductor (numerous sub-genera, Trias.—Rec.), the stout *Unicardium* (Trias.—Cret.), *Corbis* (Jur.—Rec.) in which a fine radial ornament is seen in the depressions between the strong concentric ridges, and *Diplodonta* (Eoc.—Rec.) in which the teeth 2 and 3*b* are bifid.

4. **Chamacea.**—Fixed forms, inequivalve, closely analogous to the simpler Rudistes, but derived at a later period probably from Lucinacea.

The only genus is *Chama* (Fig. 24, *d*, Cret.—Rec.), which is fixed usually by the left valve (some species by the right). The umbones are strongly prosogyral, the fixed valve larger and the free valve lid-like. The exterior has a scaly appearance.

5. **Mactracea.**—Derived from *Diplodonta* (Lucinacea), with which they agree in having tooth 2 bifid, and differ in being sinu-palliate and having the ligament internal (resilium). Ornament concentric, striate.

*Mactra* (Fig. 24, *c*, Eoc.—Rec.) is oval in form. *Ensis* (the razor-shell, Rec.) has taken to burrowing, and so has acquired the oblong shape common among Desmodonts (see later). It is, in fact, a homœomorph of *Solen*, from which it is distinguished by its heterodont teeth.



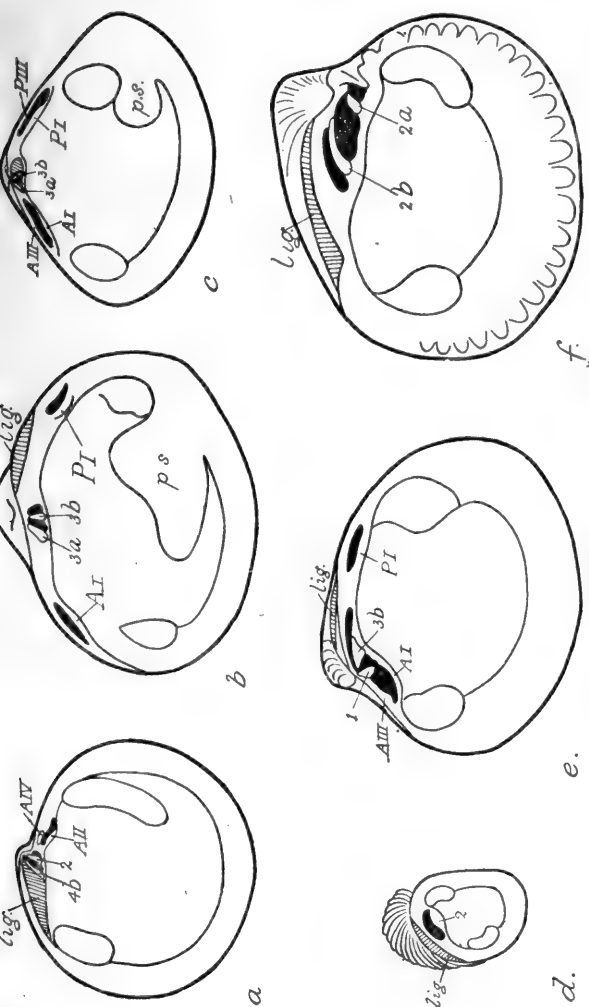


FIG. 24.—HETERODONT LAMELLIBRANCHS.

In all, teeth are white, sockets black; *a, d, f*, interiors of left valves; *b, c, e*, interiors of right valves. *a, Lucina (Codakia) sp.*, Recent. ( $\times \frac{1}{2}$ .) *Codakia* differs from the typical *Lucina* in the position of the ligament, which has become internal (a resilium). *b, Tellina obliqua* J. Sowerby, Pliocene. ( $\times \frac{1}{3}$ .) *c, Maetra antiquata* Spengler, Recent. ( $\times \frac{1}{4}$ .) *d, Chama squamosa* Solander, Eocene. ( $\times \frac{1}{3}$ .) *e, Cyprina islandica* Linné, Pliocene. ( $\times \frac{1}{2}$ .) *f, Venericardia planicosta* Lamarck, Eocene. (Natural size, small specimen.) *a, c*, Original; *b, d, e, f*, after S. V. Wood.

6. **Tellinacea**.—Sinu-palliate. Ornament concentric striate.

*Tellina* (Fig. 24, *b*), one of the commonest of seaside shells, dates from the Jurassic. *Donax* (Eoc.-Rec.) is opisthogyral, and has a short posterior side (like *Nucula*).

B. WITH TEETH OF CYRENOID TYPE:  $\frac{1, 3a, b}{2a, b, 4b}$ .

1. **Cyprinacea**.—Concentric ornament, rarely more than striate; valve-margins smooth. Umbones anterior.

Various early Jurassic forms, too rarely found with hinge decipherable, have been shown by Prof. Douvillé to be the originators of this type of hinge. Better known are *Cyprina* (Fig. 24, *e*), a sub-circular shell with beaks curved forward, crowding out the anterior cardinal tooth, abundant in the colder seas (Jur.-Rec.); *Trapezium* (*Cypricardia*), a somewhat four-sided form (Jur.-Rec.); and *Isocardia* (Mio.-Rec.), with highly spiral umbones.

2. **Astartacea**.—Concentric (striate or costate) ornament, never radial; valve-margins usually crenulate. Ligament external (except in *Crassatella*.) Integri-palliate. Trias.-Recent.

The chief genera are the nearly circular *Astarte* (Fig. 23, *e*) with numerous sub-genera, the trapezoidal *Opis* (Mesozoic) and *Crassatella* (Cret.-Rec.)

3. **Cyrenacea**.—Fresh-water habitat. Concentric striate ornament; valve-margins smooth; integri- or sinu-palliate. Umbones fairly central.

Anterior and posterior lateral teeth well developed. The chief genera are *Cyrena* (Jur.-Rec.) and *Corbicula* (Eoc.-Rec.), already described.

4. **Carditacea**.—Radial ornament; valve-margins crenulate; umbones anterior, leading to a lengthening of the teeth  $2b$  and  $3b$ . The chief genera are *Cardita* (Jur.-Rec.) and *Venicardia* (Fig. 24, *f*, Cret.-Rec.), the

latter being distinguished by the great height and thickness of the hinge-plate and large size of the teeth.

5. **Veneracea.** — Concentric ornament, striate or costate; occasionally radial also. Valve-margins smooth or crenulate; umbones anterior. Sinu-palliate.

The chief genera are *Meretrix* (Eoc.-Rec.), already described; *Venus* (Cret.-Rec.), differing from it by its smaller, pointed pallial sinus, absence of lateral teeth, and crenulate valve-margins; and *Dosinia* (Cret.-Rec.), lenticular, with deep and narrow pallial sinus.

## II. Fixed Branch.

Fixation may be temporary or permanent, by a byssus or by cementation of the shell. The development of a byssus tends to the abortion of the anterior part of the body including the anterior adductor, to the development of ears, and to an inequivalve condition.

### I. ARCACEA.

Equivalve; isomyarian; internally porcellanous; hinge-line with radial teeth, becoming secondarily taxodont; cardinal area and ligament amphidetic. Ornament radial or concentric. Fixation never more than temporary.

This sub-order has generally been associated with the Nuculacea as Taxodonta, but its history shows that the taxodont structure of the hinge is not primary as in *Nucula*, but is derived from a type in which the greater part of the hinge is occupied by long horizontal teeth, a few short oblique teeth being present at the anterior end or in the centre. These characters, as well as the amphidetic cardinal area, indicate a relationship to the next order, Pteriacea, from which the Arcacea diverge in (a) having lost the nacreous interior, and (b) being almost always equivalve. Chief genera: *Arca* (Eoc.-Rec., with doubtful records back to the Silurian), somewhat

quadrilateral in shape, with long straight hinge with vertical teeth and radial ribs (Fig. 25, *a*); *Pectunculus* [*Glycimeris*], already described (Cret.-Rec.); *Cucullæa* (Dev.-Rec.), shaped like *Arca*, but with long horizontal teeth except under umbo, and a raised edge to the posterior adductor impressions.

## II. DYSODONTA.

Usually inequivalve; hetero- or mono-myarian; frequently with anterior and posterior "ears," and a right anterior byssal notch. Cardinal area (if present) and ligament amphidetic. Fixation temporary or permanent, by byssus or cementation.

I. **Pteriacea.**—Inequivalve (except *Perna* and *Gervillia*); anisomyarian; internally nacreous; with ears; frequently with a byssal notch below the right anterior ear; hinge-line straight, without teeth or with vestiges of an actinodont type. Silurian to Recent.

A very large and varied sub-order, in which there is a general tendency (*a*) to the inequivalve condition, the left valve being the more convex; (*b*) to the lengthening out of the hinge-line by the formation of "ears" or "wings"; (*c*) to the disappearance of the anterior adductor. The interior is nacreous, the outer layer prismatic; cardinal area and ligament amphidetic; hinge teeth very feebly developed. *Pteria* [*Avicula*] (Devonian? to Recent) differs from *Pseudomonotis* (already described) in its more oblique shape and well-marked left anterior ear (Fig. 25, *c*, *c'*); *Pinna* (Jur.-Rec.) is acutely triangular in shape; *Conocardium* (Dev.-Carb.) is equivalve, inflated, the anterior ears forming a sort of tube (Fig. 25, *b*). These genera are all costate. *Perna* (Trias.-Rec.), *Gervillia* (Trias.-Eoc.), and *Inoceramus* (Jur.-Cret.) have the ligament partly sunk into the hinge-line, and fixed into a long series of ligament-pits (Fig. 25, *d*, *d'*); these genera are con-

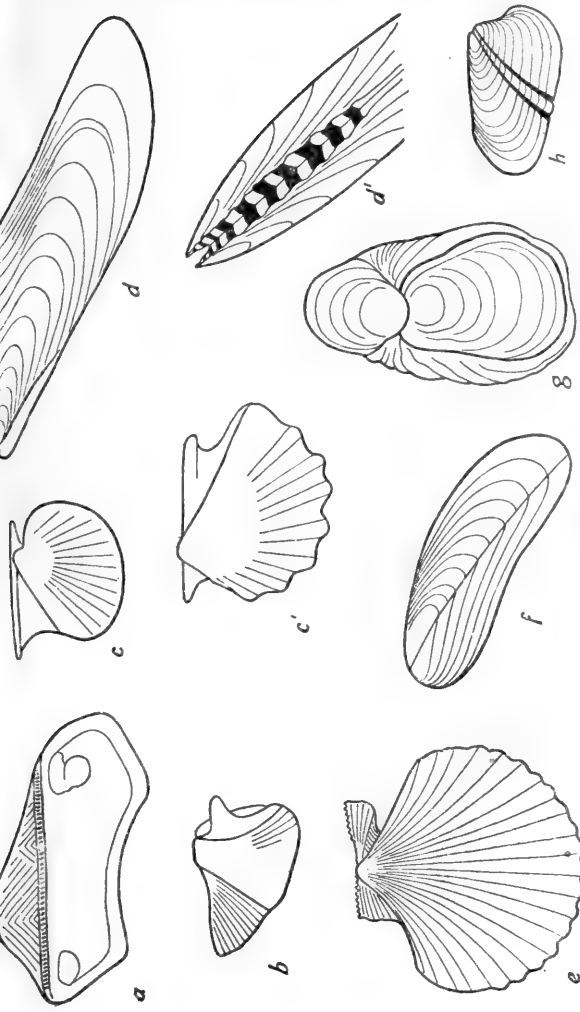


FIG. 25.—FIXED AND BURROWING LAMELLIBRANCHS.

*a*, *Arca biançula* Lamarck, Upper Eocene. Interior of right valve. ( $\times \frac{1}{2}$ .) Shows large triangular area, straight taxodont hinge, adductor impressions and pallial line. (After S. V. Wood.) *b*, *Conocardium aleiforme* (J. de C. Sowerby), Lower Carboniferous. Left side view. ( $\times \frac{1}{2}$ .) (After de Koninck.) *c*, *c'*, *Pteria* (*Oxytoma*) *costata* (J. Sowerby), Bathonian. *c*, Exterior of right valve; *c'*, exterior of left valve. (Natural size.) (After Morris and Lycett.) *d*, *Gervillia sub-lanceolata* d'Orbigny, Aptian. ( $\times \frac{1}{2}$ .) *d*, Left side view; *d'*, dorsal view of hinge-line, ligament-pits white between black. (After Woods.) *e*, *Chlamys opercularis* (Linné), Pliocene. Right valve. ( $\times \frac{1}{2}$ .) Byssal notch seen under anterior ear. (After S. V. Wood.) *f*, *Modiola scalprum* J. Sowerby, Lower Lias. Left side view. ( $\times \frac{1}{2}$ .) (After Goldfuss.) *g*, *Gryphea arcuata* Lamarck, Lower Lias. Right side view. ( $\times \frac{1}{2}$ .) (After Buwignier.) *h*, *Orthonota triangulata* Salter, Silurian. Right side view. ( $\times \frac{1}{2}$ .) (After Phillips.)

centrically ornamented, as a rule: the two first are equivalve, without curved beaks, while *Inoceramus* is inequivalve, and has beaks incurved. This last attains great size and thickness in the Upper Cretaceous, just before extinction, showing the same senile characters as *Hippopodium* or some brachiopods—growth of the shell-margin being quite out of proportion to actual increase of length. Many other genera might be named.

2. **Anomiacea**.—Inequivalve; monomyarian; internally nacreous; without ears; byssal notch (at least in early life) converted into a perforation (which may afterwards close up); no hinge-teeth; ligament amphidetic, internal.

*Anomia* (Jur.—Rec.) with the above characters is occasionally found fossil. *Placunopsis* (Jur.) resembles *Anomia*, but the right valve is not perforate and is fixed by cementation.

3. **Pectinacea**.—Usually inequivalve; monomyarian; interior lamellar, sub-nacreous; with thin external ligament and thicker resilium, both amphidetic; teeth on either side of resilium, well-developed or vestigial; usually with ears, sometimes with a byssal notch. Ornament usually radial. Some genera fixed by byssus or cementation, others active swimmers. Silurian to Recent.

These shells resemble the Pteriacea in (*a*), being usually inequivalve, (*b*) usually having the hinge lengthened by "ears," (*c*) having an amphidetic area and ligament, and (*d*) having a byssus, and consequently in many cases a notch under the right anterior ear. On the other hand, the ligament tends to sink into the position of a resilium, between the teeth; the anterior adductor is entirely lost, making the shell monomyarian; and the internal layer is sub-nacreous. The chief genera are *Chlamys* (Trias.—Rec.), both valves rather flat, with good byssal notch (Fig. 24, *e*); *Pecten* (Cret.—Rec.), with very

convex right and flat left valve, and no byssal notch; *Pterinopecten* and *Aviculopecten* (Sil.-Carb.), with long hinge and ears not sharply marked off: all these have feeble hinge-teeth, and are ornamented with radial costæ. In *Spondylus* (Jur.-Rec.) the cardinal area is large, especially on the right valve, which is attached; the hinge-teeth are large and curved; the surface is radially costate and spiny. *Plicatula* (Trias.-Rec.) is flatter and without the large area. *Lima* (Carb.?-Rec.) is equivalve, inequilateral, toothless or nearly so, and with a very feeble byssal notch.

4. **Ostracea**.—Inequivalve; monomyarian; interior lamellar, sometimes sub-nacreous; hinge-line short, without teeth, with thick amphidetic ligament; without ears or byssal notch; ornament concentric-striate, or radial (often very coarse). Fixed by left valve.

These are the oysters. Their very short hinge-line makes the amphidetic ligament shorter than high and usually triangular in shape. The subdivision into genera is unsatisfactory, as the characters that have been relied upon are such as recur again and again on independent lines of descent. Thus strongly costate forms have been named *Alectryonia*; forms with the beaks curved spirally backwards, *Exogyra*; those with concave right valve and large overhanging left umbo, the shell being fixed only in early life and breaking off by its own weight later, *Gryphæa* (Fig. 24, *g*); but these are probably all false or polyphyletic genera, consisting of a number of species belonging to different oyster-stocks which have assumed similar characters by convergence. True genera consist of species derived from the same immediate stock. Polyphyletic genera can be recognized by differences in the ontogeny of their several species. *Gryphæa* in particular is a series of senile (phylogerontic) forms, the change of growth-direction being similar to that seen in the huge

forms of *Inoceramus* of the Upper Cretaceous, or *Hippopodium* of the Lias.

*Ostrea* is possibly as old as Carboniferous, and is abundant from the Jurassic onwards. *Gryphæa* is mainly Jurassic; *Exogyra*, Upper Jurassic and Cretaceous.

5. **Mytilacea**.—Equivalve; heteromyarian; interior nacreous; umbo anterior; hinge-line short, without teeth, or with very obscure cardinal teeth; ligament opisthodontic; no ears or byssal notch, but a slight byssal gape; shell elongated in an oblique direction. Ornament concentric or partly radial. Marine or fluviatile.

This sub-order is typified by the common marine mussel, *Mytilus*. The shell is always elongated in an oblique direction and tends to a triangular shape, the apex being formed by the umbo, which is at or near the anterior end of the hinge-line and is never conspicuous, the base of the triangle being the posterior border. The area is generally obscure, but apparently amphidetic, but the ligament is opisthodontic. Hinge-teeth are wanting or indistinct. Early genera such as *Modiolopsis* (Ord.-Sil.) and *Myoconcha* (Carb.-Cret.) are less heteromyarian than the rest. *Modiola* (Fig. 25, f, Dev.-Rec., maximum in Jurassic) is more quadrilateral than *Mytilus*, the beaks not being so far forward. *Lithophagus* [*Lithodomus*] (Carb.-Rec.) is flask-shaped, and bores into corals, thick shells such as *Perna*, or rocks on the sea-bottom: casts of its borings sometimes puzzle the fossil-collector. *Dreissensia* (Eoc.-Rec.) and *Congerina* (Mio.-Plio.) are fresh-water forms, having the anterior adductor borne on a myophoric plate. It has been suggested that these are not true Mytilacea, but homœomorphs derived from some other stock, but there is little evidence for this.



## III. Burrowing Branch.

## DESMODONTA.

Usually equivalve, tending to an oblong shape; often gaping; isomyarian; internally nacreous or porcellanous. Hinge-line simple, usually one cardinal tooth in each valve; ligament opisthodontic. With long siphons; usually sinu-palliate. Ornament concentric-striate, rarely radial.

A number of Palæozoic genera belong to this branch, but, owing to imperfect preservation, are not capable of being further classified: such are *Orthonota* (Fig. 25, *h*, Sil.), *Grammysia* (Sil.-Dev.), and *Edmondia* (Carb.-Permian). The Mesozoic and later forms can be more definitely grouped.

1. **Anatinacea.**—Equi- or inequivalve; hinge with one cardinal tooth in each valve, opisthodontic ligament, with or without resilium; internally nacreous (with some exceptions); sinu-palliate.

*Pleuromya* (Trias.-Lower Cret.) is elongate-oval, with fairly strong concentric ornament, and the right valve slightly overlaps the left along the hinge line. *Pholadomya* (Jur.-Rec.) has been already described; it is almost the only Anatinacean with radial ornament, and is divided into a number of sub-genera according to shape and ornament. *Thracia* (Trias.-Rec.) is inequivalve, the right valve being the larger; *Panopea* (Cret.-Rec.) has a thick shell, gaping at both ends; *Saxicava* (Cainozoic and Recent) is a rock-borer, with the pallial line represented by a series of disconnected marks. The last two are non-nacreous.

2. **Myacea.**—Equi- or inequivalve; ligament internal, on a horizontal resiliophore; internally porcellanous; sinu-palliate.

*Corbula* (Trias.—Rec.) has already been described. *Mya* (Eoc.—Rec.) differs in being almost equivalve, and gaping at both ends; the anterior adductor is long and narrow, and the pallial sinus deep.

3. **Adesmacea**.—Borers in stone or wood, with highly-modified shell, in which the whole hinge-apparatus becomes obsolete, while various accessory shelly structures are added to the valves until finally the latter form an insignificant part of the skeleton.

*Pholas* (Jur.—Rec.) has well-developed valves, though they do not articulate, and is one of the few desmodonts with radial ornament. The inner layer of the shell is reflected over the hinge-line and covers the umbo; there is a curved rod projecting from the interior of the umbo, for the attachment of a pedal muscle, and accessory plates on the outside in the region of the umbo. *Teredo*, the "ship-worm" (Jur.—Rec.) bores in floating wood, and has two small, short valves which are of little service as a covering to the body, while the immensely long siphons are encased in a calcareous tube.

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### III

## THE GASTROPODA

THE Gastropoda, or Snails, are much more active animals than the Lamellibranchia, most of them crawling about in search of their food, which they take into the mouth by means of the radula—a rasping tongue set with chitinous teeth. The head and foot are permanently outside the mantle-chamber, which is consequently much reduced in size, with a small opening, and in nearly all cases lies on one side of the body. This last feature is part of a profound asymmetry which affects all parts of the body except the head and foot. In the mantle-chamber of primitive genera are a pair of gills much like those of *Nucula*; these are reduced to one as a part of the asymmetry of higher forms, and disappear altogether in the air-breathing forms, the whole mantle-chamber then serving as a lung-sac. Except in these last, a ciliary mechanism exists for the purpose of respiration, and in many it also serves to remove the excrement from the mantle-chamber, while in some it even collects microscopic food (though it cannot convey it to the mouth, which lies outside the mantle-chamber). The gastropod shell is distinguished from that of lamelli-branches by not being divided into right and left valves:

it is therefore described as *univalve*. The simplest form of this shell is an elliptical cone, the aperture occupying the whole base; but in the great majority of cases the shell is a cone coiled in a helicoid spiral.

In many cases there is a horny or calcareous plate (operculum) which closes the apertures of the shell when the animal withdraws into it. This, however, is never hinged to the shell, and the idea that it represents a second valve like that of lamellibranchs has no justification whatever.

Gastropods are the only class of molluscs that inhabit the dry land, as well as fresh and salt waters. They are known from all the geological systems, but it was only in the Cainozoic era that they became really abundant. From the Eocene period down to the present day, they constitute, with lamellibranchs, the main part of the invertebrate fauna preserved as fossils.

1. ***Emarginula fissura*** (Fig. 26), found fossil in the crags of East Anglia and still living in British seas, is an example of an almost symmetrical gastropod. It is shaped like a cone, with an elliptical base and the apex bent over in the plane of the major axis, which thus appears to be a plane of symmetry. More careful examination with a lens shows, especially in youthful examples, that the apex is curled in a spiral to one side, so that there is no perfect plane of symmetry. The side on which the spiral lies is the right side, the direction in which the apex points being posterior (with reference to the animal's anatomy). The anterior margin has a deep, parallel-sided slit. The outer surface is ornamented by alter-

nately strong and weak radial ribs, crossed by concentric ridges (growth-lines), except the apex, which is smooth. Internally there is seen a horseshoe-shaped scar, marking the position of the muscles by which the animal pulls the shell tightly down upon the surface to which it clings by its broad, muscular foot. The opening of the horseshoe marks the position of the head.

The notch at the anterior margin indicates the importance of ciliary mechanism in this genus, for it lodges a process of the mantle containing the exhalent aperture.

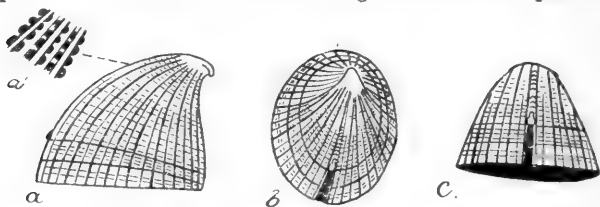


FIG. 26.—*EMARGINULA FISSURA* (LINNÉ), PLIOCENE. ( $\times 2$ .)

*a*, Right side view; *a'*, small portion of surface greatly enlarged to show the ornamentation which is only diagrammatically shown in the other figures; *b*, view from above; *c*, anterior view. Slit, in *b* and *c*, black: at its upper end is seen the callus, and above this the band. (Original.)

Shell-growth in gastropods takes place as in lamelli-branches, at the shell-margin and by thickening of the internal layer: the apex of the shell corresponds to the umbo. The presence of a marginal notch, however, causes an interruption to the continuity of the region of growth. Hence to prevent the notch from becoming deeper and deeper as growth proceeds it is filled up at the inner end by a deposit of shell-substance like that of the inner layer: in time this forms a band from the apex to the slit that in some species of *Emarginula* is very prominent.

This marginal slit, in one form or another, is characteristic of an important series of gastropods, whose generally primitive character is confirmed by the fact that they formed a much larger proportion of the Palæozoic than of the modern gastropod fauna.

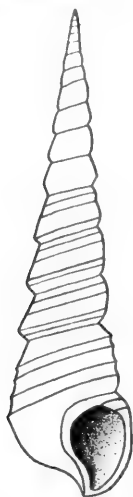


FIG. 27.—TURRITELLA IMBRICATARIA, LAMARCK, EOCENE.  
(Natural size.) (After Deshayes.)

2. **Turritella imbricata** (Fig. 27) is a very common fossil in the Barton beds of the Hampshire coast, and the Bracklesham beds of the Selsey peninsula. Its shape approaches that of a very acute cone, but it is formed of a tube coiled in a spiral, and increasing steadily in size from the apex of the cone downwards, which is the direction in which growth takes place. Each turn of the spiral is called a *whorl*, and all the whorls except the

last collectively form the *spire*. Lines drawn at a tangent to opposite sides of the spire will meet beyond the apex at an angle of  $11^{\circ}$ , which is the *spiral angle* of this particular species. The spiral line which marks the visible junction of one whorl with the next is called the *suture*. The side of each whorl forms an apparently convex curve, but this is seen under a lens to be made up of eight concave curves, the ends of which correspond to seven more or less conspicuous ridges which run spirally round the shell from apex to base, bearing on them a vast number of fine and close-set tubercles. Between and parallel to these ridges are much finer lines, from four to twelve in each interval. These are all crossed by very fine growth-lines, parallel to the margin of the aperture.

The *aperture*, or mouth, of the shell is oval in shape. When the shell is placed in the usual position chosen for figures of gastropods—apex upwards\*—the mouth is seen on the right-hand side of the base (this being a right-handed spiral or *dextral* shell, as was also *Emarginula*). The margin of the aperture is called the *peristome*; it is divided into *inner lip* (near the middle line) and *outer lip*. Living species of *Turritella* have a horny operculum, which fits into the aperture when the animal is completely withdrawn into the shell; but this, being horny, is not found fossil.

If a vertical section is cut through the axis of the spiral, it is seen that the inner faces of the whorls are

\* This is the accepted position in English works, but in French works it is usual to place the apex downwards.



united into a solid pillar extending from base to apex—the *columella*.

The outline of the whorls and detail of the surface-ornament are specific characters of *T. imbricataria*: all the other characters described (except where common to all or many gastropods) are generic characters of *Turritella*. A shell of this shape, with long spire, and last whorl not conspicuously larger than the last but one, is described as *turreted*. The possession of a solid columella is denoted by the term *imperforate*; the simple outline of the peristome is indicated by the term *holostomatous*. These terms will be more clearly understood when the contrary terms are illustrated.

3. ***Natica multipunctata*** (Fig. 28) is a common fossil in the masses of accumulated shells found in East Anglia and known as Crag, and it still lives at the present day, though only in warmer seas, as the Mediterranean. The shape is very unlike that of *Turritella*, the last whorl forming the greater part of the external surface, the spire being very low, and having a spiral angle of  $120^{\circ}$ . The whorls are highly convex, nearly semicircular in outline, but flattened or even slightly concave near the suture. The large size of the last whorl is not due to an abrupt increase of sectional area, but to the mode of coiling, the greater part of each whorl being concealed by the next: this can be realized either by following in imagination the extension of the last whorl which would result from further growth, or by making an actual section through the vertical axis. Such a section would also show that instead of being united centrally into a columella the

whorls are coiled around a central cavity, the *umbilicus*, the presence of which makes this a *perforate* shell.

The aperture is nearly semicircular, the inner lip being straight. In the adult animal, a fold of the mantle extends out over the inner lip, and secretes an extension of the inner layer of the shell, which more or less completely closes over the umbilicus. This deposit is called *callus*.

The surface of *N. multipunctata* is nearly smooth, being

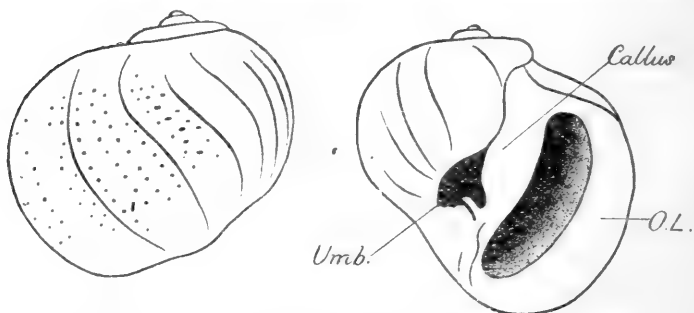


FIG. 28.—*NATICA MULTIPUNCTATA*, S. V. WOOD, PLIOCENE.  
(Natural size.)

*O.L.*, Outer lip; *Umb.*, umbilicus. (After S. V. Wood.)

only marked by fine lines of growth and by the punctations to which it owes its trivial name. In the Crag specimens the lines of growth are often irregular, some—often several near together—being more prominent than the rest. As in lamellibranchs and brachiopods, such irregularities denote interruptions to the steadiness of growth, possibly periods of starvation or of a greatly varying supply of calcareous matter.

Species of the genus *Natica* are world-wide, frequent-

ing sandy bottoms in shallow water. In time they range from at least the Triassic period. They are carnivorous, using their radula to bore circular holes in lamellibranch shells, as well as those of other gastropods, through which they feed on the animal within. Shells thus bored are very common among the fossils of the Crag, and of the Miocene of Touraine. *Natica*, however, is only one of the genera which bores in this way, and it is itself sometimes a victim to this mode of attack.

4. **Cerithium serratum** (Fig. 29) of the famous "Calcaire Grossier," the Paris building-stone, of Eocene age, is a turreted shell, different from *Turritella*, not only in its more elaborate ornamentation but in the form of its aperture, the anterior end of which is produced into a well-marked channel, the *anterior canal*. The shell attains a length of 75 mm. (3 inches). The spiral angle is about 20°. The whorls are flat-sided; in the first 10 mm. the ornamentation is weak and then it suddenly becomes strong. It consists in each whorl of an upper row of prominent compressed tubercles, 12 or 13 to a whorl, just below the upper suture; a row of very fine tubercles, about 30 to a whorl, three-quarters down the side of the whorl; and a row of rather larger tubercles, 25 to a whorl, just above the lower suture. These rows are crossed by fine lines of growth, which on the last whorl are seen to have the form of a reversed **S**, though on the whorls of the spire the lower limb of the **S** is concealed. These growth-lines are parallel to the margin of the outer lip. The aperture is pear-shaped (the anterior canal forming the stem of the pear); its long axis is at

27° to the axis of the spire; the anterior canal is nearly straight, but with a slight twist which tends to bring it more in line with the spire-axis, about two-thirds the length of the aperture proper, and nearly half its width. The shell is imperforate. Having an anterior canal it is *siphonostome*, *Natica* and *Turritella* being *holostome*.

Many species differing in details of ornament from *C. serratum* will equally well illustrate the genus in the

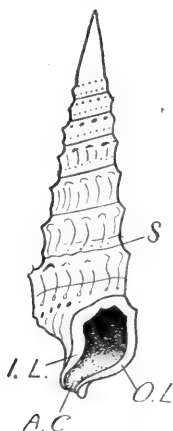


FIG. 29.—*CERITHIUM SERRATUM*, LAMARCK, EOCENE. ( $\times \frac{1}{2}$ .)

*A.C.*, Anterior canal; *I.L.*, inner lip; *O.L.*, outer lip; *S*, suture.  
Details omitted near apex. (After Deshayes.)

broad sense. The original genus *Cerithium* has now been split up into numerous smaller genera. Recent species are all marine, and though the group is world-wide, the most typical species are tropical. The genus is known fossil from the Jurassic upwards, and had a wide geographical distribution until at least the Miocene period.

5. **Rimella rimosa** (Fig. 30) is found in the Barton beds of the Hampshire coast, and belongs to a family which is nowadays almost confined to tropical seas. In shape it differs from turreted shells in that the anterior part of the last whorl (and of other whorls, though this is not seen externally) is drawn out to a point of such length that the last whorl almost repeats the shape of

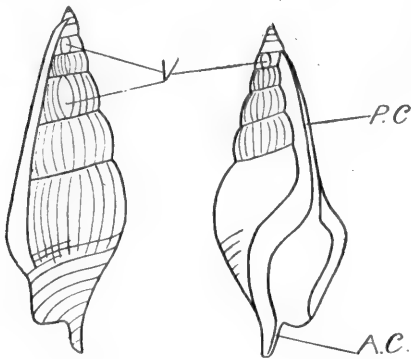


FIG. 30.—RIMELLA FISSURELLA (LAMARCK), EOCENE.  
(Natural size.)

This species is very close to *R. rimosa* (Solander). A.C., Anterior canal ; P.C., posterior canal ; V, varices. (After Deshayes.)

the spire in inverted position : such a shell is spindle-shaped or *fusiform*. The aperture and anterior canal take part in this drawing-out. The outer lip is thickened, and the posterior end of the aperture is drawn out into a long narrow channel (*posterior canal*) which runs right up the spire in close contact with it. This canal is analogous to the notch of *Emarginula* and its allies, but does not indicate any near affinity with them,

The surface-ornament consists of numerous slightly-curved vertical ridges (corresponding to growth-lines), the intervals between which are marked by finer spiral lines, which become broader and flatter as they cross the vertical ridges.

Careful examination of a well-preserved specimen shows two things: first, that the actual apex is obtuse, and the first four whorls are quite smooth; second, that at intervals the place of about three of the vertical ridges is taken by a much broader and more conspicuous elevation. These elevations, called *varices*, agree in character with the thickened outer lip of the aperture; they are in fact a series of outer lips successively abandoned as the shell grew larger. It is evident that a shell with an elaborate aperture like that of *Rimella* cannot possibly maintain the form of its aperture by steady growth, as *Natica* or *Turritella* can do with its simple aperture. It must either form its aperture once for all and abandon further growth, or it must alternate between periods of rapid shell-growth without the specialized aperture, and periods in which no growth takes place and the elaborate aperture is in full use. The latter is the case with *Rimella*: in place of the occasional irregularities of the growth-lines of *Natica* we have periodical growth-periods. What each of these represents in actual time cannot be stated with certainty, but probably less than a year.

Another point to be noticed is that none of the varices of *Rimella* show any sign of an old posterior canal. This does not mean that posterior canals were not formed until the adult stage, since immature specimens are found

having a posterior canal: it therefore means that each posterior canal is actually absorbed during the growth-period that follows its abandonment. This suggests the possibility that in some genera the whole of the special structures at the aperture might be absorbed when growth restarts. These considerations have a bearing upon some features found in Cephalopoda (p. 160).

It may be mentioned that in one genus of gastropods, *Distortrix* (very rare as a fossil) the method is adopted of forming an enlarged aperture and afterwards recovering



FIG. 31.—TRIVIA AVELLANA (J. SOWERBY), PLIOCENE. ( $\times \frac{3}{2}$ .)

A.C., Anterior canal; P.C., posterior canal. (Original.)

the normal whorl-form, not abruptly as in other genera, but gradually: the result is an extraordinary and puzzling distortion of form.

6. **Trivia avellana** (Fig. 31), found living in British seas and fossil in the Crag, is a small hemi-ellipsoidal shell in which no spiral coiling is recognizable externally, because the last whorl completely envelops and hides the spire. Such a shell is said to be *convolute*. The aperture is very narrow, nearly parallel-sided and slightly curved, with slight anterior and posterior canals; the outer lip is thickened. The whole surface is ornamented

by ridges disposed more or less at right angles to the aperture but without the steady parallelism of the spiral ridges of a turreted shell: these ridges extend over the edges of both lips, which are therefore said to be toothed.

*Trivia* is a genus of the family *Cypræidæ*, the Cowries. The typical *Cypræa* is a tropical genus, which includes the money-cowry and many large and richly coloured species. It differs from *Trivia* in having the outer surface of the shell smooth and polished by the deposit of an extension of the inner layer by lobes of the mantle which extend out and lap over it. In the youthful shell the spire is visible though very short, and only as the adult stage is reached does the shell become convolute.

7. **Fusus porrectus** (Fig. 32), of the Barton Clay, is a many-whorled, fusiform shell. The aperture is pear-shaped, and is drawn out into a narrow, straight anterior canal, nearly three times the length of the aperture itself. The whorls are very convex in outline, ornamented by nine spiral ridges of unequal strength, crossed by a large number of varices (12 to a whorl except in some of the earliest whorls); where they cross, the spiral ridges are particularly prominent. In the part of the last whorl corresponding to the anterior canal (a part concealed in the other whorls) the varices die away and the spiral ridges are numerous and more uniform. If the shell is perfect at the apex, the first two whorls are seen to be quite different from the rest—smooth and globose, coiled on an axis inclined at an angle to that of the rest of the shell. This early stage, so markedly different from the adult stage, is termed the *nucleus* or *protoconch*.



*Fusus* is a marine genus, now confined to sub-tropical seas, but, as in so many other cases, found in Britain in the Eocene period. It is rare in earlier formations, but is recorded as far down as the Upper Jurassic.

8. **Planorbis discus** (Fig. 33) is a common fossil in the Bembridge Limestone (Lower Oligocene or Sannoisian) of the Isle of Wight. The upper surface is flat (spiral angle  $180^{\circ}$ ), with a rather deep hollow in the centre.

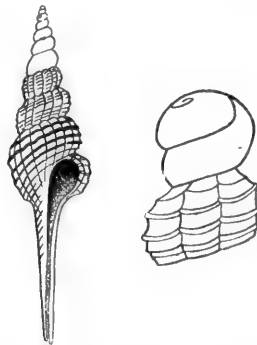


FIG. 32.—*FUSUS PORRECTUS*, SOLANDER, EOCENE.

Left-hand figure, natural size (ornament omitted from earlier whorls); right-hand figure, protoconch and post-embryonic whorl. ( $\times 18$ ) (Original.)

The greatest diameter (30 mm. in full-grown shells) can almost be measured on this upper surface, the margin being rounded and the outline below quickly turning inwards at an angle of  $35^{\circ}$  to the upper surface; in the centre of the under surface is a shallow umbilicus, about one-third the diameter of the shell. The aperture for two-thirds of its extent has an elliptical outline, but in contact with the inner whorl this changes to a concave

curve which meets the general elliptical curve at nearly a right angle. The shell is thin and fragile, and smooth, except for faint growth-lines.

The number of whorls is few : on following these carefully inwards on the upper surface it is seen that only the last whorl and a half (in large specimens) has a flat upper surface ; inwards from thence the surface becomes convex, and after another turn it plunges downwards rather rapidly, forming the hollow already noted. The

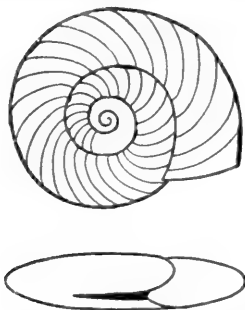


FIG. 33.—*PLANORBIS DISCUS*, EDWARDS, OLIGOCENE.  
(Natural size.) (After Edwards.)

The lines of growth are too strongly marked in the upper figure.

actual initial part of the shell is thus invisible from the upper surface, but is plainly visible below, in the centre of the umbilicus if the latter is free from matrix. It is clear therefore that the young shell is not only very different in shape from the adult (more like *Natica*), but is a left-handed or sinistral spiral. Indeed it is open to argument whether the adult shell is not still sinistral, the flat surface which has been described as upper being really under. This is the more likely to be the correct

interpretation, since the anatomy of the animal shows it to be actually sinistral. Other cases are known where the nucleus or protoconch is sinistral and the adult shell dextral, and such shells are termed *heterostrophic*.

Many species of *Planorbis* are found in the same beds, and several are also found living in our streams and ponds, it being a purely freshwater genus. Although differing in details of shape and proportions from the species described above, their general likeness to it is obvious, and in all cases the sinistral character of the young shell can be recognized.

The classification of the Gastropoda is a very unsatisfactory matter for the palæontologist. The features which zoologists have found to be the best basis for a natural classification leave no mark upon the shell, and there are not, as there are in lamellibranchs, important shell-characters that can be made a basis for broad divisions. If gastropods were entirely or mainly extinct, we should be driven to make a shell-classification, but it would be quite obviously artificial. As it is, there are few extinct genera which are not obviously related to recent forms, so we have to accept the zoological classification and place these extinct genera with their nearest allies.

The fundamental division is based upon a difference in the nervous system : in one main sub-class, the Strepto-neura, the twisting of the body which brings the anus round nearly to the head has twisted the nerve-loop which supplies the gills into a figure-of-8 ; in the other, the Euthyneura, it has left it straight. The latter sub-class

falls naturally into two divisions, the Opisthobranchiata, marine forms with gills, and the Pulmonata, terrestrial and freshwater forms in which the mantle-chamber is converted into a lung-sac. These two latter groups are so distinct that many systematists raise them to the rank of sub-classes, and as this is convenient for palæontological purposes we will do so here. No shell character can be pointed to as distinctive of either of these three sub-classes; nevertheless, any one who is familiar with gastropod shells generally would feel little hesitation in placing a genus he had never seen before in its proper sub-class. He would not find it easy to state his reasons, as they would consist in combinations of characters, positive and negative, which could only be stated with many qualifications. Among other general facts that he would have in mind would be the much larger proportion of fossil genera belonging to the Streptoneura than to the Euthyneura (for in the latter, and especially in the opisthobranchs, there is a tendency towards the reduction and final disappearance of the shell); and the restriction to freshwater deposits of Pulmonata and a few genera of Streptoneura.

#### SUB-CLASS: STREPTONEURA.

#### ORDER: ASPIDOBANCHA.

SUB-ORDER: *Docoglossa*.—This includes the limpets, forms with shells like *Emarginula*, but without the notch. Forms undistinguishable from the common modern limpet, *Patella*, date from the Silurian, and allied recent genera are also known as fossils.

**SUB-ORDER: Rhipidoglossa.**—This includes all the remaining nacreous gastropods with others that are porcellanous. Palæontologically they may be divided into two series, according to the (a) presence or (b) absence of the lateral slit (described in *Emarginula*.)

(a) *Fissuridea* resembles *Emarginula* in shape, but the notch becomes closed in at an early age by the union of the margin and forms a “key-hole” in front of the apex; as the shell grows this perforation becomes larger, by resorption of the shell, until it occupies the whorl apex and is far from the margin. In *Haliotis*, the “ormer” of the Channel Islands or “Venus’ ear,” new notches are formed as the earlier are first closed around and eventually filled in, so that at any time one notch and several perforations are in use. The important fossil genus *Pleurotomaria* (Fig. 34, a, Sil.–Rec.) is spirally coiled and has a slit, the filling in of which gives rise to a spiral band, towards which the lines of growth are indented in a V-like manner. The geological history of *Pleurotomaria* is similar to that of *Pholadomya* or *Trigonia* among lamellibranchs: world-wide in its distribution up to the Cretaceous period, it then became restricted and now survives only in the seas of Japan and the East and West Indies.

*Bellerophon* (Fig. 34, b, Sil.–Perm.) is one of the few gastropod shells which is coiled symmetrically, so that it resembles externally a cephalopod shell (but has no internal septa): the last whorl more or less completely envelops the others, leaving either a very narrow umbilicus on each side, or none. *Euomphalus* (Fig. 34, c, Sil.–Trias.) is a discoïdal shell—that is, one in which the spiral angle is increased to 180° or even more, so as to become a re-entrant.

(b) Among genera without a lateral notch, the most important are *Trochus* (Sil.–Rec.), a conical shell with

a flat base and an aperture wider than high (Fig. 34, *d*); *Turbo* (Sil.-Rec.) differing from *Trochus* in having a convex base and a nearly circular aperture, so that if placed apex downwards it is seen to resemble a spinning-top: this form is described as *turbinata*; *Nerita* (Jur.-Rec.), globose, imperforate with semicircular aperture and thick, often grooved, lips; *Neritina* (Eoc.-Rec.), similar, but with thin shell and lips, a fluviatile snail (Fig. 34, *e*).

#### ORDER: CTENOBRANCHIA.

Divided into a number of sub-orders on a basis of tongue-structure, the only convenient palæontological division is into holostome and siphonostome forms.

(a) **Holostome.**—*Scalavia* (Trias.-Rec.) is turreted, with circular aperture, strong, sharp vertical ridges and finer spiral lines. *Solarium* (Jur.-Rec.) is conical, with obtuse spiral angle, umbilicus very wide and deep, and four-sided aperture. The *nucleus* (or larval shell) is *heterostrophic*, as in *Planorbis*, as can easily be detected on a well-preserved specimen.

*Littorina* (Jur.-Rec.), the periwinkle, somewhat resembles *Turbo* in form, but is not nacreous. *Natica* and *Turritella* have already been described. *Vivipara*, or *Paludina* (Jur.-Rec.), is turbinata with rounded apex, rounded whorls and a sub-circular aperture: it is a fresh-water form (Fig. 34, *g*).

The family *Capulidæ* is an interesting case of degeneration: it has taken to microscopic food and a fixed habit; in consequence the shell reverts to a more or less limpet-like form. There is therefore some uncertainty as to whether certain fossils belong to this family or to the *Patellidæ*. *Capulus* (Fig. 34, *f*) shows a trace of spiral curvature at the apex; *Crepidula* (Cret.-Rec.), the slipper-limpet, has a slipper-shaped shell, and forms arch-like colonies, one individual on

top of another; *Calyptraea* (Cret.-Rec.), the bonnet-limpet, or Chinaman's hat, is depressed-conical, with a spiral shelf in the interior; *Platycevas* (Camb.-Trias), limpet-like, with spirally-rolled apex, often found adhering to the ventral surface of crinoids, on which it was in some degree parasitic. The *Capulidæ* attained their acme in the Silurian and Lower Devonian, particularly of Bohemia, where many strange forms occur, including some which are high-conical and almost cylindrical.

The family *Melaniidæ*, with the turreted genera *Melania* (Jur.-Rec.) and *Melanopsis* (Cret.-Rec.), is transitional to the siphonostome group, the latter genus having an anterior canal and the former not. *Melania* (Fig. 34, *h*) is distinguished from *Turritella* by the shape of the whorls, which gave a step-like outline to the shell, and the greater strength of the vertical ornament, which develops strong tubercles or spines.

(b) **Siphonostome.**—*Cerithium* has been described already. Closely allied to it is *Potamides*, which at present lives in mangrove swamps and the estuaries of tropical and sub-tropical rivers. There is no absolute way of distinguishing this genus from *Cerithium* by shell-characters alone, though the opercula are distinct, and in the fresh shell there is a dark green *periostracum* (external non-calcareous layer of shell, rarely preserved in fossils). Consequently the reference of fossil species to *Potamides* is partly based upon their occurrence along with unquestionable fresh-water shells. *Potamides* is divided now into several sub-genera: it is known from the Cretaceous upwards, and had a much wider distribution in the Eocene and Oligocene periods than now, being common in the strata of the Isle of Wight. These two genera are members of the family *Cerithiidæ*, of which other members occur as far back as the Triassic period. In these early genera the anterior canal is very feebly

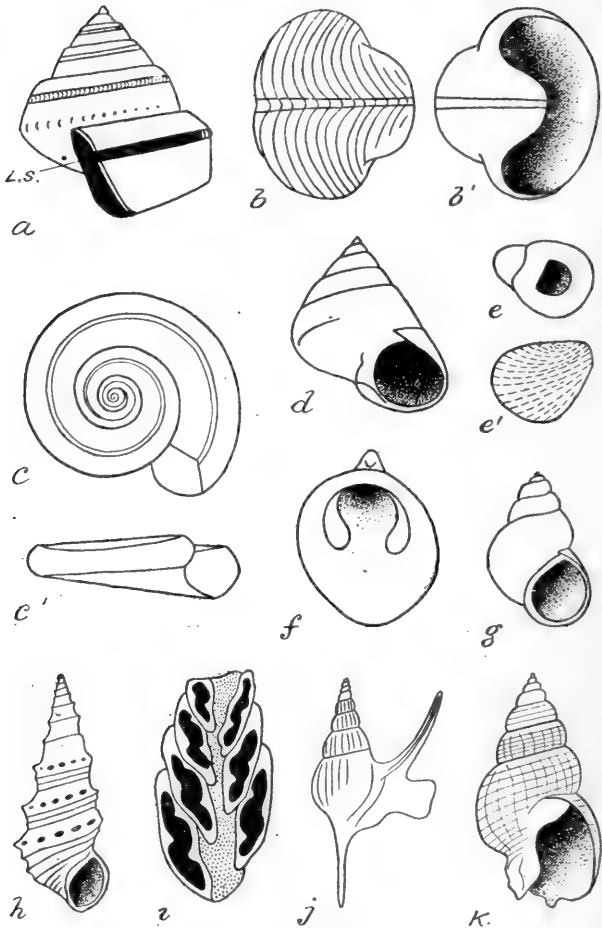


FIG. 34.—GASTROPODS.

*a*, *Pleurotomaria mosensis* Buvignier, Upper Jurassic. ( $\times \frac{1}{2}$ .) (After Buvignier). L.S., Lateral slit. *b*, *b'*, *Bellerophon hiulcus* J. de C. Sowerby, Lower Carboniferous. ( $\times \frac{1}{2}$ .) (After de Koninck.) *c*, *c'*, *Euomphalus pentangulatus* J. Sowerby, Lower Carboniferous. ( $\times \frac{1}{2}$ .) (After Goldfuss.) *d*, *Trochus inornatus* Buvignier, Upper Jurassic.



marked, so that its development must have taken place gradually within this family.

In the Mesozoic rocks there is found another family, the *Nerinaeidae*, some members of which have great superficial resemblance to *Cerithium* in form and ornament, so that they can only be distinguished by taking vertical sections through the shell (Fig. 34, *i*). It is then seen that the cavity of each whorl is more or less constricted by internal spiral ridges (not confined to the columella as any are that occur in *Cerithium*). In extreme cases these ridges are so developed that only a narrow space of complicated form is left for the snail's body; for instance, in *Ptygmatis*, a common genus in the English Lower Oolites.

*Rimella* belongs to the family *Strombidae*, other genera of which have the outer lip expanded and sometimes branching in a finger-like manner. The family ranges from the Jurassic period to the Recent, and though abundantly represented in the British area up to and in the Eocene period, it is now confined to the Indo-Pacific province, the Mediterranean and West Indies. The closely-allied family *Aporrhaidae*, however, with similar digitations to the outer lip (Fig. 34, *j*), and having the same range in time, is essentially Atlantic in its modern distribution, and the species *Aporrhais pes-pellicani* is common in the British seas.

*Trivia* and the *Cypraeidae* have already been mentioned.

FIG 34.—GASTROPODS (continued).

( $\times \frac{3}{2}$ .) (After Buvignier.) *e*, *Nerita aperta* J. de C. Sowerby, Oligocene. ( $\times \frac{3}{2}$ .) (After Edwards.) *f*, *Capulus ungaricus* (Linné), Pliocene. ( $\times \frac{3}{2}$ .) (After S. V. Wood.) *g*, *Vivipara lenta* (Solander), Oligocene. ( $\times \frac{3}{2}$ .) (After Deshayes.) *h*, *Melanatria inquinata* (Defrance), Eocene. ( $\times \frac{3}{2}$ .) (After Deshayes.) *i*, *Nerinea moreana* d'Orbigny, Upper Jurassic. ( $\times \frac{3}{2}$ .) (After Buvignier.) *j*, *Aporrhais parkinsoni* Mantell, Gault. ( $\times \frac{3}{2}$ .) (After Starkie Gardner.) *k*, *Nassa reticosa* (J. Sowerby), Pliocene. ( $\times \frac{3}{2}$ .) (After S. V. Wood.) In several cases the ornamentation is omitted from the earlier whorls for the sake of clearness of outline.

Allied to them is *Pyrula* (Cret.-Rec.), another of the forms, now exclusively tropical, found in the British Eocene: a pear-shaped form with very short, obtuse spire, and very large aperture with thin outer lip.

Another group of siphonostomes is represented by the whelks, *Buccinum* and *Nassa* (Tertiary and Recent), the former of boreal and the latter of general distribution. These are elongate-oval imperforate shells with spires of moderate length, wide apertures and short anterior canal, ornamented by coarser vertical and finer spiral lines. In *Buccinum* the canal is in line with the long axis of the aperture; in *Nassa* (Fig. 34, *k*) it makes a considerable angle with it. The latter genus is also distinguished by crenulations on the interior of the outer lip. Another allied genus is *Neptunea* [*Chrysodomus*], a boreal form, nearly smooth, notable for its left-handed species which abound in the Red Crag (Fig. 35, *a*)

*Murex* (Cret.-Rec.) differs from the whelks, firstly in having a very long and narrow canal, the edges of which bend over until they all but meet (split-tube structure), and a very rounded aperture; secondly, in the thickening of the mouth-border, from which and along the anterior canal there often arise long spines which repeat the split-tube structure. These mouth-borders persist as varices, often of great regularity in arrangement, there being exactly three to a whorl, so that those of successive whorls continue one another in a vertical (or very slightly oblique) line up the spire; it has been stated that in these forms one turn of the spire represents a year's growth. In other cases the varices are more numerous. In *Typhis* (Eoc.-Rec.) the anterior canal and spines become perfectly tubular. *Murex* is now widely distributed except in the cold seas, *Typhis* is more closely confined to warm waters, but, like so many others, is found in the British Eocene.

*Fusus* has been described; allied to it is *Clavella* (Fig. 35, *b*), an abundant Eocene form, now represented by a single Polynesian species. It differs from *Fusus* in being smooth and in the shape of the whorls, which have rather flat sides terminated above by a horizontal shelf; *Sycum*, or *Leiostoma* (Eocene), is another smooth form, differing in its much shorter spire and less clearly defined canal.

The *Volutilidæ* (Cret.-Rec.) consists of somewhat fusi-form shells, though without the sharp demarcation of the anterior canal seen in *Fusus*, the aperture being long and somewhat parallel-sided. Their special feature is the development of spiral plaits or ridges on the columella, which define grooves along which slide the tendons by which the animal pulls itself into the shell. The commonest fossil genus is *Volutilithes* (Cret.-Rec.), a richly ornamented form, abundant in the British Eocene (Fig. 35, *c*), but now represented by a single South African species. *Aurinia*, or *Scaphella* (Fig. 35, *e*), a smooth form with very rounded apex, is found in the British Pliocene, and now lives in warmer seas.

Another fusiform shell with aperture shaped as in the *Volutilidæ* is *Pleurotoma* (Cret.-Rec.), in which there is a posterior canal which takes the form of a notch at a little distance from the suture (Fig. 35, *d*), recalling the lateral slit of *Pleurotomaria*, and like that causing an inflection of the growth-lines, but not closed by a special secreted band. This abounds in species in the British and other Tertiaries, and in the warm seas to-day. *Conorbis* (Eocene) is similar, but with narrower aperture, forming a transition to *Conus* (Cret.-Rec.), with very short, depressed spire, narrow, parallel-sided aperture, and posterior canal close to the suture: its distributional history is like that of *Pleurotoma*, but it is more closely restricted to tropical seas to-day.

Brief mention must be made here of a specialized

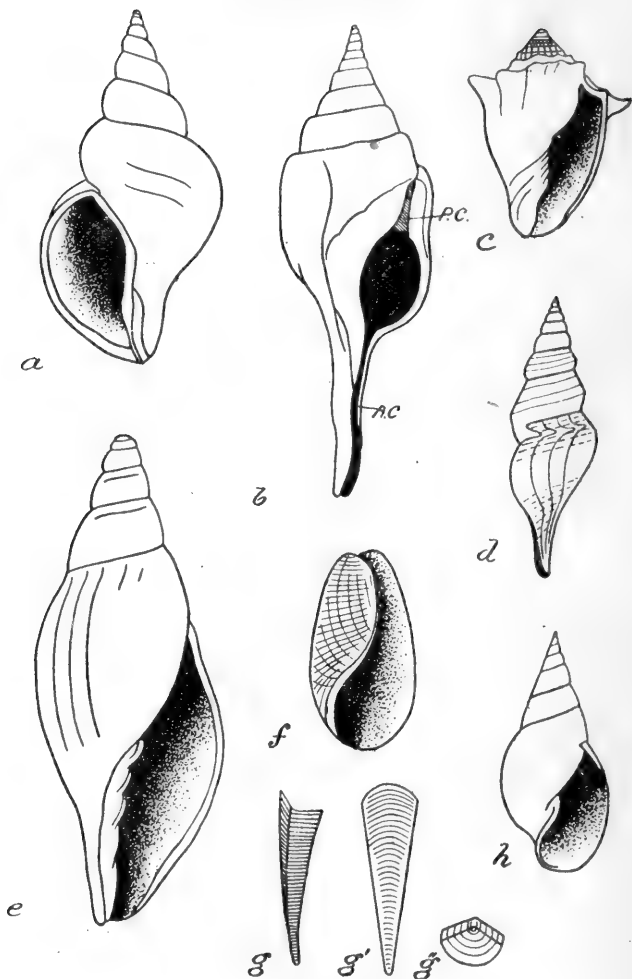


FIG. 35.—GASTROPODS.

- a, *Neptunaea contraria* (Linné), Pliocene. ( $\times \frac{1}{2}$ .) (After Harmer.)  
 b, *Clavella longeva* (Lamark), Eocene. ( $\times \frac{1}{2}$ .) (After Deshayes.)  
 A.C., Anterior canal; P.C., posterior canal. c, *Volutilithes athleta*

group of ctenobranchs, the Heteropoda, whose shells are very thin and transparent and symmetrical in their coiling. Both these changes from typical gastropod characters indicate adaptation to a pelagic life—that is, one of swimming in the open sea. Transparency is the most effective form of camouflage for a pelagic animal which has nowhere to take cover, and the lop-sided shell, which does very well for a bottom-crawler, would be a serious impediment to active swimming. Heteropoda are very abundant in the Mediterranean and other warm seas; but fossil examples are rare. The symmetrical character of the shell of *Bellerophon* led to its being at one time placed among the heteropods, but its shell is much thicker, and the presence of a slit indicates its rhipidoglossal affinities. In the Gault occurs a little shell of similar form, *Bellerophina*, which would have better claim to be considered a heteropod, were it not that it had a nacreous inner layer.

#### SUB-CLASS: OPISTHOBRANCHIA.

The **Opisthobranchia** are divided into two sub-orders, Tectibranchia and Nudibranchia. The latter are shell-less and unknown fossil. The former is divided into a number of families, but on a basis of shell-form they may be very roughly grouped into (1) more or less turbinate forms, such as *Actæon*; distinguished from Streptoneura of similar shape by the strongly-marked folds on the columella, and (2) forms such as *Bulla* and *Scaphander* (Fig. 35, *f*), with a more or less completely con-

FIG. 35.—GASTROPODS (continued).

(J. Sowerby), Eocene. ( $\times \frac{1}{2}$ .) (After Deshayes.) *d*, *Pleurotoma transversaria* Lamarck, Eocene. ( $\times \frac{1}{2}$ .) (After Deshayes.) *e*, *Scaphella lamberti* (J. Sowerby), Pliocene. ( $\times \frac{1}{2}$ .) (After S. V. Wood.) *f*, *Scaphander edwardsi* (J. de C. Sowerby), Eocene. ( $\times \frac{1}{2}$ .) (After Dixon.) *g*, *Hyolithes princeps* Billings, Lower Cambrian. ( $\times \frac{5}{8}$ .) *g*, Side view; *g'*, back view; *g''*, operculum. (After Walcott.) *h*, *Limnæa fusiformis* J. Sowerby, Oligocene. ( $\times \frac{5}{8}$ .) (After Edwards.)

volute shell, distinguished from *Cypræa*, etc., by the shape of the aperture (narrow posteriorly, widened anteriorly). There is also a pelagic group known as the *Pteropoda*, occupying a similar position among opisthobranchs to that of the *Heteropoda* among Streptoneura, their shells having become superficially symmetrical, and very thin and translucent, by adaptation to a swimming life in the open sea.

The Pteropoda, according to the investigations of Prof. Pelseneer of Ghent, do not form a natural group, being composed of two series derived from separate families of opisthobranchs. Nevertheless the name is a convenient one and may well be used if it is understood that it has not an exact taxonomic value. Pteropods abound in all the modern oceans to such an extent that where there is moderately shallow water far from land their shells form an important proportion of the foraminiferal ooze on the sea-floor—so-called pteropod ooze (at greater depths their thin shells dissolve before reaching the bottom). In the Cainozoic rocks of the Mediterranean region, similar pteropod-bearing deposits are known, and some pteropod shells have been described from the Cretaceous; but the entire absence of pteropods from the pelagic Chalk of Europe, where they might particularly be expected, seems to show that this specialized group was then at the very beginning of its existence; and it is not surprising that the Jurassic and Triassic rocks contain no certain remains of pteropods. It is therefore startling to find in the Devonian rocks abundant shells indistinguishable from those of the modern pteropod *Styliola*; and from thence downwards to the Cambrian there are found a number of genera which, though less closely similar to modern forms, are yet more like pteropods than anything else (*Hyolithes*, Fig. 35, g, *Conularia*, *Tentaculites*, etc.). Recently, among the

wonderfully preserved fossils from the Middle Cambrian of British Columbia, Mr. Walcott has found a *Hyolithes* showing swimming organs closely resembling those of modern pteropods. It is impossible that pteropods can have existed before the opisthobranchs from which they are derived, and no opisthobranch is known before the Carboniferous period. It is also very unlikely that any group should have abounded in the Palæozoic era, have lain hidden through the Mesozoic, and have again become abundant in the Cainozoic. The most probable explanation is that we have here again a case of homœomorphy, due perhaps to adaptation to like conditions. These Palæozoic forms should therefore be removed from the Pteropoda and placed provisionally in a separate order for which the name Conularida may be used. It is quite likely that this is not a natural group: some of its members may possibly have been tube-secreting annelids.

#### SUB-CLASS: PULMONATA.

These are terrestrial or freshwater forms, with shells of very variable shape, but always thin and unornamented (except by colour, which is sometimes preserved in fossils). *Planorbis* has been described; other fresh-water forms are *Limnæa*, with long pointed few-whorled spire and oval aperture (Fig. 35, *h*), and *Physa*, of somewhat similar shape, but sinistral. Among land-snails are *Helix*, the common snail, *Pupa*, which has a cylindrical form, the maximum diameter being attained very early, and *Glandina*, resembling *Limnæa* in form.

All these genera are common in the numerous freshwater beds of the Tertiary. Previous to that freshwater deposits are scanty. The oldest, in the Devonian, have yielded no gastropods, though they contain freshwater lamellibranchs; and in the Coal Measure no freshwater

pulmonates are found, but there are a few terrestrial forms, such as *Dendropupa* and *Archæozonites*, genera almost identical with the *Pupa* and *Zonites* (allied to *Helix*) of to-day. The oldest known freshwater pulmonates appear to be *Physa* and *Planorbis* of the Purbeck beds.

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(See under "Mollusca Generally," p. 92.)

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## IV

### THE CEPHALOPODA

THE present-day Cephalopoda (cuttle-fish, squid, octopus and nautilus) are the most highly organized of Mollusca. They agree with gastropods in having a rasping tongue, but the crawling foot is replaced by a series of powerful arms around the mouth, and the mantle and body-wall become muscular swimming organs. While the crawling life of gastropods has made them asymmetrical, and only a few have acquired a superficial symmetry through taking to a swimming life, nearly all cephalopods retain the perfect bilateral symmetry, while as active voracious animals their sense-organs have become highly developed. Only a few extinct forms are asymmetric, and these may well have been crawlers exclusively, while the rest of those known as fossil may, like the modern members of the class, have been at least capable of swimming and sometimes swimmers exclusively. The habitat of cephalopods is more restricted than that of gastropods, being exclusively marine.

Most of the modern cephalopods, such as the cuttle-fish and squid, show no sign of a shell externally, though it is to be found in a modified condition buried in the interior of the body; some, as the octopus, have

none at all. Only three living genera have an external shell: that of *Argonauta*, the "paper nautilus," is of a special type peculiar to it, and need not be considered here; that of *Spirula* is almost embedded in the mantle, but is of the same general type as the completely external shell of *Nautilus* (the "pearly nautilus"). This last is a spirally-coiled univalve shell, divided internally into chambers, and the same general type is found in an enormous number of extinct Cephalopoda. As the spiral coiling introduces a complication into the structure, it will be convenient to describe first the similar but straight shell of the extinct genus *Orthoceras*, filling up the gaps in our knowledge by reference to the living nautilus. There are a great many species of *Orthoceras*, ranging in age from uppermost Cambrian (Tremadocian) to Triassic, but as none of these is so common as to be obtainable with certainty for examination, and it may often be necessary to take several species to demonstrate the full structure, the description here given is generic instead of specific.

1. **Orthoceras.**—The shell (Fig. 36) is a cone approaching to a cylinder (sometimes circular, sometimes elliptical in plan), and ending in a more or less blunt rounded apex. In extremely rare cases there is found attached to this apex what looks like a small shrivelled-up bladder, and this is probably the horny equivalent of a globular calcareous body in *Spirula*—the *protoconch*, or initial shell, secreted in early life. The main shell (or *conch* as it is sometimes called) is divided internally into chambers by partitions (*septa*), which are convex towards

the protoconch and are perforated in (or near) the centre by an opening around which the septum extends like a bottle-neck (Fig. 36, *S.N.*). At the opposite end from the protoconch a considerable portion of the cavity of the

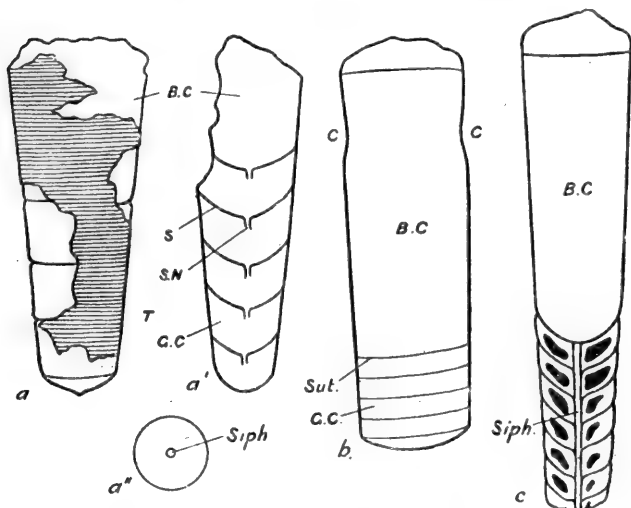


FIG. 36.—ORTHO CERAS.

*a, a', a''*, *O. capax* Barrande, Silurian. *a*, Cast of body-chamber and three gas-chambers, part of test remaining (shown by fine striations); *a'*, median section of a similar broken specimen; *a''*, view of end broken along a septum. *b*, *O. decipiens* Barrande, Silurian, cast showing perfect body-chamber with constriction, septa more closely set than in *O. capax*. *c*, *O. capillosum* Barrande, Silurian, median section showing perfect body-chamber without constriction, gas-chambers partly filled, and continuous siphuncle. (All after Barrande.) *B.C.*, Body-chamber; *C*, constriction; *G.C.*, gas-chamber; *S*, septum; *Siph.*, siphuncle; *S.N.*, septal neck; *Sut.*, septal suture; *T*, test.

shell is undivided, forming the *body-chamber*, lodging the animal's body. The rest are *gas-chambers*, containing (in *Nautilus*) a gas secreted from the blood, resembling atmospheric air but with more nitrogen.

Through the central perforations of the septa ran a living cord, the siphuncle, through all the gas-chambers back to the protoconch. While the animal was growing new shell continually was being added to the aperture or "mouth" of the body-chamber; while at intervals the animal moved forwards in its body-chamber, and secreted behind it a new septum. Thus any given septum was formed at a rather later time than the part of the external shell with which it is in contact—a fact that must never be forgotten. The line of junction of the edge of a septum with the external shell is termed the *suture* (more precisely the *septal suture*, for in coiled cephalopods the term *suture* is also used in the same sense as in gastropods, for the line of external contact of the whorls). The septal sutures are invisible externally, but when the shell is removed the internal cast shows them.

The ornamentation of *Orthoceras* is usually of a very simple character; consisting of growth-lines parallel to the margin of the aperture—usually only fine striæ, at other times with stronger rings at intervals. The actual aperture of the body-chamber is rarely preserved (the thin shell, unsupported by septa, being easily crushed); but in a few perfect specimens the aperture is seen to be a simple circle, which may or may not have just behind it a circular constriction (Fig. 36, *b*).

2. ***Nautilus radiatus*** is a fairly common species in the Lower Chalk, and the following description applies to it, but, with slight alterations, would serve for many other species. It is a shell symmetrically coiled in a plane-spiral, so tightly that each whorl nearly conceals

the whorl within, leaving only a very deep and narrow *umbilicus* on each side. The shape of the whorl-section thus comes to be that shown in Fig. 37 (right-hand figure), and the outline may be divided into a peripheral area, a pair of lateral areas, a pair of umbilical zones, and an impressed area, of which the last is concave, the rest more or less convex (see Fig. 49, *e*, for these

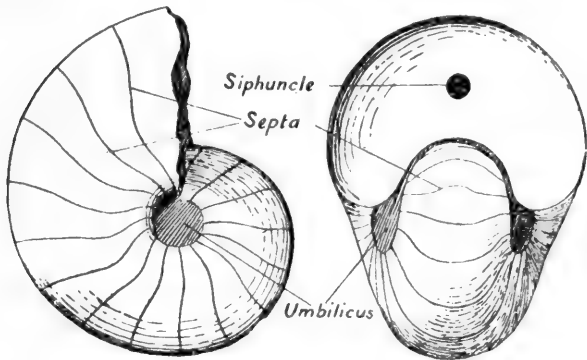


FIG. 37.—NAUTILUS ALBENSIS, D'ORBIGNY, CENOMANIAN, DERIVED (CAMBRIDGE GREENSAND).

Internal cast. Body-chamber at least missing. Umbilicus filled with phosphatic matrix. Side view and front view. (Natural size.) (Original.)

terms). The peripheral area is known from the anatomy of living species to be ventral, so that the umbilical and impressed areas are dorsal. The ornamentation consists of a series of slight corrugations which are essentially growth-lines, and correspond to the aperture-margin, but owing to the spiral coiling there has to be more rapid growth on the ventral than on the dorsal side, and the growth-lines are not parallel as they practically are in

gastropods, but radiating: in cephalopods they are therefore usually termed the *radial lines*. These lines are very faint near the umbilicus, but become more distinct in the outer part of the lateral areas, where they swing backwards and cross the peripheral area in a curve which is concave forwards (towards the aperture). This is called the *hyponomic sinus* (cf. Fig. 45, *a'*), and corresponds to an embayment of the aperture occupied by the funnel or

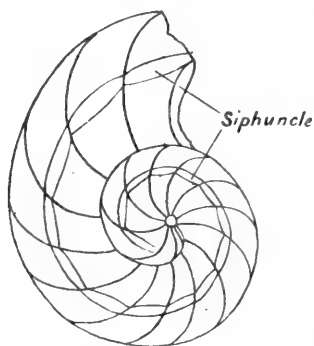


FIG. 38.—NAUTILUS EXCAVATUS, J. DE C. SOWERBY, INFERIOR OOLITE.

Approximate median section (not accurately median at the centre).  
(Natural size.) (Original.)

hyponome, an organ by which the nautilus ejects water from the mantle-chamber and so projects itself through the sea. This hyponomic sinus is characteristic of most Nautiloidea, though wanting in the primitive species of *Orthoceras*. If the fossil is broken, the septa are seen to be concave forwards as in *Orthoceras*, with the siphuncle placed rather nearer the dorsal side (Fig. 37, right-hand figure). On the cast the sutures are seen to run radially

outwards from the umbilicus for half the height of the lateral area, then to swing forwards, and to cross the peripheral area with a very slight backward curve: they thus contrast sharply with the radial lines, of which they cross four or more in their course.

3. **Asteroceras obtusum** (Fig. 39) is the index-fossil of one of the zones of the Lower Lias. Specimens of this or closely allied species are familiar to visitors to Lyme Regis. The shell is of a light yellow-brown colour, but is usually only preserved in fragments, the fossils being essentially internal casts. The shell is spirally coiled in a plane—or bilaterally—symmetrical spiral. Each complete turn of the spiral is termed a *whorl*. The number of whorls cannot usually be counted, the central being hidden by rock-matrix which is difficult to remove, but usually four or more can be counted: they become larger rather rapidly from the centre outwards. The body-chamber occupies rather less than half the last whorl: it is filled with a grey matrix of argillaceous limestone, while the gas-chambers are filled with brown crystalline calcite. The visible part of the shell encircled by the last whorl is called the *umbilicus*. Unlike that of gastropods this forms a concave area on both sides equally. The spiral line of contact between each whorl and the next is the *whorl-suture* (corresponding to the suture of a gastropod, but present on both sides of the ammonite).

A plane-spiral shell is measured as follows: the *diameter* is measured from the outer edge of the aperture (or if the shell is imperfect, of the latest part preserved)

straight across the centre to the opposite edge. The measurement of a single whorl in the same direction gives its *height*; at right angles to this is its *thickness*. In an ammonite with strong ribs, such as *Asteroceras*, this thickness will vary very much according as it is measured at or between the ribs. The *width* of the umbilicus is measured from whorl-suture to whorl-suture along the same line as the diameter. These are the most important dimensions, and it is their relative proportions, rather than their absolute amounts, that are of value for comparison of one species with another. As, however, these proportions frequently alter in the process of growth, the actual size of an ammonite measured must always be stated. The four essentials of ammonite measurement are, then—(1) diameter; (2) height of last whorl; (3) thickness of last whorl; (4) width of umbilicus. The first may be stated in millimetres, the others as percentages of the first. Thus for a particular specimen of *Asteroceras obtusum* we express these dimensions thus:

$$145, 36, 27\text{-}31, 41.$$

The 27-31 refers to the difference of thickness between and at the ribs.

For comparison we give measurements of two allied species, *Asteroceras redcareense*:

$$118\cdot5 : 36, 30\text{-}34, 37\cdot5,$$

and *Asteroceras olifex*:

$$88 : 34\cdot5, 25\text{-}27, 38.$$

A glance at the three formulæ shows us that *A. redcareense*



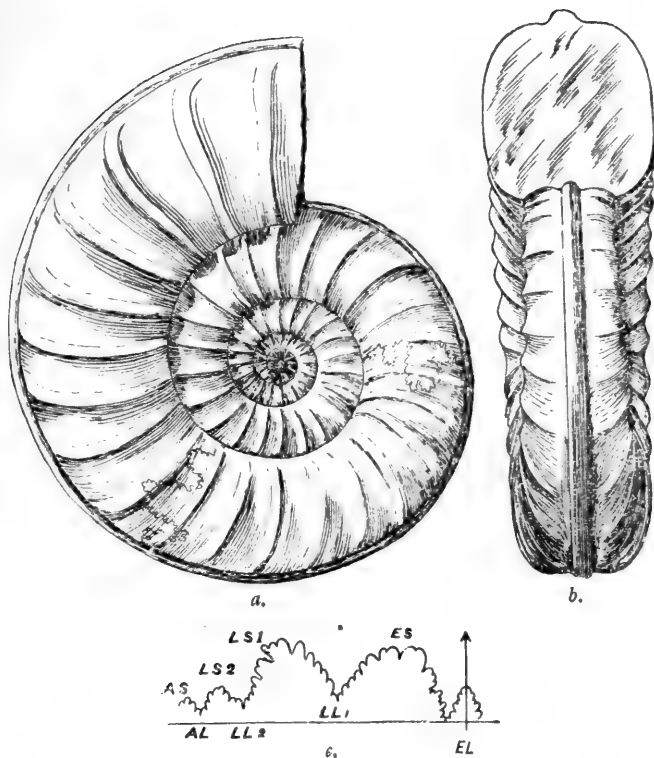


FIG. 39.—*ASTEROCERAS OBTUSUM*, J. SOWERBY, SINEMURIAN  
(LOWER LIAS), LYME REGIS.

- a*, Side view; *b*, apertural view ( $\times \frac{1}{2}$ ), (Original); *c*, suture-line (after d'Orbigny. The arrow denotes the middle line of the periphery and points towards the body-chamber; the horizontal line is the guide-line. *EL*, External lobe; *ES*, external saddle; *LL1*, *LL2*, first and second lateral lobes; *LS1*, *LS2*, first and second lateral saddles; *AL*, *AS*, auxiliary lobe and saddle.

is thicker, *A. olifex* thinner than *A. obtusum*, while both are less widely umbilicate.

If we place the specimen so that the aperture faces us (apertural view, Fig. 39, *b*) we see the shape of the whorl in cross-section. It is somewhat elliptical, and the outline may be divided into six parts, corresponding to six regions on the surface of the whorl: (1) the somewhat flattened *peripheral* or *external* area or *venter*, which bears a broad rounded *keel* in its middle line; (2) and (3) the *lateral areas*, one on each side, slightly convex but with a general direction approximately parallel to the plane of symmetry; (4) and (5) the *inner* or *umbilical areas*; one on each side, which slope inwards to the whorl-sutures; and (6) the concave *impressed area*, invisible except when the whorl is detached from the shell, lying between the two whorl-sutures and in close contact with the next inner whorl. The ratio between the height of this overlapped part of an inner whorl and the height of the outer whorl which overlaps it is the *amount of indentation* of the outer whorl; while the ratio between it and the total height of the whorl of which it forms part is the *amount of inclusion* of the inner whorl. In *A. obtusum* the former is about  $\frac{1}{7}$ , the latter about  $\frac{2}{7}$  (the height of the outer whorl being about double that of the next inner). These ratios are low when the umbilicus is wide (as in *Asteroceras*), but they increase as it becomes narrower.

The spiral line along which the peripheral area meets the lateral area is called the *peripheral margin*; that on which the lateral and inner areas meet is the *umbilical margin* (as for descriptive purposes the umbilicus is taken

to include the inner area of the outer whorl, but not for purposes of measurement). In *Asteroceras* these margins are not sharply defined, as they are in some ammonites.

The ornament of *Asteroceras* consists of a series of strong ribs, which start at the umbilical margin and run almost straight outwards until near the peripheral margin, where they bend decidedly forwards and die away. Between their ends and the median keel, the periphery forms a shallow groove on either side. The forward bend of the ribs shows that the aperture instead of having a hyponomic sinus, as in *Nautilus*, has a median projection or *rostrum* (*cf.* Fig. 45, *f*).

The ribs are well spaced-out, their distance apart being proportionate to the height of the whorl; thus in the last whorl of the specimen figured it gradually increases from 8 mm. to 16 mm. (as measured in the middle of the lateral area). Careful examination of the inner whorls shows that the ribs there are not so smooth as in the outer whorls: each is thickened to form a *tubercle* about the middle of the lateral area. This ammonite, as it grew up, suffered a degeneration (*catagenesis*) of its ornament, from more to less complex.

The ribs and tubercles are not thickenings of the shell, but corrugations, and therefore show as well on the cast as when the shell (or *test*) is present.

The septal sutures (Fig. 39, *c*) are very different from those of *Orthoceras* or *Nautilus*: they are thrown into a series of forward and backward curves, each of which is further puckered up or frilled. The forward curves (convex towards the body-chamber) are called *saddles*, the

backward curves are *lobes*. The visible suture-line (without the portion on the impressed area) consists of (1) a median *peripheral* or *external lobe*, divided into two by a small pointed saddle, (2) a pair of *external saddles* on the peripheral margins, followed on each side by (3) the *first* or *superior lateral lobe*, (4) the *first* or *superior lateral saddle*, (5) the *second* or *inferior lateral lobe*, (6) the *second* or *inferior lateral saddle*, (7) an *auxiliary lobe*, (8) an *auxiliary saddle*, (9) another *auxiliary lobe*. Both lobes and saddles are much subdivided, but the numerous subdivisions are all approximately equal. The first lateral saddle is much larger than the second, and lies but little above the centre of the lateral area.

If we draw a straight line from the centre of the ammonite to the ends of the external lobe (*normal line* or *guide-line*), we see that all the other lobes fall short of this line, the first lateral lobe most of all.

4. **Xipheroceras planicosta** is another ammonite from the zone of *A. obtusum*. It is common at Lyme Regis, but far more beautiful specimens are, or were, found in a bed of limestone at Marston Magna near Yeovil—the “Ammonite Marble” or Marston Marble, at one time much used for ornamental purposes, and still generally obtainable in small fragments from mineral dealers. In both localities the usual specimens are small (diameter about 2 cm.), larger ones (5 or 6 cm.) are rare and probably not identical in species. The dimensions of one of the small size are

Whorl-section reniform (kidney-shaped) in inner whorls, becoming higher and less broad later. Amount of indentation one-tenth, of inclusion one-sixth (at 20 mm. diameter). When the umbilicus is clean there can be seen in the centre a small globular *protoconch*, with six whorls around it (up to 20 mm. diameter). The first two whorls or so are quite smooth, then fine striæ appear; after another whorl and a half obscure ribs are seen, and about the end of the fourth whorl well defined ribs appear. At the 20 mm. diameter the ribs are about 2 mm. apart, and run as follows: starting in the steep inner area they first slope backwards, then curve round to a truly radial direction on the umbilical margin, from which they curve very gently to a slight backward slope on the outer half of the lateral area; at the peripheral margin they swing forward and cross the periphery without interruption in a forwardly-convex curve, but at the same time they become much broader and lower (as though modelled in a plastic substance and then pressed down). The fine striæ on and between the ribs follow the same direction, which shows that here as in *Asteroceras* there was no hyponomic sinus to the aperture but a rostrum, though not a very prominent one. Larger specimens of this (or nearly allied) species show that soon after attaining 20 mm. diameter the ribs begin to show signs of tubercles at the peripheral margin, and in some the flattened peripheral rib tends to divide into a bundle of three ribs. In another species (*X. ziphus*) the tubercles are developed into long spines. Thus the early species of *Xipheroceras* show an increasing strength and

complexity or *anagenesis* of ornament with advancing age, in contrast to the *catagenesis* of ornament in *Asteroceras*. It also shows decided change in whorl-shape.

The body-chamber of these small specimens occupies just over half a whorl, and the last two or three septa are usually crowded together—a feature common in the last septa of large ammonites. This suggests that the small size of these ammonites was not due to premature death, but that they were a small species. Larger species of the same genus are for the most part rather later in time, so that the genus shows *anagenesis* in size as well as in ornament.

The suture-line of *Xipheroceras* is (at 20 mm. or less) like a much-simplified *Asteroceras* suture, except that there are no auxiliary lobes and saddles, and the lateral lobes do not lie so much in front of the peripheral. In older shells the subdivision of the lobes and saddles becomes much more complex.

These four examples of cephalopods have been chosen for description as easily obtainable, so that readers can verify the descriptions on actual specimens. The next few examples are less common, and will be described more briefly.

5. **Tetrameroceras obovatum** (Fig. 40) is one of several more or less ellipsoidal species found in the Lower Ludlow shales of Herefordshire and Shropshire. It is about 110 mm. long, 58 mm. wide, and 75 mm. high. Preserved as a cast, it is seen that about one-half of the shell is body-chamber, the rest consisting of about nine gas-chambers. The whole shows a very slight curvature,

the side which we shall presently recognize as ventral being slightly concave: such a curvature is the opposite to that of *Nautilus*, where the ventral side is convex. This is expressed by saying that *Tetrameroceras* is endogastric, *Nautilus* exogastric. A more striking difference from both *Orthoceras* and *Nautilus* is the form of the aperture, which is greatly narrowed in the centre, forming a slit only 3 mm. wide. This widens at the ventral end

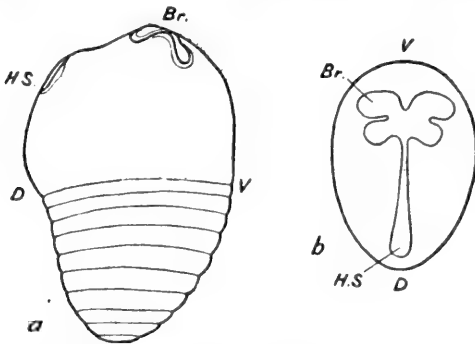


FIG. 40.—TETRAMEROCERAS OBOVATUM (BLAKE), SILURIAN  
(LOWER LUDLOW BEDS).

*a*, Side view; *b*, apertural view. ( $\times \frac{3}{8}$ .) (After Blake.) *Br.*, Brachial portion of aperture; *H.S.*, hyponomic sinus; *D*, dorsal side; *V*, ventral side.

into an oval, at the dorsal end into a four-lobed expansion. Evidently the animal was permanently shut in its body-chamber, and could only protrude two pairs of arms for obtaining food by the larger four-lobed aperture, and the swimming funnel by the other. The latter therefore represents the hyponomic sinus and fixes the side towards which it lies as ventral. In other species contemporary with this there may be openings for only

one pair of arms (genus *Gomphoceras*) or for three or four pairs.

6. **Meloceras** [**Cyrtoceras**] **elongatum** (Fig. 41, a) is found in the Upper Silurian limestone of Bohemia. It is compressed-elliptical in section and curved in form, the curvature decreasing from youth to age (*i.e.*, from apex to body-chamber), and the plane of curvature being that of the major-axis of the ellipse. It attains a length of 80 to 90 mm. of which nearly a third is body-chamber. The septa have the simple form seen in *Orthoceras*, but are more closely set than in that genus, their distance apart being only about one-sixth the major axis of the cross-section. The siphuncle is close to the convex margin, and forms a continuous calcareous tube, constricted as it passes through the septa. The shell is only ornamented by fine striæ, the course of which shows a very slight hyponomic sinus on the convex margin, which is therefore ventral. Thus this species is exogastric, and the siphuncle is ventral (its usual position when not central). There are other species attributed to the same genus which are endogastric.

7. **Cophinoceras** [**Gyroceras**] **ornatum** is found in the Middle Devonian limestone of the Eifel. Compared with the last it has a stronger curvature, so that it forms a complete spiral of at least a whorl and a half, but there is no contact between the whorls. It is depressed-elliptical in section (*i.e.*, the long axis of the ellipse is at right angles to the plane of coiling). The only ornament seen on the cast is a paired series of rather coarse and



ill-defined tubercles along the peripheral margins, but on the shell itself the periphery is marked by longitudinal ridges and transverse striæ. The septa are farther apart than in *Meloceras*; the siphuncle in the same position.

8. **Ophidioceras simplex** (Fig. 45, *b*), from the Silurian of Bohemia, is a flat-sided spiral shell, 35 mm. in diameter, of several whorls which are just in contact, except that a very small portion of the last whorl becomes straight and so separates from the next inner whorl. The aperture is constricted and Y-shaped, the hyponomic sinus (the stem of the Y) being towards the periphery, so that the shell is exogastric (as are most, if not all, of the spiral cephalopods). The sides are ornamented by simple ribs, interrupted by a keel on the periphery.

These three examples illustrate stages in the transition from a straight shell like *Orthoceras* to a tightly coiled one like *Nautilus*. At one time these different degrees of curvature were regarded as marking different genera, and generic names were given accordingly. Now it is recognized that they are evolutionary stages which may have been passed through by different stocks at the same or at different times. Names for these stages are useful. Following Mr. Buckman in modifying the more cumbersome terms of Hyatt, we may call the straight shell an *orthocone*; the curved one which does not form a spiral, a *cyrtocone*; the open spiral, a *gyrocone*; the spiral with whorl-contact, an *ophiocone*. The terminology does not at present distinguish between evolute ophiocones like *Ophidioceras*, in which the whorls merely touch, and those in which, by tighter coiling, the inner whorls become

more or less included by the outer. By tighter and tighter coiling (a continuation of the same process which led from cyrtococone to ophiocone) the umbilicus becomes smaller and smaller until we reach the *sphærocone* with no umbilicus or a very small one, as in *Nautilus*.

If these stages represent a real evolutionary series, we ought to find (1) that they follow one another in time, and (2) that the ontogeny of forms in the later stages should show traces of the earlier stages.

As to the first point, remembering the imperfection of the palæontological record, and the fact that different stocks must have gone through similar developments at different times, we must not expect too much. Orthocoines are known from the Lower Cambrian to the Trias, and are pretty equally distributed though getting scarcer after the Carboniferous. Cyrtocoines are known from the uppermost Cambrian, but are most abundant in the Silurian and Devonian; gyrocoines, rare in the Silurian, are abundant in the Devonian, and then become rarer; ophiocoines, though known from the Ordovician and Silurian, are rare until the Devonian and Carboniferous; while sphærocoines first appear in the Carboniferous and continue to the present. Thus, on the whole, the known sequence in time agrees with the expected sequence.

As to the second point, allowing for the tendency to hurry through ancestral stages during ontogeny, the evidence is satisfactory. The theoretically earlier stages do often precede the later in ontogeny, as may be seen in several illustrations (Figs. 41, *b*; 45, *a*).

At the same time, ontogeny shows evidence of

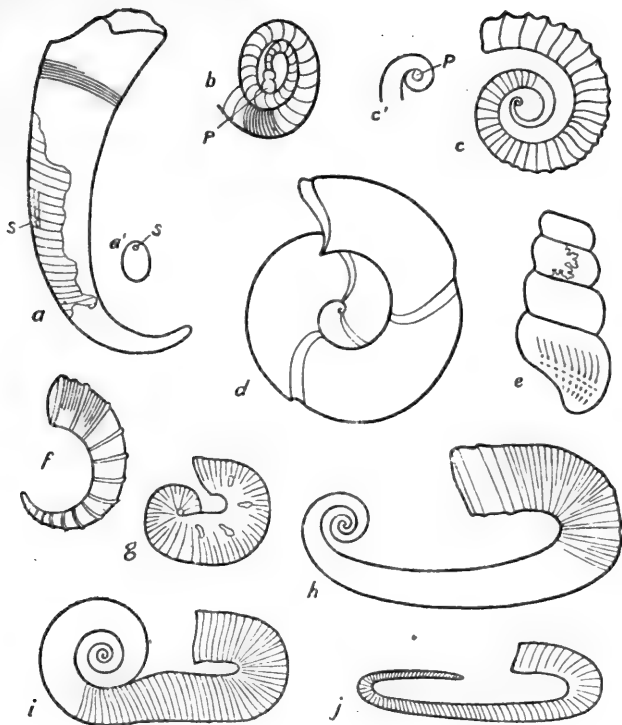


FIG. 41.—CEPHALOPOD COILING CYCLE.

*a, a'*, *Meloceras* [*Cyrtoceras*] *elongatum* Barrande, Silurian. ( $\times \frac{1}{2}$ .)  
 Cyrtocoene: *a*, side view, striate ornament indicated at one place, part of test removed, showing suture-lines and part of siphuncle (*s*); *a'*, cross-section. *b*, Inner whorls of *Agoniatites fecundus* (Barrande), Middle Devonian ( $\times 3$ ), showing orthocone, cyrtocoene, and ophiocone stages; *P*, protoconch. *c*, *Spiroceras calloviense* (Morris), Upper Jurassic (Kellaways Rock), ( $\times 2$ ); *c'*, initial part ( $\times 10$ ); *P*, protoconch. This shows uncoiling from serpenticone to cricocone. *d*, *Morphoceras dimorphum* (d'Orbigny), Bajocian. Ornament omitted. Shows uncoiling, sphærocene to serpenticone; also five constrictions. *e*, *Turrilites bechei* Sharpe, Cenomanian. Ornament omitted except on last whorl, and one suture-line indicated. *f*, *Toxoceras bituberculatum* d'Orbigny, Neocomian. Toxocone. *g*, *Scaphites equalis* J. Sowerby, Cenomanian. Scaphiticone, beginning as sphærocone and ending in a hook. *h*, *Ancyloceras pulcherrimum* d'Orbigny, Barremian. Cricocone changing to toxocone, with hook-like end. Ornament omitted except near aperture. *i*, *Macroscaphites ivani* (Puzos), Barremian. ( $\times \frac{1}{2}$ .) Serpenticone uncoiling, with hook-like end. Ornament omitted except on body chamber. *j*, *Hamites*, Albian. A generalized figure. *a, b, c*, After Barrande; *e*, after Sharpe; the rest after d'Orbigny. All  $\times \frac{1}{2}$ , unless otherwise stated.

another tendency—that of *reversion* in old age to earlier stages. Thus *Meloceras elongatum* tends to an orthocone stage by lessening of curvature; *Ophidioceras* reverts abruptly to the same. In Palæozoic times examples of this are not very frequent, but among Mesozoic Cephalopoda a tendency to uncoil is common: the next few examples will illustrate this.

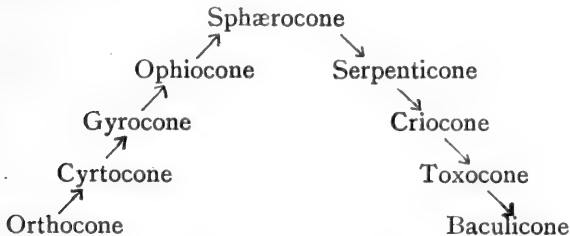
**Spiroceras calloviense** (Fig. 41, *c, c'*) is a common fossil in the Kellaways Rock of Wiltshire. At first sight it appears to be a gyrocone, but close examination shows that it begins with a globular protoconch, around which the tube-like shell winds closely for more than one whorl, after which its curvature diminishes and it continues as an open (evolute) spiral. As this is a stage in an *uncoiling* process it must not be called a gyrocone: the term applied is *criocone*.

**Toxoceras** (Fig. 41, *f*) is a genus of which various species are known from Cretaceous rocks. It has the form of a cyrtocone, and the protoconch and initial part of the conch never seem to be preserved, so that direct evidence of uncoiling is wanting; but as it occurs so late in time, and has sutures like those of contemporary coiled and uncoiling forms, it is reasonable to regard it as a stage in uncoiling (*toxocone*).

**Baculites** (Fig. 46, *l, l'*) is a long, straight, compressed form, found in the uppermost Cretaceous strata. Its initial stages are usually lost, but in specimens from South Dakota they have been found to be substantially similar to those of *Spiroceras*, the closely-coiled stage

lasting rather longer. It is thus the final stage of uncoiling (*baculicone*).

These three forms illustrate the reversal of the process which led from orthocone to ophiocone. There are many indications that the closely-coiled forms which precede them in the Jurassic and Cretaceous are themselves derived from sphaerocones, so they may be termed *serpenticones*. Thus we have a double series, one of increasing curvature (*anagenesis*) and one of decreasing curvature (*catagenesis*).



Such a double series forms an *evolutionary cycle*. It should never be possible to confuse the corresponding stages of the upward and downward series, because (1) the ontogeny of a perfect specimen should show some trace of the stages earlier in the series, and if this fails (2) there are other features, such as the sutures, which have their own independent anagenesis and catagenesis, and their stages will never exactly correspond with the coiling stages. Thus we find degenerate suture-lines in Cretaceous serpenticones, but not in criocones, etc. This is an example of the principle of *irreversibility* in evolution, according to which an organism which reverts to

the condition of one of its remoter ancestors never does so entirely: it retains features acquired by its intermediate ancestors. It should thus always be possible to distinguish degenerate from primitive forms.

As with the anagenetic series, so with the catagenetic: the same stages are passed through by different stocks at different times. Uncoiling forms, including a baculicone, occur as early as the Noric (Upper Triassic), where they are contemporaneous with the last orthocones; but it is not until the Cretaceous that they become abundant.

Just as the early ophiocones often show a tendency to revert to the straight form in old age, so the uncoiling forms show a tendency to coil again in old age, producing hook-like body-chambers. *Ancyloceras* ends thus after a criocone stage, *Macroscaphites* after a serpenticone stage, while *Scaphites* passes direct from sphærocone to this hook. *Hamites* (initial stages unknown) makes two hook-like bends. All these are Cretaceous (Fig. 41, *g-j*), but in the Jurassic period *Æcoptychius* had the form of *Scaphites* (but different ornament), and there were a number of sphærocones which showed a tendency to uncoil in old age (*scaphitoids*). Sometimes there are signs in ontogeny of uncoiling followed by re-coiling.

All these forms so far described are bilaterally symmetrical, but there are a few asymmetrically-coiled forms (*turricones*), resembling sinistral turreted gastropods, mainly Cretaceous (*e.g.*, *Turrilites*, Fig. 41, *e*) but with one example in the Noric; and one extraordinary form (*Nipponites*) which can best be described as a three-dimensional zigzag. By analogy with the gastropods,

which are mostly asymmetric and crawlers, but in which the few swimming or floating forms become symmetric, we may suppose these few asymmetric cephalopods to have been crawlers (*benthic*), while the rest were, at the least, not confined to the bottom, even if they were not habitually swimmers (*nektic*) or floaters (*planktic*).

The thin shell with its large volume of gas-chambers must have been a very light object in the animal's life-time, enabling the animal to rise or sink in the sea with ease, as does the modern *Nautilus*. After death it might float and be carried by currents to a considerable distance. Thus the three surviving species of *Nautilus* live in the Polynesian seas between Sumatra and Fiji, but their empty shells are found on the coast of Japan and elsewhere; the three species of *Spirula* live in deep sub-tropical waters, and only about half a dozen specimens of the animal have ever been found, but the empty shells are found in great numbers on the coasts of New Zealand, and are also known in the Banda Sea, the Canary Islands, West Indies, etc., and have even been found on the Cornish coast. Thus it *may* be the case with fossil cephalopods that the geographical distribution of the shells is far wider than that of the living animals. Mr. Buckman points out, however, that in travelling long distances such delicate shells could not escape injury; so that when we find (as we frequently do) fossil cephalopods with the most delicate structures preserved uninjured, it is reasonable to suppose that they lived where they are now found; but when we find the shells

showing signs of travel—broken body-chamber, abraded surface, or general damage, they may fairly be regarded as having floated from a distance.

In the process of burial on the sea-floor, the sediment would fill the body-chamber, and penetrate through the septal neck into the first gas-chamber, which it could only fill up to the level of the entry. A little might penetrate into the second chamber, but beyond that it would have great difficulty in making its way unless the shell was broken in places (though fine calcareous mud is sometimes found in the air-chambers of apparently unbroken shells). The empty chambers would rarely remain empty, however: water would permeate them and deposit materials from solution. Thus in calcareous rocks the chambers are usually filled or partly filled with crystalline calcite; in clays, with pyrite or marcasite. Where very little sediment was being deposited, they were often filled with calcium phosphate. As a consequence, fossil cephalopods, especially those of large size, are usually very heavy objects, and it needs an effort of imagination to realize them as possibly floating animals. Further, the thin shell itself may have been removed, in one of two ways: by solution in the rock, or by flaking away during extraction, so that we have an internal cast. When the ornament is a corrugation, not a thickening, of the shell, it shows as well on the cast as on the shell, but the casts are at once distinguished by their showing the septal sutures, which of course are on the inner, not the outer, surface of the shell.

Sometimes the shell itself may be replaced by silica or



pyrites: in which case no sutures are visible on the surface. Only the finest ornament in cephalopods is usually a thickening (*capillæ*) or thinning (*striæ*) of the shell, but there are cases among ammonites where protuberant parts of the surface—whether corrugations (*costæ*) tubercles or keel (*carina*)—have their cavities cut off from the general shell-cavity by a partition, so that the cast fails to show these elevations or shows them in a much smaller degree than the shell-surface. Mr. Buckman terms these tubular structures *septicostæ* (found in dactyloids), *septitubercles* (in deroceratids), and *septicarinæ* (in many oxycones). The partitions are wanting in the greater part of the body-chamber, being found in its posterior part and in the gas-chambers, so that they are secreted by the hinder part of the mantle, and like the chamber-septa are later in date than the adjacent shell. These structures may be of considerable stratigraphical value—*e.g.*, serving to distinguish Upper Lias dactyloids from Upper Jurassic perisphinctids, even in fragments.

Among existing Cephalopoda two orders may be recognized, distinguished by the number of gills and various other features. The order Tetrabranchiata (four-gilled) includes the single genus *Nautilus*; all other living forms belong to the Dibbranchiata (two-gilled). It has been usual to extend this classification to extinct forms, but while many of these are so evidently allied to the recent forms that they can safely be assigned to one or other of these orders, there is one very important series of fossils which diverges quite as much from the nautiloids in some respects as do the dibranchs. It is there-

fore advisable to recognize three orders, and to one of these no name having reference to gills can be applied since gills are not preserved in the fossils.

The three orders may be briefly characterized thus, but it must be understood that as the two other orders diverge from the ancestral order Nautiloidea, there are transitional forms which may not conform strictly to the definitions.

1. The **Nautiloidea** are the ancestral and most conservative order. Commencing as orthocones at the end of the Cambrian period, they pass through the intermediate stages to the sphærocone in the Palæozoic era, but subsequently remain without further change down to the present time. Only a very few forms, and those quite early, show any tendency to uncoil.

Generally distinctive features are—(1) the protoconch is not calcareous and is nearly always shed; (2) the septal sutures are either simple circles or they become slightly wavy; they are never frilled; (3) the siphuncle is usually near the centre of each septum, very rarely is it in contact with either margin; (4) the septal necks point away from the body-margin; (5) there is a hyponomic sinus.

2. The **Ammonoidea** contrast with the steady-going Nautiloidea: they had a short life and a merry one. Diverging from primitive Nautiloidea at the end of the Silurian epoch, they hurry through the early stages of coiling, and in the Mesozoic era begin to uncoil. Some of them uncoil completely as early as the late Triassic period; others at various stages in the Jurassic; others after some uncoiling start coiling-in again; but in the Cretaceous period uncoiling becomes very general and is followed by the abrupt extinction of the order (though coiled forms also persist to the last).

General distinctive features are more difficult to state than in the case of the Nautiloidea, because of the great

changes through which the order passes, but the following may be given :

(1) The protoconch is calcareous and is never shed ; (2) the septa are like those of nautiloids in the most primitive families, but soon become folded and eventually frilled at the edges, so that the suture-lines attain a very high degree of complexity ; (3) the siphuncle migrates to one of the margins, in the great majority to the periphery ; (4) the backwardly directed septal necks (*retrosiphonate*) soon become replaced by forwardly projecting *septal collars* (*prosiphonate*) ; (5) the hyponomic sinus is present in most Palæozoic genera, but afterwards disappears, and may be replaced by a rostrum.

3. The **Dibranchiata** vary so much in shell-structure that it is difficult to make any statement that shall apply to the whole order. The main feature is the general subordination of the chambered shell (*phragmocone*) to other skeletal structures, resulting in a great delay of the tendency to coil. The septa are simple, the siphuncle more or less marginal and retrosiphonate.

Among the large number of Palæozoic nautiloids we may choose a few for mention.

(1) Genera retaining the straight form of *Orthoceras*, but distinguished from it by peculiar features of the siphuncle. In *Endoceras* (Ord.-Sil.) the siphuncle is nearly half the width of the shell and the septal necks are funnel-like and fit in to one another, forming a continuous tube. In *Actinoceras* the siphuncle is central, and swells out in each gas-chamber, but is constricted as it passes through the septa. Internal casts of the siphuncle of a gigantic species of this type resemble a row of vertebræ (*Huronion vertebralis*) when weathered out from the Ordovician limestone of Drummond Island, Lake Huron.

(2) Orthocones or cyrtocones which acquire peculiar

features when full grown. *Tetrameroceras* (p. 136) is an instance; *Gomphoceras* (Ord.-Sil.) is an exogastric form with T-shaped aperture; *Phragmoceras* (Sil.) an endogastric gyrocone. In *Ascoceras* (Sil.), after growing as an orthocone to some length, the shell suddenly expanded, the earlier portion was detached, and the few septa that were afterwards formed are so strangely shaped that the gas-chambers are on the dorsal instead of the posterior side of the animal.

(3) Ophiocones (Fig. 45, *a*) are found in the Devonian and are abundant in the Carboniferous. Sphærocones begin with *Solenocheilus* of the Carboniferous, and *Nautilus* (Trias.-Rec.) continues this form. *Hercoglossa* (Trias.-Cainozoic) and *Aturia* (Cainozoic) are remarkable as mimicking the Devonian clymenids (see below), both in the folding of their septa and the dorsal position of the siphuncle.

(4) Uncoiling forms are very rare among nautiloids, and are confined to early times. *Lituites* is Ordovician, *Ophidioceras* (Fig. 45, *b*) is Silurian: both are ophiocones (sometimes beginning as cyrtocones) which revert to orthocone form, the former at an early period of its life, the latter only in old age. Otherwise the Nautiloidea seem to have found stability and permanence in the sphærocone stage.

The Ammonoidea are more interesting to the geologist than are the Nautiloidea, because of their great value as zone-fossils, which arises from the wonderful vitality of the stock, which during six geological periods threw off swarm after swarm, each going through an evolutionary cycle with rapidity and then either dying out or giving rise to a new stock repeating a similar cycle, until at last exhaustion is reached in the Cretaceous period and the whole order dies out.

Examples of some of the most highly organized ammonoids (*Asteroceras*, *Xiphoceras*), as well as of degenerate forms (*Spiroceras*, *Toxoceras*, *Baculites*) have already been described. Examples of the most primitive forms will now be given.

In the Upper Devonian shales of Budesheim in the Eifel district of Western Germany, there are found great numbers of internal casts of small tightly-coiled cephalopod shells, in pyrites oxidized on the surface to a rich brown colour. They rarely exceed 15 mm. in diameter, but they are practically complete shells, since they show the cast of the body-chamber as well as the septate portion. They vary very much in relative thickness and degree of involution, so that a number of different species are distinguishable,\* but if the septal sutures are examined they can at once be sorted into two series. We choose an example of each to describe.

4. **Manticoceras** [**Gephyroceras**] **retrorsum** has (in the specimen shown in Fig. 42) a diameter of 15 mm. and its proportions are—

15: 53, 57, 20.

The body-chamber, so far as preserved, is not quite half the last whorl in length. The umbilical margin falls very steeply, almost perpendicularly near the aperture, but less steeply in the earlier-formed part of the last whorl. The lateral and peripheral areas seem at first sight to pass insensibly into one another, but very careful examination reveals a very faint longitudinal depression about  $2\frac{1}{2}$  mm. on either side of the middle line: this is

more pronounced in the earlier formed part of the last whorl. It may be taken as marking the peripheral margin.

The ornamentation, as seen in the cast, consists of two quite independent series of lines—(1) a series of very faint ribs, most clearly seen at the peripheral margin, where they are less than 1 mm. apart. They are curved with a forward concavity on the lateral area, and at the peripheral margin they bend backwards and cross the periphery in a deep curve like the hyponomic sinus

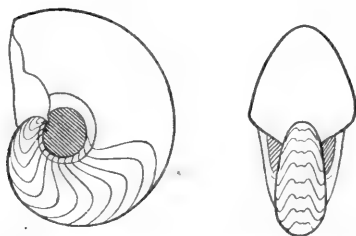


FIG. 42.—MANTICOCERAS AFF. RETRORSUM (VON BUCH), UPPER DEVONIAN; BUDESHEIM, EIFEL. ( $\times 2$ )

Cast of an immature example; the faint ornamentation omitted; umbilicus filled with matrix; numerous suture-lines behind the body-chamber. (Original.)

of Nautiloidea. (2) The other ornament is a series of much finer and closer irregularly-sinuuous lines, about five to each of the ribs, to which they are not parallel, but run obliquely back from the umbilical margin in a curve which is at first convex forwards and is afterwards reversed.

The suture-line (septal suture) is of a kind intermediate between those of a *Nautilus* and an ammonite: lobes and saddles are well-defined, but entirely free from frilling (*goniatitic type*). There is a broad peripheral lobe,

divided into two by a small median saddle; a wide external saddle on each side, and a rounded lateral lobe (Fig. 47, *b*). It is the special feature of the family *Gephyroceratidae* that the external lobe and saddle are so wide that the latter comes to lie in the middle of the lateral area; hence many authors call it the "lateral saddle." In ontogeny the little median saddle appears late, so that there can be no doubt that the divided lobe

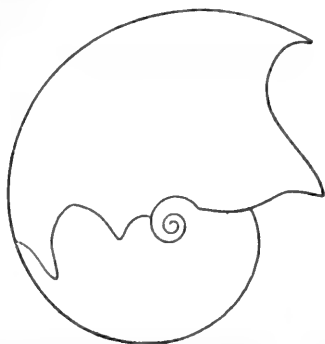


FIG. 43.—MANTICOCERAS RHYNCHOSTOMA J. M. CLARKE, UPPER DEVONIAN; BIG SISTER CREEK, ERIE COUNTY, NEW YORK, U.S.A. ( $\times \frac{1}{8}$ .)

Adult, with rostrum and lappets. Last suture-line only shown.  
(After Clarke.)

of which it forms part is the external lobe and not a pair of lobes.

Although the Eifel specimens are never much larger than the specimen described, in beds of the same age in New York there have been found specimens of a closely-allied species which grew to a great size: in these the hyponomic sinus disappeared in age and was replaced by a forward projection or *rostrum* (Fig. 43).

5. **Tornoceras simplex** is said to attain a diameter of 75 mm., but it is not often that specimens are found much larger than that figured, the size and proportions of which stated in the method already explained are

$$14.5 : 55, 47.5, -.$$

The umbilicus is either entirely closed, or too small to be measured accurately.

The body-chamber extends through about half a whorl (it may be longer). The cast is nearly smooth, but shows growth-lines (radial lines) whose course is similar to that of *Manticoceras*. The suture-line, however, is quite different: the external lobe is narrow and undivided; on each side of it is a rounded external saddle, a rounded lateral lobe and a rounded lateral saddle (Fig. 47, c). It is the lobe that comes in the middle of the lateral area, so that the contrast with *Manticoceras* is striking.

6. **Gastrioceras carbonarium** (Fig. 44) occurs in some abundance in the marine bands which form the "roofs" of certain coal-seams in the Lower Coal Measures of Lancashire and Yorkshire. Specimens have been found as much as 160 mm. in diameter, but a more usual size is about 30 mm. and one of these small specimens gives the following proportions (the query to the last item denotes difficulty of measurements owing to the umbilicus being filled with tough shaley matrix):

$$30 : 45.5, 60, 40?$$

The inner area falls very steeply from the umbilical



margin. The periphery is arched and cannot be marked off from the lateral area. The greater part of the surface is marked by very fine striæ, which on the lateral area are straight and radial but cross the periphery in a forwardly-concave curve, indicating a much shallower hyponomic sinus than in the Devonian forms already described. The striæ are not uniform, but are arranged in bundles, which in passing from the periphery towards the umbilicus take on the character of ribs and

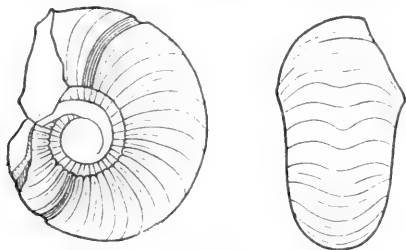


FIG. 44.—GASTRIOCERAS CARBONARIUM (VON BUCH), WESTPHALIAN (COAL MEASURES), LANCASHIRE. (Natural size.)

Immature; two constrictions shown; the striate ornament indicates a hyponomic sinus (right-hand figure). (Original.)

at the umbilical margin project slightly as blunt tubercles. At intervals of about half a whorl there occur "constrictions"—*i.e.*, depressions of the shell, 1 mm. or more in width, following exactly the course of the ornament-lines.

These constrictions are analogous to the varices of gastropod shells: each one was originally formed just behind the apertural margin (as in *Orthoceras decipiens*, though in that species there is only one), and it may be presumed that its formation was followed by a period of

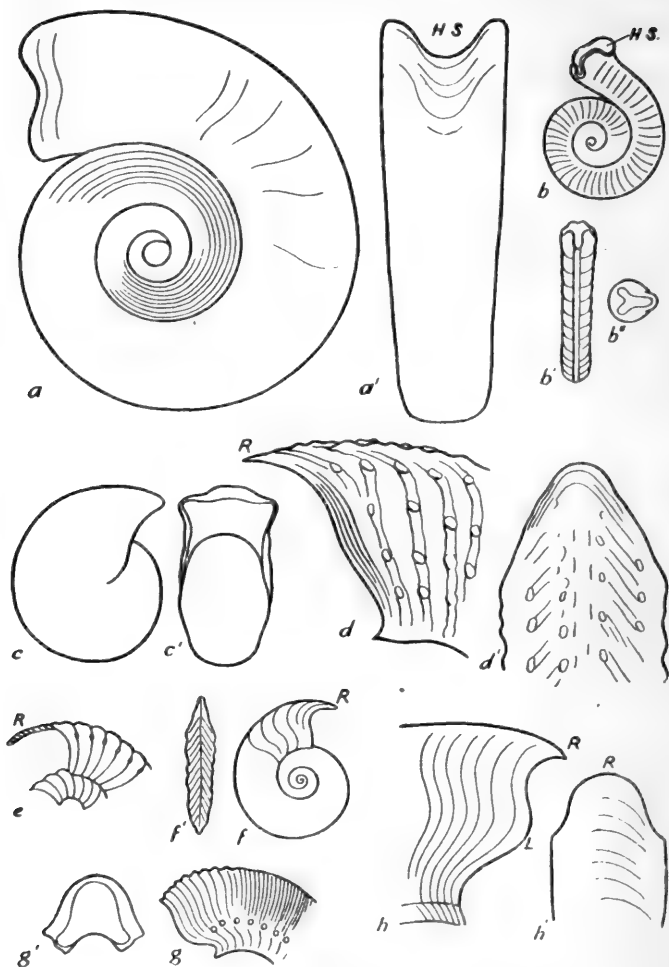


FIG. 45.—APERTURAL MARGINS OF CEPHALOPODA.

*a*, *Discitoceras leveillianum* (de Koninck), Carboniferous Limestone, Clane, Ireland. *a*, Side view, showing gyrocone stage in centre, passing into ophiocone; there are indications of the radial and longi-

cessation of growth, after which renewed growth went on rapidly for half a whorl when another constriction was formed.

Most specimens preserve the shell, but even where it is chipped away no suture-lines can be seen. This is because the body-chamber was over a whorl in length: only on the inner whorls of broken specimens can the suture-line be seen (Fig. 47, *d*). It resembles that of *Tornoceras* in having a lateral lobe and saddle, but the lobe is pointed instead of rounded; while the external is divided by a median saddle which is much more prominent than that of *Manticoceras retrorsum*.

These three Palæozoic species are conveniently described as "goniatites," being characterized by suture-lines with simple lobes and saddles.

FIG. 45.—APERTURAL MARGINS OF CEPHALOPODA (*continued*)

tudinal ornament. *a'*, Peripheral view, showing hyponomic sinus (*H.S.*) (After Foord and Crick.) *b*, *Ophidioceras simplex* Barrande, Silurian, Lochkov, Bohemia. *b*, Side view, showing ophiocone finally uncoiling, and aperture with hyponomic sinus (*H.S.*). *b'*, Peripheral view; *b''*, apertural view. (After Barrande.) *c*, *Arcestes distinctus* (Giebel), Noric (Alpine Trias). Sphærocone; no distinct hyponomic sinus, rostrum, or lappets. (After Quenstedt.) *d, d'*, *Protrachyceras archelaus* (Laube), Ladinic (Alpine Trias). Apertural region, showing broad rostrum. (After Mojsisovics. *e*, *Paltopleuroceras pseudocostatatum* (Hyatt), Domerian (Middle Lias). Long crenulate rostrum. (After Quenstedt.) *f, f'*, *Pleydellia subcompta* (Branco), Yeovilian. Showing relation of radial line to apertural margin. (After Buckman.) *g, g'*, *Reineckia extincta* (Quenstedt), Vesulian. Showing tendency to constriction of aperture, absence of distinct rostrum and lappets, and relation of radial line to apertural margin. (After Quenstedt.) *h, h'*, *Brasilia effricata* S. Buckman, Aalenian, Bradford Abbas, Dorset. Showing very broad rostrum, no definite lappets, and relation of radial line to apertural margin. (After Buckman.) (All  $\times \frac{1}{2}$ .) *H.S.*, Hyponomic sinus; *L*, lappet; *R*, rostrum.

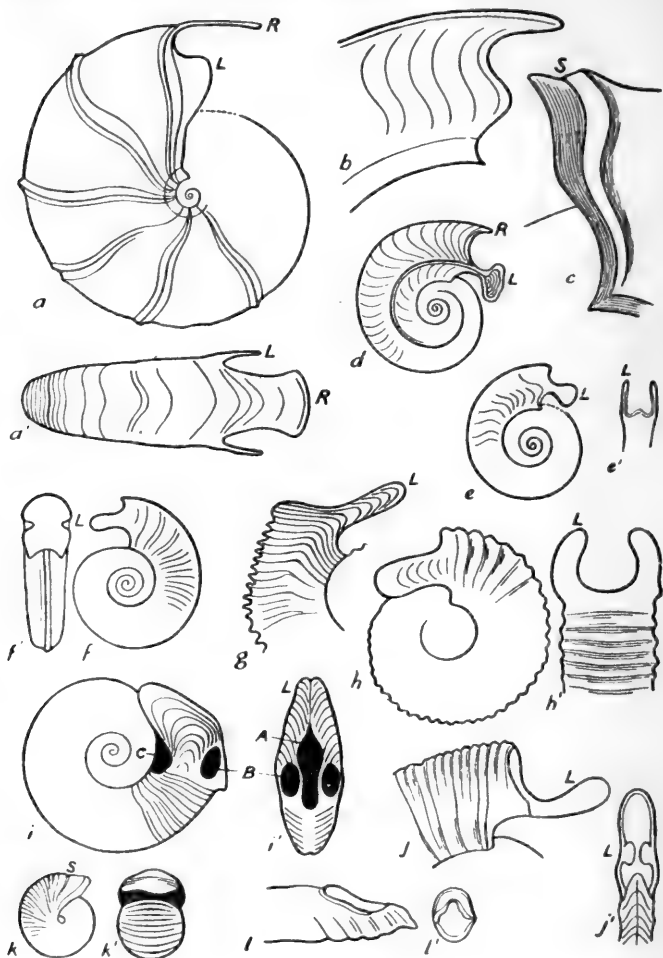


FIG. 46.—APERTURAL MARGINS OF CEPHALOPODA.

*a, a'*, *Phylloceras mediterraneum* Neumayr, Vesulian, near Digne (Basses Alpes). ( $\times \frac{1}{2}$ .) Showing rostrum and lappets (unusual in *Phylloceratinae*) and a number of varices, only parallel to apertural margin if

## GENERAL CHARACTERS OF AMMONOIDS.

The body-chamber of the typical ammonoids varies from half a whorl to over two whorls in length. The aperture of nearly all Devonian forms has a hyponomic sinus on the periphery, but in the Carboniferous period some of the goniatites lose this, and begin to develop a slight forward projection (*rostrum*) in its place. In the Triassic and early Jurassic periods this rostrum becomes more and more prominent, until in some cases it projects as a narrow rod with a length greater than the height of the whorl (Fig. 45, *c-f*). Sometimes the rostrum may

FIG. 46.—APERTURAL MARGINS OF CEPHALOPODA (*continued*).

rostrum and lappets are excluded. (After Haug.) *b*, *Hildoceras* sp., Whitbian (Upper Lias). Rostrum, lappet, and radial line. (After Wright.) *c*, *Lucya cavata* S. Buckman, Aalenian (*concava* zone), Bradford Abbas (Dorset). Constriction behind aperture. (After Buckman.) *d*, *Oppelia fusca* (Quenstedt), Vesulian, Œschingen (Württemberg.) Lappet constricted at base; relation of radial line to apertural margin well shown. (After Quenstedt.) *e*, *e'*, *Fontannesia curvata* S. Buckman, Bajocian (*discites* zone), Bradford Abbas (Dorset). Very feeble rostrum, constricted (spoon-like) lappets. (After Buckman.) *f*, *f'*, *Witchellia deltafalcata* (Quenstedt), Bajocian. Rostrum almost lost, lappets bent inwards to constrict aperture. (After Quenstedt.) *g*, *Cosmoceras elizabethæ* (Pratt), Callovian (Lower Oxford Clay), Christian Malford (Wilts). Long lappets, no rostrum; relation of radial line to apertural margin. (After Quenstedt.) *h*, *h'*, *Otoides* sp., Bajocian, Lauffen (Württemberg). Incurved lappets, no rostrum; no evidence of lappets in radial line. (After Quenstedt.) *i*, *i'*, *Morphoceras pseudo-anceps* (Ebray), Vesulian, St. Honoré-les-bains (Nièvre, France). ( $\times \frac{2}{3}$ .) Lappets and bifurcated rostrum uniting to divide aperture into five orifices—*A*, median hyponomic orifice; *B*, paired opening, probably for eyes; *C*, paired opening for arms. (After H. Douvillé.) *j*, *j'*, *Siemiradzkaia comptoni* (Pratt), Callovian. Long incurved lappets, no rostrum, a constriction shown some distance behind aperture; radial line parallel to constriction, not to apertural margin. (After Quenstedt.) *k*, *k'*, *Sphæroceras brongniarti* (J. Sowerby), Bajocian, Spherocone, aperture depressed, without rostrum or lappets. (After Quenstedt.) *l*, *l'*, *Baculites* (*Cyrtochilus*) *baculoides* (Mantell), Cenomanian, Chardstock (Somerset). (After Crick.) All  $\times \frac{1}{2}$ , except where otherwise stated. *R*, rostrum; *L*, lappet; *S*, constriction.

project outwards as a horn, or even be curled backwards (Fig. 52). Genera with a prominent rostrum are found onwards to the Cretaceous period, but in certain Lower Jurassic forms a pair of lateral protuberances (*lappets*) appear, and as these increase the rostrum diminishes until it may disappear altogether (Fig. 46, *a-h*). Genera with large lappets are confined to the Upper Jurassic. In many cases the lappets tend to close in the aperture, the extreme case being that of *Morphoceras* (Fig. 46, *i*), where the aperture is even more completely subdivided than in the Silurian *Tetrameroceras*.

The constrictions already described in *Gastrioceras* are found in various other ammonoids, sometimes at intervals throughout life (Fig. 41, *d*), sometimes only in very early stages of growth. As we have seen in gastropods, all specializations of the apertural margin must have interfered with the simple growth of the shell, and we must suppose, either that they were not formed until the shell had attained its full size, or that, if formed, they had to be resorbed before growth could continue. Either of these suppositions may be true in particular cases. In a number of genera constrictions do occur at intervals throughout the length, and in one case (*Perisphinctes* and allied genera) there are sometimes found peculiar markings (*parabolæ*) at intervals which may indicate the places where lappets were resorbed.

In the body-chamber of some ammonites there is frequently found a pair of symmetrical calcareous plates, which together form a heart-shaped body (*aptychus*). Similar aptychi are found apart from ammonites, though

in strata in which they occur, and there are even certain Jurassic shales in the Alps which are full of aptychi, but contain no ammonites. As the former are made of calcite, while the shells are aragonite, more easily destroyed by solution, this is not surprising. In one unique example, from the Inferior Oolite of Dundry Hill, Somerset, the aptychus was found in its natural position, closing in the aperture of the shell, so that it evidently acted as an operculum. The two halves of the aptychus were permanently united in *Scaphites* (*synaptychus*); in the *Avietidæ* and *Amaltheidæ* and some Palæozoic genera, a single horny plate (*anaptychus*) served as an operculum, and many ammonoids possibly had no operculum of any kind.

The septa of ammonoids always show a tendency to folding at the margin, giving rise to more or less complexity in the suture-line. We know nothing of the meaning of this folding, puckering, and frilling, but the various resulting patterns of suture-line are of the greatest value in tracing affinities and classifying ammonoids; so that careful attention must be paid to its details. The number of lobes and saddles is extremely small at first (Fig. 47), but increases during the newer Palæozoic era, some families then having a very large number (Fig. 47, *e*, *f*). In the typical families of the later Mesozoic the number tends to keep within certain limits, and to bear a close relation to the degree of involution of the shell. The following description applies especially to those genera in which this relation holds, and needs some modification to apply to the Palæozoic

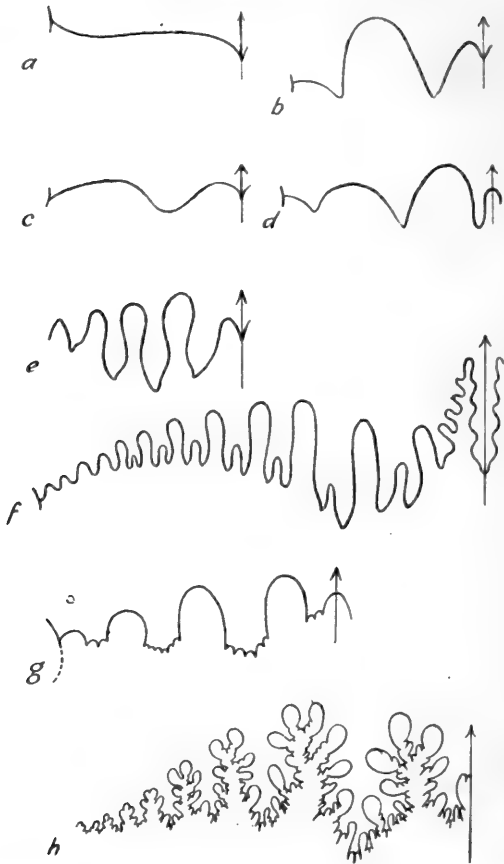


FIG. 47.—SEPTAL SUTURES OF EARLY AMMONOIDEA.

Each figure has the umbilical margin on the left and the middle line of the periphery on the right. The arrow points towards the body-chamber. *a*, *Anarcestes*, Devonian; *b*, *Manticoceras*, Devonian; *c*, *Tornoceras*, Devonian; *d*, *Gastrioceras*, Carboniferous; *e*, *Prolecanites*, Carboniferous; *f*, *Medlicotta*, Permian; *g*, *Paraceratites*, Triassic; *h*, *Phylloceras*, Jurassic. *a-f*, After Crick; *g*, after Perrin Smith; *h*, after d'Orbigny.



forms with either very few or very many lobes and saddles.

Beginning at the periphery, we find there a median *external lobe* (also called *peripheral* or *siphonal*), usually divided in the middle by a small saddle. Flanking this lobe on either side, at about the peripheral margins, is a pair of *external saddles*. On each lateral area are two lobes and two saddles (first or superior, and second or inferior lateral). If we are dealing with an evolute shell there remains only a median *internal lobe* (also called *dorsal* or *antisiphonal*). In the case of shells tending towards the involute, additional lobes and saddles are developed below the lateral lobes: these are called *auxiliary* lobes and saddles, and their number increases with the degree of involution, though not at the same rate in different families.

The degree of complexity of the suture-line serves as a general indication of age. Simple, undivided lobes and saddles indicate the Devonian or Carboniferous period (Fig. 47, *a-e*); in the Permian, subdivision begins (Fig. 47, *f*). The Triassic period is specially characterized by ammonoids with broad rounded saddles and denticulate lobes (*ceratitic* sutures, Fig. 47, *g*), but alongside these are others with highly complex sutures. In the Jurassic period the ceratitic type is absent, and the highly complex (*ammonitic*) suture is alone found (Fig. 47, *h*, 48, *a-h*). This latter also characterizes the Cretaceous period, but in sub-tropical and tropical regions there are Cretaceous forms (*pseudo-ceratites*) in which the suture-line reverts by catagenesis to something like the common Triassic type (Fig. 48, *i, j*).

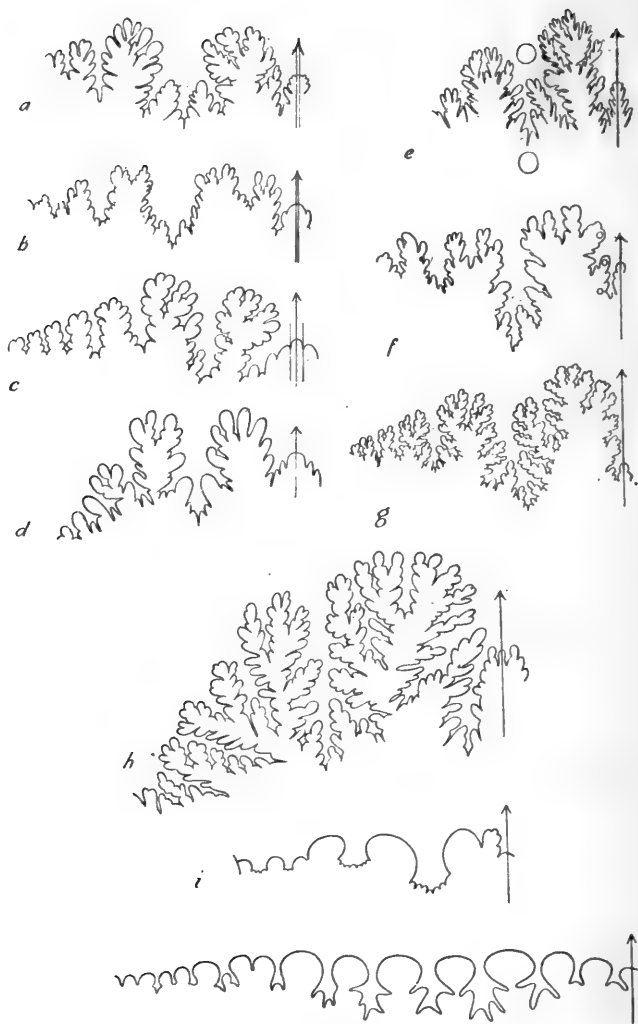


FIG. 48.—(For description see p. 165.)

The shape of the whorl-section varies greatly: it may be rounded, quadrate, cordate, sagittate, depressed, etc. (Fig. 49). These various forms, in combination with different degrees of involution, of rapidity of growth, and of change with advancing age, give rise to an enormous variety of shell-forms, to some of the commonest of which special names are given. Thus, when increase of size is slow, so that for a given diameter there are many whorls, and there is a wide, shallow umbilicus and a square periphery, the resemblance to a cart-wheel suggests the term *rotiform*; but with a rounded periphery, as though the wheel were pneumatically-tyred, the term *planulate* is used (Fig. 49, *a, b*). *Discoidal* means much compressed with an acute periphery, usually with very small umbilicus. When the whorls are depressed, with broad periphery and rather deep umbilicus, the ammonite if placed on its side suggests the shape of a crown, especially if (as is common) it has a row of tubercles or spines along the lateral margin: such an one is *coronate* (Fig. 49, *f*). Mr. Buckman uses the term *oxycone* for discoidal forms and those approaching them (Fig. 49, *c, d*), this being a stage which corresponds to the sphærocone but differs from it in being compressed; and *cadicone* for the extreme form of the coronate type, with very deep conical umbilicus (Fig. 49, *i*).

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FIG. 48.—SEPTAL SUTURES OF JURASSIC AND CRETACEOUS AMMONOIDEA.

Arrangement as in Fig. 47. Circles in *e* denote the position of tubercles. *a*, *Paltopleuroceras*, Domerian; *b*, *Grammoceras toarcense*, Yeovilian; *c*, *Oppelia*, Upper Jurassic; *d*, *Caloceras*, Hettangian; *e*, *Derocheras*, Charmouthian; *f*, *Cosmoceras*, Callovian; *g*, *Hoplites*, Lower Cretaceous; *h*, *Perisphinctes*, Upper Jurassic; *i*, *Tissotia*, Upper Cretaceous; *j*, *Metengonoceras*, Upper Cretaceous. *a-h*, after d'Orbigny; *i*, after H. Douvillé; *j*, after Hyatt.

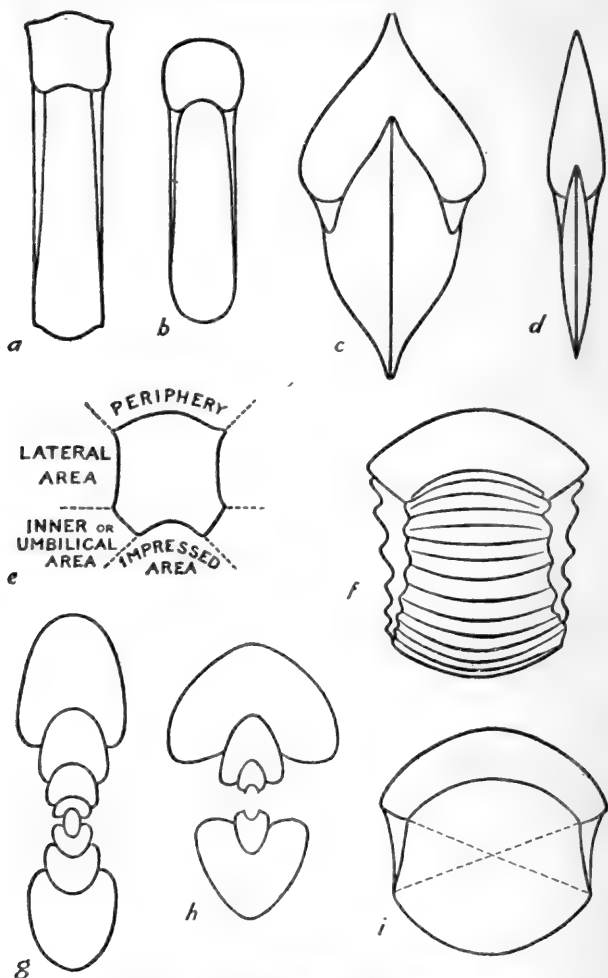


FIG. 49.—WHORL-SHAPE IN AMMONOIDEA.

All except *e*, *g*, and *h* are apertural views. *a*, *Microderoceras*, lat-umbilicate, rotiform, whorl-section quadrate. *b*, *Dactylioceras*, lat-umbilicate, planulate, whorl-section rounded. *c*, *Chamousettia*, angust-

The ornamentation of ammonoids falls under a few definite heads. Primitive genera are smooth, and so are many higher forms in early youth. The smooth stage is generally followed by a *capillate* stage, in which there is a pattern of fine raised lines on the surface; and this by *subcostate* and *costate* stages, in which the much more prominent features called *ribs* (*pilæ*, *costæ*) are developed: these are really corrugations of the shell, and usually appear as strongly on the cast as on the exterior; when they do not, it is because an internal partition or septum is formed under each rib, as in the planulate ammonites of the Upper Lias. A still later stage is the *tuberculate* or *spinous*, when portions of the ribs stand out prominently either with rounded or pointed ends. These stages follow one another in the given order (anagenesis of ornament), though any one of the intermediate stages may be skipped in the hurrying-on of development. After the last stage, catagenesis may often take place, and the shell which is tuberculate in youth may become costate or even smooth in old age.

The ribs, or capillæ, run in a straight or curved direction from the umbilicus to the periphery; their course is

FIG. 49.—WHORL-SHAPE IN AMMONOIDEA (*continued*).

umbilicate, lenticular oxycone, whorl-section cordate. *d*, *Amaltheus*, angust-umbilicate, discoidal oxycone, whorl-section sagittate. *e*, Diagram based on *Aspidoceras* to explain areas of whorl-surface. *f*, *Erymnoceras*, coronate, whorl-section greatly depressed (periphery and umbilical area practically meet, excluding any lateral area). *g*, *Perisphinctes*, section showing early whorls of depressed crescentic shape, changing later to compressed and planulate. *h*, *Quenstedtoceras*, section showing early compressed whorls, changing later to broad and somewhat depressed. *i*, *Cadoceras*, a cadicone, greatly depressed whorls, deep conical umbilicus (indicated by dotted lines). *a*, *b*, *c*, *d*, *f*, *i*, After d'Orbigny; *g*, after Dumortier and Fontannes; *h*, after R. Douvillé.

constant through the various stages of development, and is a good guide to the affinity between different species. This course is termed the *radial line* of the species, and it bears a close relation to the form of the apertural border. Thus, if there is a rostrum and lappets without any constriction behind, the radial line will be more or less sickle-shaped or *falciform* (Figs. 46, *f, h*; 47, *d*), but if there is a constriction it will be straight (Fig. 47, *j*). A rostrum without lappets gives rise to a radial line like an inverted L, or Greek  $\Gamma$  (*gammi-radiate*, Figs. 39, *a*; 45, *d, e*).

The ribs sometimes cross the periphery quite straight (Fig. 46, *h, k*); more often with more or less of a forward bend, owing to the general presence of a rostrum (Fig. 45, *f*). The absence of a forward bend in the ribs does not, however, prove the absence of a rostrum (Fig. 46, *a*); it may mean that rostra were produced at intervals and resorbed. In many forms the ribs are interrupted on the middle of the periphery, either by an elevated *keel* (*carinate* periphery, Fig. 39, *b*) or by a median groove (*sulcate* periphery, Figs. 45, *d*; 46, *i*) or by a keel flanked by grooves (*carinati-sulcate*).

The radial ornament is in some families crossed by longitudinal lines.

The classification of the ammonoids is by no means in a settled state yet, and it is necessary to have some acquaintance with the development of ideas on the subject. A hundred years and more ago, all ammonoids whose shells were normally coiled with the whorls in contact were given the one generic name *Ammonites*, while those which showed peculiar modes of coiling

received special names such as *Hamites*, *Scaphites*, *Turritites*, and *Baculites*. Leopold von Buch in 1830 pointed out the importance of the suture-line and separated from *Ammonites* the Palæozoic species as *Goniatites* and the most typical Triassic species as *Ceratites*. D'Orbigny added several to the list of genera based upon peculiarities of coiling. This classification remained unchanged until 1865: it was inconsistent and lop-sided. Based mainly on coiling—a feature that may vary during the life of the individual—it yet united under the one name, *Ammonites*, species with all degrees of involution, from those in which the whorls only just touched to those which were completely involute, yet it separated off under a distinct name those in which the whorls just failed to touch. The number of species of *Ammonites* too was too enormous, whatever conception might be held of a genus.\*

Von Buch had indeed divided *Ammonites* into some sixteen groups, but these were based upon external form and ornament only; while Montfort (1808) and de Haan (1825) had separated off certain groups under distinct generic names, but these had been ignored. In 1865 Suess in Europe, and in 1867 Hyatt in America, independently and almost simultaneously started the subdivision of the genus *Ammonites*. Their method of work was rather different. Suess (whose work was quickly carried on by Waagen and Neumayr) defined a few large natural groups and gave them generic names. Hyatt,

\* Nevertheless, if used colloquially, the word "ammonite," in the sense of the old generic name, will always remain a useful one

inspired and started on his work by Louis Agassiz, confined himself to the ammonites of one small division of time and divided them with much greater minuteness. Thus it happened that one of Waagen's genera (*Arrietites*) was equivalent to a whole family of Hyatt's. The American worker also initiated the method of using individual development (ontogeny) as an essential criterion in classification. This double start led to some confusion in the naming of Jurassic ammonites, which Mojsisovics and Gemmellaro, working on the almost untouched mass of Triassic and Permian species, were able to avoid. Numerous later workers have added greatly to the recognized number of Ammonite genera—work which is not always greeted by stratigraphers with the thanks which it deserves, but which is inevitable once the evolutionary conception of a genus is accepted.

#### GENERAL HISTORY OF THE AMMONOIDEA.

As so often happens, the apparently most primitive genera are not the earliest. The orthocone *Bactrites* indeed is doubtfully reported from the Silurian, but is not known in the Devonian until nearly the end of the Middle epoch of that period; while *Gyroceras* [*Mimoceras*], which starts as a gyrocone and continues as an ophiocone, is known from the Middle Devonian only. At the very beginning of the Devonian there appear two genera in the ophiocone stage, *Anarcestes* (Fig. 47, *a*) and *Agoniatites* (Fig. 41, *b*), the very simple sutures of which have led most palæontologists to place them in a family *Nautilinidæ*, though they might perhaps better be regarded as at the base of separate other families. Towards the end of Middle Devonian time, a new family *Magnosellaridæ*



appears (*Tornoceras*, etc.), characterized by the appearance of small external and large lateral saddles (Fig. 47, *c*). In the Upper Devonian flourished the remarkable family *Clymeniidae*, in which the siphuncle is on the inner or dorsal margin, instead of the peripheral margin. In the same period lived the *Gephyroceratidae* and *Magnosellaridae* (typified respectively by *Manticoceras* and *Tornoceras*, already described). With the beginning of the Carboniferous period the Devonian genera vanish, while two new families appear—the *Glyphioceratidae* in which the peripheral lobe comes to be divided by a small saddle, and surface-ornament first begins to be noticeable (*Glyphioceras*, *Gastrioceras*) and the *Prolecanitidae* in which the number of lobes and saddles is much increased, and they come to have a narrow tongue-like shape (*Prolecanites*, Fig. 47, *e*). This family attains much greater complexity of suture in the Permian, especially in *Medlicottia* (Fig. 47, *f*) and in *Cyclolobus* and *Popanoceras*, which seem to be transitional from this family to the Triassic *Arcestidae*. The type-genus of this last, *Arcestes* (Fig. 45, *c*), is notable for the extreme length of body-chamber, which, in combination with the U-shaped whorl-section due to combined depression and involution, must have resulted in a most extraordinarily shaped animal.

Along with these in the Trias are found the families *Ceratitidae* and *Meekeceratidae* (the latter also Permian, Fig. 47, *g*), in which the suture-line is generally "ceratitic," or in some genera rather more complex. The former family attains to costate and tuberculate ornament, but the latter are smooth, compressed, discoidal forms. In the *Trachyceratidae* (Fig. 45, *d*) the surface becomes ornamented by intersecting radial and longitudinal lines, with tubercles at the intersections, and the periphery is more or less sulcate. The suture-line is ceratitic, but with saddles notched somewhat as in *Asteroceras*. Another

family in which involute, compressed forms with acute periphery predominate is the *Pinacoceratidæ*, in which the suture ranges from ceratitic to the most highly complex kind known in any ammonoid. These are the principal Triassic families, none of which survive that period.

The classification of the Jurassic ammonites is in a very unsettled state at present. Mr. Buckman, the chief English investigator of them, proposes the following provisional scheme (the terms involved are explained farther on):

- I. Suture-line phylloidal, no keel, no aptychus or anaptychus. Families *Phylloceratidæ*, *Lytooceratidæ*.
- II. Suture-line phylloidal, passing to complex and much inflected; no keel in most, when present it arises late, after elaboration of suture-line; with aptychus or anaptychus.
- III. Suture-line with saddle of ceratitic outline, more or less serrated but generally remaining fairly simple; keel usually developed at a very early stage; elaboration of suture-line, if any, coming later; with aptychus or anaptychus.

I. While most of the Mesozoic families of ammonites are short-lived, rapidly attaining their acme and dying away in a single geological age or little more, the two families of this branch are exceptional in enduring with little modification through the Jurassic and Cretaceous periods. They are also peculiar in having a narrower geographical distribution than most other families, their headquarters being in the subtropical waters of "Tethys"—the ocean which occupied the site of the present Alpine-Himalayan mountain-systems and the Mediterranean region. Only at intervals of time did a few representatives succeed in migrating into the colder seas of what is now Central and Northern Europe. The

Phylloceratidæ are distinguished by their suture-line (Fig. 47, *h*), in which the saddles are subdivided by little lobes (lobules) into ovoid "cells," constricted posteriorly (phylloids); by the general absence of ornament other than striæ; and by the general tendency to complete involution in the shell (Fig. 46, *a*).

The Lytoceratidæ also have a "phylloidal" suture, but it often becomes so complex that this character is obscured; long lateral branches to the median internal lobe are characteristic. They tend to an evolute form, though with exceptions, and in the Cretaceous period yield a large proportion of the uncoiled forms (*Macroscaphites*, *Ancyloceras*, some species of *Crioceras*). In both these families constrictions may occur at intervals, and in the Lytoceratidæ these are sometimes marked on the exterior of the shell not by depressions, but by conspicuous elevations ("flares").

II. and III. It will be convenient to describe the rest of the Jurassic ammonites in historical order, indicating their taxonomic position by the number II. or III. in parentheses.

The Jurassic period opens with the Hettangian age, characterized by the first appearance of ammonites in Northern Europe. These belong to the family Psiloceratidæ (II., Fig. 48, *d*). The genera vary from nearly smooth (*Psiloceras*) to strongly costate (*Schlotheimia*). The latter genus survives to the end of the Sinemurian age, which is mainly characterized by the Arietidæ (III.), a family with uninflected sutures, simple straight ribs bending forward on the periphery (*Asteroceras*, Fig. 39, etc.) and a keel. The whorl-section is usually quadrate, but in the degenerate *Oxynoticeras* it becomes acutely sagittate: this and similar oxycones persist into the next age. Alongside of the Arietidæ in their acme are found not only some survivors (*Schlotheimia*) from a previous age, but also the

primitive ancestor of forms which attain their acme later—*Microderoceras birchi* being the first. This is a widely umbilicate planulate form, whose inner whorls show anagenesis from smooth to costate and tuberculate. *Xipheroceras* (p. 134) is an allied form, later in time. From some such form may have sprung the Deroceratidæ (II.), which attain their acme in the Charmouthian stage—forms with rounded whorl-section, costate tuberculate or spiny, and a highly ornate, much inflected suture (Fig. 48, *e*). Alongside these are found two other families—the Liparoceratidæ (III.), which begin as “capricorns” much like *Xipheroceras*, and rapidly develop into multi-tuberculate unkeeled sphærocones with uninflected suture-line, and the Polymorphidæ (II., Fig. 46, *e*), with an inflected suture, which also begin rather like capricorns, but become bi-tuberculate (two tubercles on each side) and develop a keel later on. Here also appear *Celoceras pettos*, the first Jurassic coronate type, ancestral to the dominant families of the Upper Jurassic; and *Echioceras*, a genus which like the Polymorphidæ passes from a planicostan to a keeled stage, and may be ancestral to the Hildoceratidæ so important a little later.

In the Domerian stage, there is an irruption of a new family, Amaltheidæ (III.), which have several features in common with the Arietidæ, but in which discoidal forms predominate, and the keel has typically a knotted appearance (Figs. 45, *e*; 48, *a*; and Frontispiece).

The Whitbian, Yeovilian and Aalenian stages are dominated by the enormously prolific Hildoceratidæ (III.), which are already abundant in the Domerian of the Mediterranean region, though rare in Britain. They are characterized by a more or less doubly-curved or sickle-shaped radial line of ornament; the whorl-shape and degree of involution vary greatly, but there is always a keel, and the suture-line is uninflected, but differs from

that of Arietidæ in the much deeper first lateral lobe (Figs. 45, *f, h*; 46, *b, c*; 48, *b*).

In the Whitbian, the hildoceratids (*Harpoceras*, *Hildoceras*, *Pseudolioceras*) are accompanied by planulate deroceratids, some tuberculate (*Peronoceras*, *Porpoceras*), others degenerated to costate—the dactyloids (*Dactylioceras*). In the Yeovilian and Aalenian, other hildoceratids (*Lioceras*, *Ludwigia*) are accompanied by the last polymorphids, some closely resembling hildoceratids in aspect (*Dumortieria*), others quite distinct (*Tmetoceras*).

In the Yeovilian (sporadically), the Aalenian (commonly), ending in the earliest Bajocian, occur the Hammatoceratidæ (II.), tuberculate with rounded periphery and deroceratid suture-line, which develop a keel and acquire striking resemblance to hildoceratids and sonnininines, from which they are distinguished by the suture-line.

As we pass from the Aalenian to the Bajocian comes the greatest faunal change of the Jurassic: here the line between Lower and Upper Jurassic epochs should be drawn, though the old stratigraphical boundary between Lias and Oolites comes at least an age earlier. The hitherto dominant families die out suddenly, and three new series rapidly establish themselves. First are the Sonnininæ (III., Fig. 46, *f*), a sub-family of the Amaltheidæ, though separated from it, so far as present knowledge goes, by nearly three ages. They are characterized in general by a catagenesis of ornament, the inner whorls being spinose, the outer plainly ribbed or even smooth (a marked contrast to the anagenetic ornament of the Domerian amaltheids), but the suture-line becomes more elaborate as the ornament declines. The keel is in many cases a septicarina (p. 147). The Sonnininæ are almost confined to the Bajocian; but the other two new families last to the end of the Jurassic period.

One of these is the Ooppelidæ (III.), keeled forms which appear suddenly in the oxycone stage, without sign of preceding stages, and mostly remain in that stage or tend to open out into scaphitoids; they tend to produce well-marked lappets and a rostrum, so that their radial line is sickle-shaped (Figs. 46, *d*; 50); their suture-line has a smooth outline and a very prominent first-lateral saddle and deep first-lateral lobe (Fig. 48, *c*).

The other is the family Stepheoceratidæ (II.), using



FIG. 50.—LUNULOCERAS BRIGHTI (PRATT), CALLOVIAN (LOWER OXFORD CLAY), CHRISTIAN MALFORD (WILTS).  
(Natural size.)

Rostrum and lappets. Original.

that term in its widest sense: a very extensive group, which starts from a coronate stage, and goes through various developments of form—some becoming planulates directly, others sphærocones (Fig. 46, *h*), others planulates through a sphærocone stage, but all retaining the same general type of ribbing—more or less straight ribs, splitting on the lateral area into two or more which either run continuously across the arched periphery (Fig. 46, *h*) or are interrupted by a groove (Fig. 46, *i*), never a keel. The aperture may have a plain border,

or there may be lappets (sometimes long and elaborate in shape) but they never affect the course of the radial lines, though sometimes they leave indications of their former position by markings (parabolic knots) at intervals. Constrictions occur in some genera (Fig. 46, *j*, *k*). These richly varied Bajocian and Vesuvian stepheoceratids are continued into higher Jurassic stages chiefly as costate planulates known as the Perisphinctidæ (Figs. 46, *j*; 48, *h*; 49, *g*)—certainly not a true family, as they are polyphyletic, arising from several different coronate stocks.

The Bathonian age in Northern Europe was marked by an almost total disappearance of ammonites, but in the Callovian a rich fauna reappears, in which four new families appear alongside the persistent opelids and perisphinctids. These are (1) the Cardioceratidæ, presumably allied to Opeledæ: they pass from platycones to sphærocones with varying degrees of inflation (*Quenstedtoceras*, Fig. 49, *h*, *Cardioceras*), even to very stout cadicones (*Cadoceras*, Fig. 49, *i*); (2) the Pachyceratidæ, coronates; (3) the Aspidoceratidæ, at first square-whorled and evolute, later (in some genera), rounded and involute, characterized by a modification of the coronate or perisphinctid suture, in which the external saddle and first lateral lobe become very large, the lower saddles and lobes being compressed into what looks like a single complex saddle; (4) the Cosmoceratidæ, starting as closely-ribbed coronates (*Kepplevites*) but rapidly becoming more compressed and developing a periphery medianly smooth, often with marginal tubercles, while the lateral area becomes richly bi-tuberculate: long lappets are present (Figs. 46, *g*; 48, *f*). This last family hardly outlasts the Callovian, and the Cardioceratidæ die out in the Kimmeridgian; the remainder survive to the end of the Jurassic.

The Phylloceratidæ and Lytoceratidæ persisted in the Alpine-Mediterranean region right through the Cretaceous period. The latter family gives rise to some uncoiled forms (*Macroscaphites*, *Ancyloceras*, Fig. 41, *h*, *i*) in the Lower Cretaceous, but also giving off a branch family, *Desmoceratidæ*, in which the tendency is towards tighter coiling or involution: this family lasts to the Upper Cretaceous.

In the Neocomian stage of the Lower Cretaceous, the oppelids and perisphinctids persist, and a very characteristic form is *Olcostephanus* (also found in the higher

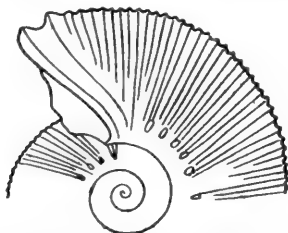


FIG. 51.—OLCOSTEPHANUS ASTIERIANUS (D'ORBIGNY)

•NEOCOMIAN. ( $\times \frac{1}{2}$ .)

Plain apertural margin, oblique to radial line of ornament. (After d'Orbigny.)

Jurassic strata), coronate to planulate, with perisphinctid aspect (Fig. 51), but a different suture-line of the "inverse" type (the lobes from periphery to umbilicus successively ending farther and farther in front of the guide-line). Besides the uncoiled forms already mentioned, *Crioceras* and *Toxoceras* (Fig. 41, *f*) are common, or more correctly criocones and toxocones, for the generic names as generally used denote groups of homœomorphs rather than true genera.

The Barremian stage is specially characterized by the *Pulchellidæ*, rather compressed involute forms with ribs of peculiar shape—broadening from umbilicus to peri-



phery, so that the spaces between them are parallel-sided and at last narrower than the ribs themselves: the ribs form sharp tubercles on the edge of the flattened periphery.

In the Aptian and Albian stages the family *Hoplitidæ* is abundant: it is regarded as derived from the perisphinctids, though it differs greatly from them both in aspect and suture-line (Fig. 48, *g*). These ammonites are rather involute, with flattened periphery, and sigmoid (doubly curved) ribs. The later species tend to be strongly bituberculate, with the ribs gathered in to the tubercles. Such species abound in the Lower Gault Clay of Folkestone, but in the Upper Gault they have almost completely disappeared and are replaced by keeled forms practically unknown in the Lower Cretaceous. The uncoiled forms most characteristic of the Gault or Albian stage are *Hamites* and *Turrilites* (Fig. 41, *e, j*).

An important family beginning in the Lower Cretaceous but extending into the Upper is the *Acanthoceratidæ*, characterized by broad straight ribs with a tendency to break up into many tubercles. Characteristic of the Upper Cretaceous are the keeled forms of the family *Prionotropidæ* (*Mortoniceras*, Fig. 52, *Schlenbachia*). In warmer latitudes there appear a number of genera known as pseudo-ceratites (Fig. 45, *i, j*), not a natural family, but agreeing in a degeneration of the suture-line which reverts to something resembling the ceratitic type of the Trias. These forms are known in Southern Europe, Syria, India, North and South Africa, South America, and the Southern United States. The catagenesis of suture is not accompanied by any loss of coiling: many of them are strongly involute. On the other hand, the uncoiled Cretaceous genera show complex sutures. *Scaphites* (Fig. 41, *g*), and *Baculites* (Fig. 46, *e*) are most characteristic of the Cretaceous beds higher than the Gault.

There are certain important lessons which the study of the enormous number of species of ammonites has impressed upon palæontologists. First is the danger of basing any idea of relationship on external form alone. Over and over again species of very similar form have proved to differ widely either in their suture-details, or

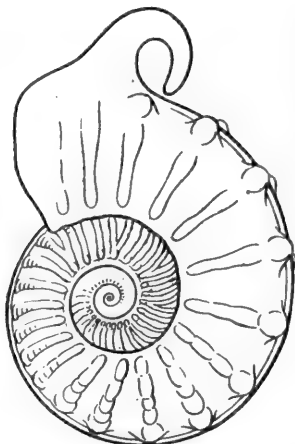


FIG. 52.—MORTONICERAS INFLATUM (J. DE C. SOWERBY),  
ALBIAN (UPPER GAULT.) ( $\times \frac{2}{3}$ .)

Ornament omitted in centre; bifurcating ribs replaced later by single multituberculate ribs. Rostrum bent backwards. (After Buvignier.)

in their ontogeny (as shown by a study of the inner whorls): such species are said to be *homœomorphs* of one another, and have more than once led, either to mistakes in zonal stratigraphy, or to the erroneous idea that certain ammonite-species have too long a range in time to be of zonal value.

Secondly, in spite of the richness of the ammonite-

faunas, the gaps in the phylogenetic sequence are impressive. Neumayr, forty years ago, first called special attention to this in a famous essay. He pointed out how at certain geological horizons there appeared abundant new ammonites which could not be the descendants of any in the earlier zones : these he termed *cryptogenetic* types. In other cases, similar forms reappeared at wide intervals, while absent from intervening strata : these he termed *sporadic* types. Two particular cases of the latter he was able to explain very satisfactorily : at various horizons in the Jurassic of South Germany (and at some but not all of the same horizons in England) there appear species of the genera *Phylloceras* and *Lytoceras* (or, as we should now express it, of the families Phylloceratidæ and Lytoceratidæ). But similar forms occur throughout the Jurassic of the Mediterranean region ; hence Neumayr's explanation of their sporadic occurrence farther north was that opportunities for migration occurred occasionally owing to geographical or climatic changes, and he expressed the belief that other sporadic and cryptogenetic types would prove to have migrated from unknown regions. Since Neumayr wrote it has been shown that many of his supposed "sporadic" types are not related to one another but are homœomorphs, as for instance various oxycones which at that time were placed on account of their form in the genus *Amaltheus*.

Cryptogenetic types are indications of the imperfection of the palæontological record, which, as Mr. Buckman points out, may be due to several causes :

1. Incomplete exploration of large areas of the earth's surface—of which indeed three-quarters is practically preserved from exploration by a covering of deep sea.

Within the last twenty years, exploration of new areas has actually revealed the ancestors of what had been cryptogenetic types (not indeed of ammonites, but of trilobites and mammals), and justified Neumayr's migration-theory.

2. Destruction of fossiliferous strata by denudation. Not only have large parts of some continents been swept bare of masses of strata that once covered them (as proved by isolated patches preserved by some accident), but it is now realized that among shallow-water deposits there has been much "pene-contemporaneous" erosion, and that in what looks like a thick conformable series of sediments there may be many gaps due to this cause.

3. New stocks begin with small members which are liable to be overlooked in collecting or in subsequent investigation; and even larger forms, if rare (and they may be rare if the stock has not yet attained dominance), are liable to be neglected.

## DIBRANCHIATA.

The most familiar fossils of this order are those known as *Belemnites*, the most typical of which are found in the Jurassic and Lower Cretaceous systems, though forms but little different also occur in the Upper Triassic and Upper Cretaceous. A typical belemnite shell consists of (1) a *phragmocone* (chambered shell) which is an orthocone or cyrtocone with a calcareous globular protoconch,

a siphuncle along the ventral margin and a forward prolongation of the dorsal region, the *pro-ostracum* (Fig. 53, *a*, *b*, *b'*) and (2) a solid *guard*, more or less cigar-shaped, with a conical hollow (*alveolus*) at the blunt end for the reception of the apex of the phragmocone. The guard is composed of fibrous calcite arranged radially; it is more often found preserved than the phragmocone, and is so resistant to wear and tear that belemnite guards are often found as derived fossils in gravels. In a few cases, sufficient traces of the body of the belemnite have been found to show that the skeleton was entirely internal, the animal growing out of all proportion to the growth of the shell, so that an ever smaller portion of the body remained within the body-chamber, and the mantle gradually enveloped the whole shell. Like its relative the modern cuttle-fish, it possessed an ink-sac and a number of arms around the mouth, though these were furnished with horny hooks not known in the cuttle-fish, and there seem to have been only six of them instead of the eight or ten of modern dibranchiates (Fig. 53, *a*).

In some of the earliest (Upper Triassic and Lower Jurassic forms) the phragmocone extends nearly to the end of the guard (Fig. 53, *c*), and in these cases it is probable that the former was still an external shell in early life and only later became enveloped in the mantle, which then began to secrete a guard around it. (This makes the name "guard" inappropriate, since it was formed when the phragmocone least needed protection). But in most later forms the alveolus only extends a

short distance into the guard, which probably began to be formed as early as the phragmocone.

The phragmocone when found alone is apt to be mistaken for an *Orthoceras*, but it can be distinguished, (1) by the marginal position of the siphuncle, and (2) by the fact that the growth-lines (*conothecal striæ*), which form its only ornament, curve forwards on the dorsal region in correlation with the presence of a pro-ostracum (Fig. 53, a).

The chief features serving to distinguish species among belemnite-guards are (1) the general shape, (2) the disposition of grooves on the surface, (3) the depth and apical angle of the alveolus. The two main shapes are the *lanceolate* and the *hastate*: in the former the diameter is constant for the greater part of the length, and the posterior end is conical; in the latter the diameter increases from the front end for some distance backwards. In cross-section either form may be circular, compressed (laterally) or depressed (dorsi-ventrally): to distinguish between the latter in the absence of the phragmocone, it is sufficient to notice the plane of symmetry of the alveolus which is the median plane. The alveolar angle varies between  $12^{\circ}$  and  $32^{\circ}$ .

A few belemnite-guards are quite free from grooves; others have a number of short apical grooves; but the majority have either a median ventral groove or a pair of dorso-lateral grooves.

The classification of belemnites is in a confused and unsatisfactory condition. Only morphological classifications have been proposed, except for limited groups of

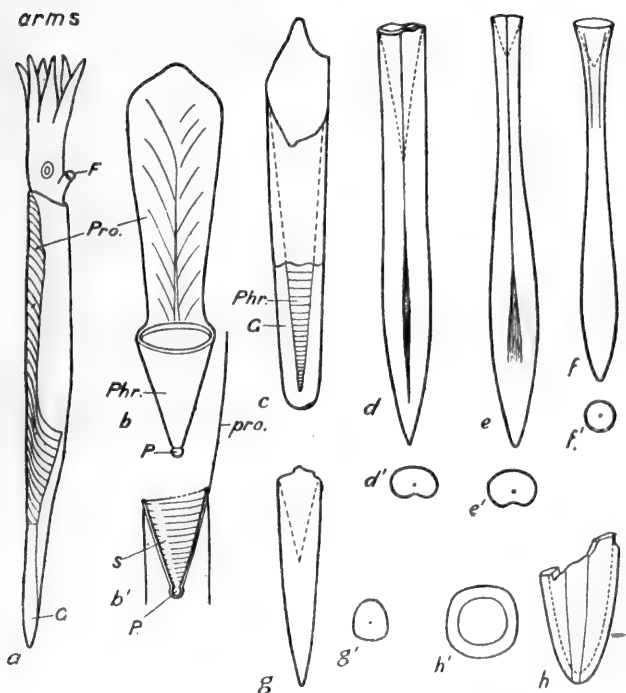


FIG. 53.—BELEMNITES.

- a*, Restoration of the living Belemnite (modified from d'Orbigny). *F*, Funnel; *G*, guard; *Pro.*, pro-ostracum. *b*, *b'*, Restoration of phragmocone, in front view and section (after Crick). *P*, Protoconch; *Phr.*, phragmocone; *S*, siphuncle. *c*, *Atractites philippii* Hyatt and Smith, Carnic, California. Guard (*G*) partly broken open showing phragmocone (*Phr.*). (After Hyatt and Smith.) *d*, *Belemnopsis bessinus* (d'Orbigny), Bathonian. *e*, *Hibolites hastatus* (Blainville), Callovian (Oxford Clay). *f*, *Hastites clavatus* (Blainville), Charmouthian. *g*, *Oxyleuthis acutus* (Miller), Sinemurian. *h*, *Caeloteuthis excavatus* (Phillips), Sinemurian. *d-h*, Ventral views: dotted lines indicate the alveolus, unbroken lines the grooves on the surface. *d'-h'*, Cross-sections, the dot marking the axis. *d*, After d'Orbigny; *e-h*, after Phillips. (All  $\times \frac{1}{2}$ , except *a*).

species, and little notice has been taken of ontogeny, although the mode of growth of the guard (by accretion) makes changes in shape and grooving recognizable.

The following is an imperfect statement of the classification most generally accepted. An asterisk denotes genera always accepted as distinct, the remainder being usually lumped in the comprehensive genus *Belemnites*.

#### A. GUARD NOT GROOVED.

*Atractites*,\* Trias, Scythic to Rhætic (guard nearly cylindrical, alveolus nearly as long as guard, Fig. 53, *c*).

*Oxyteuthis*, Sinemurian-Charmouthian (guard acutely conical, alveolus half length of guard), *e.g.* *Bel. acutus* (Fig. 53, *g*).

#### B. GUARD WITH VENTRAL GROOVE.

*Cæloteuthis*, Sinemurian (short, cylindro-conical, alveolus nearly as long as guard, groove very wide), *e.g.* *Bel. excavatus* (Fig. 53, *h*).

*Belemnopsis*, Charmouthian-Bathonian (long, cylindrical, with acute apex, groove long, deep and narrow, alveolus one-third length of guard), *e.g.* *Bel. bessinus* (Fig. 53, *d*).

*Pachyteuthis*, Charmouthian-Neocomian (stout, cylindrical, with conical apex, groove long and shallow, alveolus from one-third to two-thirds length of guard), *e.g.* *Bel. abbreviatus* (Fig. 54, *a*).

*Cylindroteuthis*, Callovian-Neocomian (long, cylindrical, groove deepest near apex, becoming indistinct forwards, alveolus about one-fourth length of guard), *e.g.* *Bel. oweni* (Fig. 54, *b*).

*Hibolites*, Aalenian-Cenomanian (hastate), *e.g.* *Bel. hastatus* (Fig. 53, *e*).

*Belemnitella*,\* Emscherian-Maestrichtian (cylindrical, with rounded and acuminate apex, alveolus one-third to one-half length of guard, ventral slit in guard along



more than half the length of alveolus), e.g. *Bel. mucronata* (Fig. 54, c).

*Actinocamax*,\* Cenomanian-Campanian (very like the last, but the part of the guard around the alveolus is imperfectly calcified, and is always more or less destroyed), e.g. *A. quadratus* (Fig. 54, d).

#### C. WITH DORSO-LATERAL GROOVES.

*Aulacoceras*,\* Trias, Ladinic to Noric (phragmocone much longer than the small hastate guard).

*Hastites*, Charmouthian-Neocomian (hastate), e.g. *Bel. clavatus* (Fig. 53, f).

*Pseudobelus*, Aalenian-Cenomanian (lanceolate, with very deep lateral grooves), e.g. *Bel. bipartitus*.

#### D. WITH SEVERAL APICAL GROOVES.

*Dactyloteuthis*, Domerian-Yeovilian (cylindro-conical up to a certain age, then suddenly elongating into a long tubular apex), e.g. *Bel. acuarius* (Fig. 54, f).

*Megateuthis*, Aalenian-Bajocian (with similar change of shape), e.g. *Bel. giganteus*.

#### E. WITH MEDIAN DORSAL GROOVE.

*Duvalia*, Callovian-Neocomian of Mediterranean province (much compressed), e.g. *Bel. dilatatus* (Fig. 54, e).

The typical Belemnoids die out at the end of Mesozoic time, except in Australia, where they are recorded from Eocene strata. In Europe, there are in the Eocene several forms, mostly very rare as fossils, which may be their descendants strangely modified before final extinction. Greater interest attaches to two collateral stocks which lead to living forms. One of these is the Eocene *Belosepia*, which forms a link between the belemnites and the recent cuttle-fish *Sepia*. The siphuncle is greatly widened, the phragmocone is transitional from its typical form to the "cuttle-bone," and the guard is in process

of reduction to the little point of a modern *Sepia*. The other transitional form is the Miocene *Spirulivrostra*, in

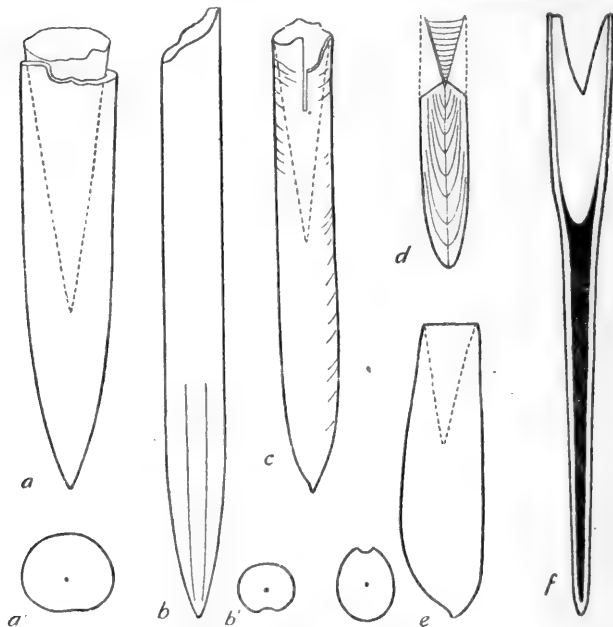


FIG. 54.—BELEMNITES.

*a*, *Pachyteuthis explanatoides* (Pavlov), Upper Jurassic. *b*, *Cylindroteuthis magnificus* (d'Orbigny), Lower Portlandian. *c*, *Belemnitella mucronata* d'Orbigny, Campanian (Upper Chalk), showing alveolar slit and groovings of surface. *d*, *Actinocamax verus* Miller, Campanian (Upper Chalk). Dotted lines indicate the destroyed part of the guard. *e*, *Duvalia lata* (Blainville), Neocomian. Some species of *Duvalia* are more compressed than this (*e'*). *f*, *Dactyloteuthis acuarius* (Schlotheim), Charmouthian. Longitudinal section, showing sudden change of shape and cavity (black). *a-c*, Ventral views; *d, f*, sections; *e*, side view; *a'-e'*, cross-sections. (All  $\times \frac{1}{2}$ d.) (*a, b*, After Pavlov; *c, e, f*, after d'Orbigny; *d*, after Crick.)

which the phragmocone is a more decided cyrtococone than in any belemnite: this leads to the recent *Spirula*, a gyrocone in which all trace of guard has disappeared.

Alongside the typical Belemnoids of the Mesozoic runs an allied stock (*Phragmoteuthis*, Trias; *Belemnoteuthis*, Upper Jurassic; *Conoteuthis*, Lower Cretaceous), in which the guard is a very thin investment of the phragmocone. By reduction of the phragmocone and guard with retention of the proostracum, this may have led to the modern squid, *Loligo*.

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## V

### THE TRILOBITA AND OTHER ARTHROPODA

1. **Calymene blumenbachi** (Fig. 55), the "Dudley locust," is a familiar fossil, beautifully preserved in the Silurian Limestone of Dudley in the Black Country, formerly much worked as a flux for the iron-furnaces, but now worked out. This was evidently an animal of very different construction from those we have hitherto considered. The main part of its body is seen to be composed of a row of very short, broad divisions (*somites*, or segments), thirteen in number, all alike except for a slight diminution in size backwards. In front is a semi-circular headpiece (*cephalon*), which shows suggestions of somites like those behind; and at the other end is a tail-piece (*pygidium*) showing very well-marked segmentation (division into somites). From end to end run two nearly parallel grooves, which divide the whole body into a median strongly-arched portion (*mesotergum*) and lateral flatter portions (*pleural regions*). The existence of these three portions of the body suggested the name *Trilobita* for the group of fossils to which *Calymene* belongs.

The trilobites are quite extinct and unknown outside the Palæozoic system. There are, however, abundant

living forms with so similar a general structure of skeleton that we can safely refer them to the same phylum. This is the great phylum Arthropoda, which includes the Insects, the Myriapods (centipedes and millipedes), the Arachnids (scorpions and spiders), the Crustacea (lobsters and crabs), and one or two minor and unfamiliar classes. In all these, the body is metamericly segmented (divided into a longitudinal series of more or less similar somites), and encased in an exoskeleton of chitin which may be hardened by a deposit of calcium phosphate; a number of the somites at the anterior end are more or less completely united into a head; and on the ventral surface is a paired series of jointed limbs (usually one pair to each segment) which fulfil the functions of locomotion (walking or swimming), the seizing of food, and in aquatic forms respiration.

Shell-growth in the Arthropoda is totally unlike that of Brachiopoda and Mollusca. The exo-skeleton is not secreted by a mantle but by the whole surface of a complex jointed body. It is a continuous cuticle, thickened and hardened to form a number of rigid pieces (*sclerites*) but remaining thin between, where flexibility is necessary. Marginal growth is therefore impossible. The growing animal at intervals bursts and casts off its whole exo-skeleton, and presently secretes a new and larger one: this is the process of *ecdysis* or *moulting*. The only way in which the ontogeny of a fossil arthropod can be determined is by the finding of a series of cast skins (or of prematurely dead animals): this has been successfully done for a number of species of trilobites.

The limbs or appendages of Arthropods are usually of the greatest importance for classification. Unfortunately the limbs of trilobites are very rarely found. The ventral exo-skeleton of aquatic Arthropods has always much more thin cuticle and smaller sclerites than the dorsal, but in trilobites it seems to have been nearly all thin cuticle, which easily decayed and allowed the limbs, themselves soft, to be lost.

*Calymene blumenbachi* is sometimes found lying flat, sometimes rolled-up exactly in the way in which the modern wood-loose rolls itself up when alarmed—that is to say, with the ventral sides of head-piece and tail-piece in close contact (compare Fig. 59, *e*). Comparison of specimens in the two conditions shows that neither head nor pygidium is flexible, but that the somites of the intermediate region (commonly called the *thorax*) are movable on one another by pivots at the sides, their dorsal portion sliding partly over one another when the animal stretched itself out, and becoming fully exposed when it rolled up.

In an ordinary-sized specimen 50 mm. long, the head measures about 16 mm. in length, the thorax 27 mm., and the pygidium 7 mm. Subsequent measurements refer to such an one, but the species sometimes attained nearly double these dimensions.

Each thoracic or *free somite* consists of a central arched portion (axis) and a pair of lateral *pleura*. The axis of the first somite is about 11 mm. wide, that of the last about 8 mm. : each consists of a prominent arch, measuring 2 mm. from front to rear, and an anterior sunken

area, of which about 1.5 mm. is visible in an enrolled specimen, but which almost disappears in a straight one. The pleura vary in width from about 12 mm. in the first somite to 10 mm. in the last; about 4 mm. from the axis each bears a prominent little forward projection, fitting into a socket in the somite in front, and serving as a pivot. In enrolled specimens the part of the pleuron external to this pivot is largely concealed beneath the somite in front. A well-marked groove divides each pleuron into a smaller anterior and larger posterior portion.

The head shows the same trilobed character as the thorax: the central part is called the *glabella*, the lateral, the cheeks or *genæ*. Evidences of segmentation are shown chiefly by the glabella; there is, however, one well-marked cross-furrow (neck or *occipital* furrow) near the posterior margin, marking off both in glabella and *genæ* a posterior somite which closely resembles a thoracic somite, but is immovably fixed to the rest of the head-shield. The other signs of segmentation are three pairs of grooves (*segmental furrows*) in the glabella, more or less transversely placed, but not crossing the centre of the glabella, which is quite smooth. The most anterior of these is very slight, the second longer or deeper, the third still longer and deeper. The two latter bend obliquely backward, so as to mark off rounded lobes joined to the rest of the glabella by a constricted base. These three furrows and the occipital furrow indicate that the head is composed of five united somites. With the disappearance of flexibility in the head, why have traces of the grooves between the somites been retained?



The reason can be understood by examining the methods of muscular attachment in Arthropoda. Where powerful muscular action is necessary the inner face of the exo-skeleton does not provide a sufficient area of attachment, and to increase that area a portion of the cuticle becomes, as it were, pushed in to the interior of the body. Such an inward process is called an *apodeme*,

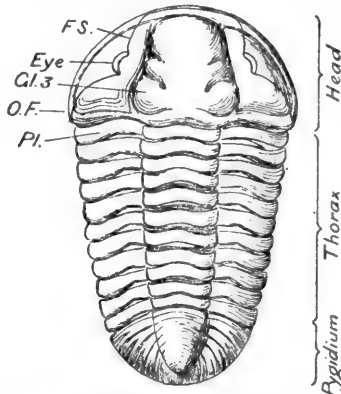


FIG. 55.—CALYMENE BLUMENBACHI, BRONGNIART, WENLOCK LIMESTONE.  
(Natural size.) (Original.)

*F.S.*, Facial suture; *Gl.3*, third lateral lobe of glabella; *O.F.*, occipital furrow; *Pl.*, pleuron.

and in the thorax of trilobites apodemes are formed in pairs at the posterior margin of each somite. The lateral furrows of the glabella occur in corresponding positions and are evidently apodemes of the head. Some trilobites have lateral furrows much more like those of the thorax than in the case of *Calymene*; in others they diverge still more from the primitive characters. Since

apodemes serve principally for the attachment of the limb-muscles, this seems to indicate that in *Calymene* the head-limbs are more specialized than in some trilobites, but less so than others. Of the nature of the head-limbs (jaws, etc.) of trilobites we know very little.

The glabella of *Calymene* becomes gradually narrower forwards. It ends bluntly, and in front of its end there is a raised border, which margins the whole head-shield, but is slightly arched up in front of the glabella.

The genæ within this raised border are only slightly convex. Each carries a large eye, opposite the first rounded glabella-lobe (third head somite). The eyes are of the compound type, found only in arthropods: instead of one adjustable lens there are many, of fixed curvature, each focusing a small segment of the field of vision on a retinula. The compound character is not well seen in *Calymene*, as the surface of the eye is smooth.

On each cheek there is seen a fine dividing line (*facial suture*), which starts at the genal angle (outer end of posterior margin of head), runs first obliquely forward, and then transversely, until it reaches the posterior margin of the eye; here it curves round the inner margin of the eye, and continues straight forward to the front margin of the head-shield, where it continues on the under-side. Just below the margin a transverse suture joins the right and left facial sutures.

The most probable explanation of the facial suture is that it is a line of easy separation to facilitate the moulting (ecdysis) of the head-shield, and especially of the eye, the lenses of which are formed from the cuticle and must

be moulted. The portion of each cheek lying external to the suture is called the *free cheek*, the remainder is the *fixed cheek*, and the glabella together with its attached fixed cheeks constitutes the *cranidium*. Loose cranidia and free cheeks are often found, probably detached in the process of moulting. In all trilobites which possess both eyes and facial suture, the eye lies on the free cheek in contact with the suture, and the adjacent part of the fixed cheek has a protuberance fitting into the outline of the eye, called the *palpebral lobe*.

If the suture cuts the lateral margin in front of the genal angle, it is described as *proparian*; if shifted so as to cut the posterior margin, it would be *opistho-parian*. That of *Calymene* is on the verge between the two.

In specimens which show the under-side of the head, there is seen, articulated to the central part of the marginal rim, a somewhat oblong plate with indented posterior margin. This is called the *labrum* (or *hypostome*), and formed a biting upper-lip to the mouth (Fig. 61).

The pygidium of *Calymene* is nearly semi-circular, the free posterior margin having much less curvature than the anterior margin which articulates with the thirteenth thoracic somite. The axis tapers backwards to a rounded termination, a little short of the actual end of the pygidium: its anterior two-thirds are divided into six well-marked somites, the remainder is unsegmented. There are six pairs of pleura, which from front to rear show an increasing backward curvature, until the last pair run straight back parallel to one another. The margin is

entire. The pygidial pleura are covered with little tubercles.

Very little is known of the limbs of *Calymene*: traces of them have been found in sections of enrolled specimens, including spiral structures which are probably gills carried on the limbs.

2. **Dalmanites caudatus** (often called *Phacops caudatus*) is another famous Dudley trilobite (Fig. 56). The most important differences between it and *Calymene* are these: The marginal rim of the head-shield is drawn out into a slight point in front and into a pair of genal spines behind. The glabella is much wider in front, instead of narrower; its lateral furrows are nearly straight and do not mark off rounded lobes as in *Calymene*, but converge towards the middle line, leaving a much narrower smooth central area. The eyes are very large, usually well-preserved, and the compound character is obvious, the surface being divided into a large number of corneal facets arranged in a very regular manner. The facial suture is very distinctly proparian, cutting the lateral margin some way in front of the genal angle and making a right-angled bend at the eye; in front it runs round the front margin of the glabella from one side to the other, not cutting the front margin of the head-shield, so that the two free cheeks form one inseparable piece. The labrum is somewhat triangular (Fig. 61, *d*).

The thorax consists of eleven somites, which differ from those of *Calymene* chiefly in the relative narrowness of the axis (about one-quarter the total width, instead of nearly one-third).

The pygidium consists of twelve or more somites, of which only ten have pleura recognizable: it is longer proportionately than that of *Calymene*, more triangular in outline, its axis narrower, and at its posterior end it is drawn out to a long spine (*mucronate*). The presence of this spine shows, by analogy with living Arthropods, that it obtained its food by thrusting its head forward

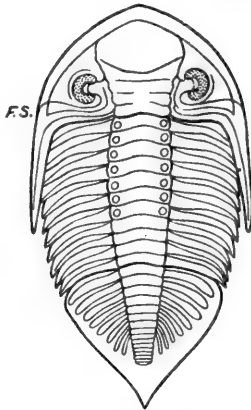


FIG. 56.—DALMANITES CAUDATUS (BRÜNNICH), WENLOCK LIMESTONE, (Natural size.) (After Salter.)

F.S., Facial suture.

into the mud, using the tail-spine as its support. The highly-developed eyes, however, show that it did not live buried in the mud: the eyes could have been no use in the search for food; they must have served to warn it of the approach of enemies. Their position, on the highest part of the head, is clear evidence that this was a bottom-living or *benthic* animal: in trilobites of *nectic*

(swimming) habit, the eyes are close to the margin of the head, so that they could look outwards as well as upwards, and in these there is never a tail-spine. We owe these observations to Prof. Dollo of Brussels. Nothing is known of the limbs of *Dalmanites*.

3. **Triarthrus becki** (Fig. 57) is a small trilobite of which very beautifully preserved specimens have been found in the Ordovician Utica Shale of Rome, New York State. In form this is much less tapering than the previous forms, and ends more bluntly behind. The semi-circular head-shield has a much less distinct marginal rim, the glabella is of almost uniform width, with lateral furrows which are but very slightly inflected from the transverse direction. In all these points the head shows much less difference from the thorax than that of *Calymene* or *Dalmanites*, so that *Triarthrus* is a more primitive form. The cheeks are each little more than half the width of the glabella; a long and narrow eye is in the centre of each; the facial sutures are opisthoparian, but cut the hind margin very close to the genal angle, running obliquely inward and forward (with a bend at the eyes) to cut the anterior margin separately at a distance apart not very much less than the width of the glabella.

The thorax consists of fourteen free somites, of which the first eight are of almost uniform width, after which a slight tapering takes place: each bears a median tubercle, as also does the last (occipital) somite of the head and the first of the pygidium. The pygidium is very short (about two-fifths as long as broad), and consists of six somites fused.

The labrum is parabolic in outline. From beside it springs a pair of long, unbranched antennæ, which are the appendages of the first head-somite, and the only pair not conforming to the general type of the rest.

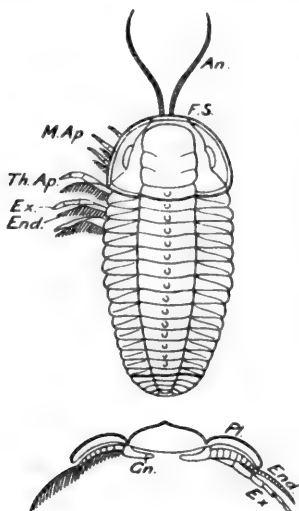


FIG. 57.—TRIARTHURUS BECKI, GREEN, ORDOVICIAN (UTICA SHALE), ROME (NEW YORK). (x 2.)  
(After Beecher, modified.)

The lower figure is a diagrammatic cross-section: on the left side the exopodite with its fringe is alone drawn, on the right the exopodite (without the fringe) and endopodite are shown. (NOTE.—The abbreviations *Ex.* and *End.* have been accidentally interchanged.) *An.*, antenna; *End.*, exopodite; *Ex.*, endopodite; *F.S.*, facial suture; *Gn.*, gnathobase; *M. Ap.*, mouth appendages; *Pl.*, pleuron; *Th. Ap.*, thoracic appendages.

Any one of the largest appendages (from the first eight thoracic somites) shows the following characters: It is attached to the ventral surface of the body by a joint called the *coxopodite*, from which a hard jaw-

process (*gnathobase*) projects towards the middle line. In the outward direction two branches spring from the coxopodite (hence the appendages are said to be *biramous*): the inner one, or *endopodite*, consists of five movable joints, not unlike one of the ordinary legs of a crab; the outer, *exopodite*, consists of one long joint followed by a great number of very short joints, the whole fringed with numerous hair-like *setæ*. Evidently the endopodite is adapted for crawling on the bottom, the exopodite for swimming through the water. The function of the gnathobase is known from the habits of modern Crustacea with very similar appendages. The right and left gnathobases in any somite approach one another to grasp any solid body between and pass it forward to the pair in front, and so on until it reaches the mouth, where it is swallowed or rejected according to its being edible or not.

Thus the appendages of *Triarthrus* perform the three functions of crawling, swimming, and seizing food, as do those of such a Crustacean as *Apus*: to these may be added probably that of respiration, for they present a large surface of thin cuticle to the sea-water in a region where it must be constantly agitated by the movements of the limbs. In more specialized trilobites we may expect a greater division of labour—some appendages will be specialized as jaws, others for crawling, and others for swimming (unless one of these two means of locomotion is lost altogether), and definite gills will appear as outgrowths from some appendages instead of the whole surface being used for respiration. In *Calymene*



there is evidence of such gills. The only indication of specialization in *Triarthrus* is that in the four pairs of head-appendages (behind the antennæ) the gnathobases are larger, and the exopodite and endopodite smaller, so that (as might be expected in the neighbourhood of the mouth) the jaw-function is beginning to predominate over the other functions.

4. **Trinucleus concentricus** (Fig. 58) is a trilobite found in the Upper Ordovician Shales of Shropshire and Wales. Complete specimens are rarely found, but the usual (though not maximum) length appears to be

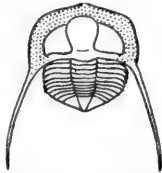


FIG. 58.—*TRINUCLEUS CONCENTRICUS* EATON, CARADOCIAN.  
(Natural size.) (After Phillips.)

about 17 mm., of which 9.5, 4.5 and 3 mm. measure head, thorax and pygidium respectively. The greatest width of the thorax is 12 mm., that of the head 18 mm. This great difference is due to the presence of a remarkable flat brim projecting from the free margin of the head, and perforated by a number of pits, arranged in four or five roughly concentric rows. This brim is about 3 mm. wide at each genal angle, where it contracts into a long, outwardly-curved genal spine, which extends back 4 or 5 mm. beyond the end of the pygidium; at the front end of the head the brim is about 2 mm. wide, so that the length of the head without the brim is about equal to that

of the thorax and pygidium. Consequently in an enrolled specimen only the head is seen on one surface, and only the thorax and pygidium with the projecting brim and genal spines on the other: in fact it is rather doubled-up than rolled-up.

The head within the brim consists of a highly raised glabella widening forwards from about 3 mm. to about 5 mm., and smooth protuberant cheeks. The glabella shows scarcely any sign of segmentation, and the cheeks show no trace of eyes or facial suture. *Trinuclеus* is thus a blind trilobite, and has probably arrived at that condition by degeneration consequent on complete adaptation to the mud-grubbing life for which its shape is so well suited. In certain species of *Trinuclеus* (or closely allied genera) there are traces of eyes in the young, and the late Cambrian genus *Orometopus*, probably the ancestor of *Trinuclеus*, has well-developed eyes and opisthoparian suture. With the loss of the eyes moulting became an easier process and a facial suture could be dispensed with, splitting taking place along the margin. The disappearance of glabellar furrows is also a specialization, and traces of them can be seen in some species of *Trinuclеus* (as *T. favus*).

The thorax consists of six somites; the axis is only 3 mm. wide, or one-fourth the total width. The pygidium is short, obtusely triangular in shape, the axis tapering, the number of somites about four.

From what has been said in the chapter on Lamelli-branchia, it will be understood that in seeking a natural classification of trilobites it is essential to distinguish

between (1) differential or static characters that keep fairly constant through one line of descent; (2) progressive characters that are likely to show similar sequences in several lines of descent; and (3) adaptative characters that may occur over and over again in the same or different branches. Let us first distinguish the progressive characters.

Arthropods are doubtless descended from the metamERICALLY - segmented worms (annelids), and have advanced beyond them by, among other things, the coalescence of a number of anterior somites (six in trilobites) to form a head: this process has been termed *cephalization*. Among trilobites only, a similar process takes place at the posterior end, somites fusing to form the pygidium (*caudalization*), so that we have forms with very small pygidia consisting of the unsegmented end of the body alone or with addition of a very few somites (*micropygous* stage), forms with a pygidium including more somites but still much smaller than the head (*heteropygous*), and forms with a pygidium as large as the head (*isopygous*). These stages were passed through independently by various lines of descent, the number of thoracic somites diminishing as the pygidium incorporated more of them.

These changes do not seem to bear any relation to habitat or mode of life, but there are others that do (adaptative characters). The ordinary trilobites seem to have lived on the sea-bottom, but to have been able both to crawl and to swim; but particular genera or families took, some to a mud-grubbing, others to a surface-

swimming life, and became adapted to those special conditions. Adaptation to life in the mud is shown by a shovel-like head; the eyes as far from the margin as possible (to be out of the mud, where they are useless) and sometimes lifted up on long stalks, or else the eyes are lost altogether; the pygidium sometimes ends in a spine. Adaptation to a pelagic life is shown by a more or less globular head with eyes near the margin, sometimes by very thin shell, peculiarly shaped pygidium, and great development of spines (as a protection).

There remain the static or differential characters, the chief of which is the course of the facial suture. Others of less value, because liable to be modified by progression or adaptation, are the form and proportions of glabella and cheeks, and of axis and pleura.

The recognition of the importance of the facial suture is due to the late Prof. Beecher of Yale, who in 1895 proposed the names *Opisthoparia* and *Proparia* for the orders with the two types of suture. Unfortunately a few trilobites, mostly blind, show neither type, and in these Beecher thought the facial suture was marginal or sub-marginal: he therefore united them as *Hypoparia*. More recent discoveries seem to show that these forms had lost their sutures through their blindness, and can be traced back partly to opistho- and partly to pro-parian ancestors. Only two orders appear necessary therefore. Of these, *Opisthoparia* is much the larger, and is divided by Prof. Swinnerton of Nottingham into sub-orders as shown below.

## ORDER I. : OPISTHOPARIA.

Facial suture cutting posterior margin.

SUB-ORDER 1. **Mesonacida**.—Long crescentic eyes close to glabella, wide free cheeks (in earliest genera, facial suture not yet developed). Nearly all in micro-pygous stage; thoracic pleuræ to a large extent free from one another, the free part (pleural spines) more and more curved back towards posterior end. Mainly Lower and Middle Cambrian, including the zonal genera *Olenellus* (Figs. 59, *a*; 61, *a*) and *Paradoxides*; the specialized pelagic *Remopleurides* is Ordovician.

SUB-ORDER 2. **Conocoryphida**.—Glabella usually parallel-sided or narrowing forwards, eyes small; thoracic pleuræ not spiny; pygidium in most cases hetero- or iso-pygous. A very large group, ranging through the whole Palæozoic era, and subdivisible into sections:

(i.) *Conocoryphina*: specialized in respect of blindness, but otherwise the most primitive; glabella with oblique segmental furrows; free cheeks extremely narrow; micro- to hetero-pygous. Cambrian.

(ii.) *Olenina*, including two main families, the earlier *Olenidæ* with broad short head, narrow glabella, tapering thorax of twelve to twenty-two somites, micro- to hetero-pygous, Cambrian (Fig. 59, *c*); and the later *Proëtidæ* with longer head, thorax of eight to ten somites, not tapering, hetero- to iso-pygous (Ord.—Perm.)—the only family surviving the Devonian (Fig. 59, *g*).

(iii.) *Ptychoparina*, including Cambrian hetero-pygous families near to Conocoryphidæ but with eyes, and two later isopygous families—*Asaphidæ* (Figs. 59, *b*; 61, *b, c*), with eight thoracic somites (Camb.—Ord.), and *Illenidæ* (Fig. 59, *d, e*) with ten (Ord.—Sil.).

(iv.) *Calymenina*, a small group in which the facial

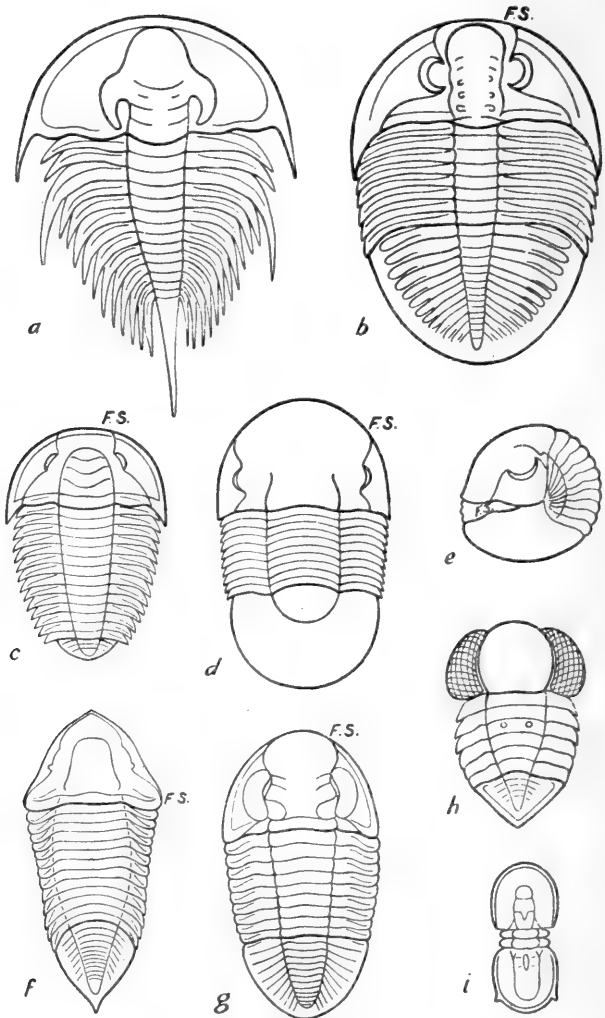


FIG 59.—(For description see p. 209.)

suture cuts the genal angle. It includes two important genera (both Ord.-Dev.)—the heteropygous *Calymene*, already described, and the isopygous *Homalonotus*, with several sub-genera, of which *Trimerus* (Fig. 59, *f*), with triangular head and pygidium, is the best known.

**SUB-ORDER 3. Trinucleida.**—A somewhat divergent series, of which the more generalized ancestral forms are not known. The *Harpedida* (Ord.-Dev.) are micro-pygous, with many thoracic somites, but specialized in having a brim like that of *Trinucleus*, except that it extends far back beyond the genal angles. *Ampyx* resembles *Trinucleus* in thorax and pygidium, but has no head-brim, has very narrow free cheeks, and a long median spine in front. *Trinucleus* (Ord.) has been described and its eye-bearing ancestor *Orometopus* (Upper Camb.) referred to already. Possibly to be placed here are two small isopygous forms—*Shumardia* (Upper Camb.) and *Æglina* (Ord.), the latter a pelagic form with enormous eyes (Fig. 59, *h*), probably a nocturnal animal descending to the depths of the sea by day and feeding at the surface at night.

**SUB-ORDER 4. Odontopleurida.**—Glabella subdivided into lobes bearing little relation to the original segmentation; free cheeks wide; micro-pygous, pygidium with pleura projecting so as to make the margin toothed

FIG. 59.—TRILOBITES.

- a*, *Olenellus thompsoni* (Hall), Lower Cambrian. Parker's Quarry, Georgia, Vermont. ( $\times \frac{1}{2}$ .) (After Walcott.) *b*, *Ogygiocaris* [*Ogygia*] *buchi* (Brongniart), Llandeilian. ( $\times \frac{1}{2}$ .) (After Salter.) *c*, *Olenus cataractes* Salter, Upper Cambrian. ( $\times \frac{1}{2}$ .) (After Salter.) *d*, *Illenus davisii* Salter, Ordovician. ( $\times \frac{1}{2}$ .) (After Salter.) *e*, *Bumastus barriensis* (Murchison), Silurian. Side view of an enrolled specimen. ( $\times \frac{1}{2}$ .) (After Salter.) *f*, *Trimerus* [*Homalonotus*] *delphinocephalus* Green, Silurian. ( $\times \frac{1}{2}$ .) *g*, *Phillipsia derbiensis* (Martin), Lower Carboniferous. ( $\times \frac{3}{4}$ .) (After H. Woodward.) *h*, *Æglina binodosa* Salter, Ordovician. (Natural size.) (After Salter.) *i*, *Agnostus princeps* Salter, Upper Cambrian. ( $\times \frac{1}{2}$ .) (After Salter.)

or lobed. Includes two pelagic families (both Ord.-Dev.)—*Lichadidæ*, with very thin crust, and *Acidaspidæ*, very spiny. The rather isolated genus *Bronteus* (Ord.-Dev.) shows some relations with these, but it is isopygous, and its pygidium has an entire margin and the axis is very short.

## ORDER II.: PROPARIA.

Facial suture cutting lateral margin. The most primitive genus is the Middle Cambrian *Burlingia*, which is micropygous, but almost as broad as long. Associated with it is the small isopygous *Pagetia*, which

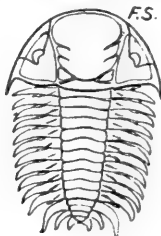


FIG. 60.—CHEIRURUS BIMUCRONATUS (MURCHISON), WENLOCK LIMESTONE.

(Natural size.) (Original.) \*

retains the facial suture lost in the commoner forms *Microdiscus* (Camb.) and *Agnostus* (Fig. 59, *i*, Camb.-Ord.). These three genera have the smallest numbers of free somites of any trilobites—2, 4 and 2 respectively.

The more familiar Proparia are only known from the Ordovician onwards: they have nearly always eleven free somites.

The *Encrinuridæ* have very narrow free cheeks with an almost straight facial suture, and small eyes, sometimes on long stalks; a long pygidium with many pleuræ, and often a still larger number of divisions of the axis. The *Cheiruridæ* (Fig. 60) have a facial suture, with right-angled



bend at the eye; pleura of free somites spiny; pygidium small, of three to five somites, with pleura projecting from margin. This family includes several remarkable pelagic forms--*Sphærexochus* (Ord.-Sil.), *Staurocephalus* (Ord.), *Deiphon* (Sil.). The *Phacopidæ* are remarkable for their highly-developed eyes, with many well-preserved lenses; the glabella is always expanded in front; the facial suture as in the last family; pygidium with entire margin. *Dalmanites* (Ord.-Sil.) has been described; *Phacops* (Sil.-Dev.) differs in the more expanded



FIG. 61.—HYPOSTOMES (LABRA) OF VARIOUS TRILOBITES.

*a*, *Elliptocephala asaphoides* Emmons, Lower Cambrian. ( $\times 3$ .) (After Walcott.) *b*, *Ogygiocaris buchi* (Brongniart), Llandeiliian. ( $\times \frac{2}{3}$ .) Dotted lines indicate outline of doublure. (After Salter.) *c*, *Asaphus tyrannus* Murchison, Llandeiliian. ( $\times \frac{2}{3}$ .) (After Salter.) *d*, *Dalmanites caudatus* (Brünnich), Salopian. ( $\times \frac{2}{3}$ .) (After Salter.)

glabella, on which the segmental furrows are obsolete, and the shorter, non-mucronate pygidium.

### General Geological History of the Trilobites.

They appear suddenly in the Lower Cambrian, with every appearance of having been long in existence already, since specialized forms like *Agnostus* appear alongside the primitive *Mesonacidæ*. Most of the Cambrian forms, however, are micropygous and unspecialized. In North America different genera and species of *Mesonacidæ* serve as zone-fossils in the Lower Cambrian (*Nevadia*, *Elliptocephala*, *Callavia*, *Olenellus*), and in Britain and Scandinavia species of *Paradoxides* serve

similarly for the Middle Cambrian, and species of *Olenidæ* for the Upper Cambrian (see Appendix I.). In the succeeding Ordovician system the trilobites attain their acme. Although with the modern narrowing of the extent of the term "family" it is no longer possible to say that all families of trilobites occur in the Ordovician, yet there are few that do not, and there is a greater abundance and variety of forms than in any other system.

Two families are especially characteristic of the Ordovician—*Trinucleidæ* and *Asaphidæ*. Both are strictly confined to the Ordovician, if we include the Tremadoc beds, which form a transition from Cambrian to Ordovician, and if we confine ourselves to Britain and Scandinavia; but asaphids have been found as low as Middle Cambrian in British Columbia. They thus afford an instance of migration as an explanation of cryptogenetic types. Asaphids are more characteristic of the Lower and Middle Ordovician, trinucleids of the Upper. Neither family survives the period, but allies of each persist into the Silurian—*Illænus* representing the asaphids and *Ampyx* the trinucleids.

In the Silurian the trilobites are still abundant, but no new families appear and many genera are extinct, especially among Opisthoparia, the Proparia now increasing in importance. In the Devonian the list of families is diminished by three—the two mentioned above as surviving into the Silurian and the *Encrinuridæ*. Lastly in the Carboniferous only one family survives, the *Proëtidæ*, represented by four genera, of which one survives into the Permian of tropical regions.

Besides their value as indices of age, trilobites may serve another purpose to the geologist. The majority being bottom-living forms (*benthic*) they were more restricted than pelagic forms in geographical extension. They may therefore assist in the delimitation of marine zoological provinces in Palæozoic times, and so help towards the reconstruction of past geographies. Such provinces are regarded by some geologists as established for the Cambrian, Ordovician, and Devonian periods, though the Silurian gives little indication of provinces. Thus, in the Cambrian of China there are trilobites belonging to genera unknown in Europe, and again in the Rocky Mountains there is another series of forms, while in Newfoundland the European faunas are found. There is therefore a probability of separate provinces between which migration was difficult.\* At the same time great caution is necessary in drawing conclusions from limited data. Evidently if two faunas from different parts of the world contain no species in common, we cannot be sure that they were contemporaneous: it may be that they belong to different zones in the system, and that one zone was never deposited in the one area, or was subsequently removed by denudation, while the same was the case with the other zone in the other area. Mistakes of this kind have been made and afterwards corrected in several cases, and it may be that the same will happen to the supposed Palæozoic life-provinces. As more detailed knowledge is obtained of the strati-

\* See Cowper Reed, "Pre-Carboniferous Life Provinces," *Records Geol. Surv. India*, vol. xl. (1910).

graphy of little-known areas like China and British Columbia, it will be possible to say with greater certainty whether they were inhabited by faunas differing from the strictly contemporaneous faunas of Europe.

**Ontogeny of Trilobites.**—Owing to the inability of the exo-skeleton to grow with the animal's growth, the adult trilobite, unlike a brachiopod or mollusc, retains no trace of its early form. The only way to trace the development of a trilobite is to find remains of a sufficient number of individuals of all stages of development (whether cases of infant mortality, or merely the skins moulted in healthy development) to be sure they belong to the same species. This has been done in a number of cases, particularly by Barrande in Bohemia and Beecher in North America, and the general course of development has been established. The earliest stage known has been termed the *protaspis* larva, and is probably the form in which most trilobites were hatched. At this stage, the whole dorsal shield is less than 1 mm. long, and consists principally of head, the thorax and pygidium being very rudimentary. The trilobation is distinct, and the glabella shows five well-marked somites. The eyes are marginal, probably as an adaptation to the free-swimming life usual in Crustacean larvæ. By repeated moults the larva passes through stages in which the post-cephalic part of the body increases in length and in number of somites, gradually attaining the adult state.

The remaining divisions of the Arthropoda must be dealt with much more briefly.

PHYLUM : **ARTHROPODA.**

Metamerically segmented animals with jointed appendages, the anterior somites fused into a head.

CLASS : **CRUSTACEA.**

Usually aquatic, and breathing by gills borne on the appendages, with one or two pairs of antennæ.

SUB-CLASS : **Trilobita.**—Classification already given.

SUB-CLASS : **Entomostraca.**—A rather heterogeneous group of primitive Crustacea, all passing through the stage of a Nauplius larva, with only three pairs of appendages. Chief orders—Phyllopora, Ostracoda, Cirripedia.

SUB-CLASS : **Malacostraca.**—With 19 somites (or in Phyllocarida a few more) the head of 5 (bearing two pairs of antennæ, 1 of mandibles, 2 of maxillæ), the thorax of 8 with walking limbs (of which the first 1, 2, or 3 may be fused with the head). Chief orders—Phyllocarida, Isopoda, Decapoda (with sub-orders Macrura and Brachyura).

CLASS : **ARACHNIDA.**

Without antennæ. Somites 18 or fewer.

SUB-CLASS : **Merostomata.**—Marine, breathing by gills. Orders—Xiphosura, Eurypterida.

SUB-CLASS : **Arachnida** (*sensu stricto*).—Terrestrial, breathing by lungs or tracheæ. Chief orders—Scorpiones, Araneæ.

CLASS : **MYRIOPODA.**

With numerous similar somites. Terrestrial, breathing by tracheæ.

**CLASS: INSECTA (Hexapoda).**

With head bearing antennæ, mandibles and two pairs of maxillæ, thorax with 3 pairs of appendages and 2 pairs of wings, and abdomen without appendages.

**Notes on the Chief Classes and Orders of Arthropoda (other than Trilobites) found Fossil.**

The **Phyllopoda** are mostly non-marine, but as common in excessively salt as in fresh waters. The form of the body and the appendages have some resemblance to those of a primitive trilobite like *Olenus*; but (1) there is no trilobation; (2) no fusion of posterior somites into a pygidium; and (3) the exo-skeleton of thorax and abdomen is thin, and to protect the hinder regions the head-shield is extended back as a loose covering. In some forms, especially in the fossil *Estheria*, this head-shield is divided into two by a median suture so as to form practically a bivalve shell: this being ornamented by sub-concentric ridges closely resembling the growth-lines of a mollusc, it is very easy to mistake *Estheria* for such a lamellibranch as *Posidonomya*. All the more is this the case, because while, in general, arthropod shells do not grow marginally but are only replaced by ecdysis, *Estheria* is stated to be a unique exception, in which the concentric lines are actually growth-lines. The following points should be looked for to distinguish *Estheria*: (1) There is no hinge-structure as in lamellibranchs; (2) the material of the shell is not calcareous but chitinous; (3) with a lens there may be seen between the apparent growth-lines a network of striæ which is never seen in lamellibranchs. *Estheria* is common from Carboniferous to Triassic. *Protocaris* is a Cambrian marine form scarcely distinct from the modern freshwater *Apus*.

The **Ostracoda** are more thoroughly bivalve than *Estheria*, as the two valves completely enclose the whole body, and they are calcareous. They never show any "growth-lines," and are nearly all of too small a size to be lamellibranchs. The Silurian *Leperditia* is a giant among ostracods, being nearly 20 mm. in length: a glance at the hinge will show that it is not a lamellibranch: there is also a tubercle on each valve, anterodorsally, which could not occur in a molluscan shell. Although the majority of ostracods are marine, it is in freshwater deposits (such as the Purbeck Marls and Wealden Shales) that they occur in such abundance as to attract attention in spite of their small size. Ostracods range from Cambrian to Recent.

The **Cirripedia** are the only arthropods which are fixed. They are all marine, and occur sparsely in formations from the Ordovician onwards. They secrete a shell of five or more pieces, which shows little analogy with that of any other arthropod; and in the works of early palæontologists such as Cuvier and the Sowerbys they will be found figured among Mollusca.

The **Phyllocarida** are an almost extinct group, mainly Palæozoic, differing from phyllopods in little else than the great restriction in the number of somites, and the lesser backward extension of the head-shield. Some forms (*Hymenocaris*, *Echinocaris*) are fairly common fossils from Cambrian to Devonian.

The **Isopoda** (wood-lice) are terrestrial forms, with a curious external resemblance to trilobites, which some palæontologists regard as a real relationship. Unlike trilobites, however, their number of somites is fixed. They are rare as fossils, though found occasionally from the Devonian upwards: one species, *Archæoniscus brodiei*, occurs in enormous numbers in certain of the Lower and Middle Purbeck beds of the South of England.

The **Decapoda Macrura** (lobsters, etc.) occur in various formations from the Triassic upwards. Well-preserved specimens are abundant in the Lithographic stone of Solnhofen, Bavaria.

The **Decapoda Brachyura** (crabs) first appear in the Middle Jurassic. A species, *Palæocorystes stokesi*, abounds in one bed in the Gault and (as a derived fossil) in the Cambridge Greensand. Other forms occur in phosphatic nodules in the London Clay.

The **Eurypterida** had the body divided into head, mesosoma, and metasoma, each of six somites. The head-appendages all bear gnathobases, none taking the character of antennæ (a fundamental distinction between Arachnida and Crustacea); they increase in size backwards, the last being a very large pair of claws. There are no walking-limbs behind the head, the appendages of the mesosoma being broad and flat, and bearing book-like gills, while the metasoma has no appendages. Behind the eighteenth somite is a telson, which varies in character from an expanded swimming organ (*Pterygotus*) to a long and narrow rod (*Eurypterus*). In early Palæozoic times this order seems to have been confined to American seas, but towards the end of the Silurian period it spread over the European area, giving rise to some gigantic forms (*Pterygotus*, a nectic form, two metres long; *Stylonurus*, benthic, one metre). Some of the Devonian and later eurypterids became adapted to a freshwater habitat, the last of these being found in the Permian, after which the order was extinct.

The **Xiphosura** are close allies of the eurypterids, differing from them in the fusion of the somites of the meso- and meta-soma into one piece. They range from Cambrian to Recent, and are mainly marine, but in the later Palæozoic some freshwater forms existed. Some of the earlier genera have a close external resemblance to



trilobites, but this is largely the effect of adaptation to similar conditions of life.

The **Scorpiones** are direct descendants of the eurypterids, from which they differ only in the effects of adaptation to a land-life. They are known from the Silurian period, and the scorpions of to-day differ very little from those of that early time.

The **Araneæ** (spiders) are derived from scorpions by a shortening of the abdominal region. They are known from the Coal Measures, but are very rare as fossils until the Oligocene, where they occur in the amber (fossil resin) of the Baltic area.

The **Myriopoda** (millipedes and centipedes) are very rare as fossils, but occur as early as the Devonian.

The **Insecta** are abundant in occasional beds, of which the Coal Measures (particularly of Commeny in France) and the Oligocene amber are the most prolific, but otherwise very rare. The earliest is recorded from the Upper Ordovician, and if not misidentified is the only land-animal known from so early a period.

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## VI

### THE VERTEBRATA

THE Vertebrata are commonly accepted as the dominant phylum of the Animal Kingdom. That position might be disputed by the Arthropoda, for the latter are certainly more all-pervading and have insinuated themselves everywhere where life is found, even into many nooks and crannies which the Vertebrata have left alone. But it is to the credit of the Vertebrata that they have almost completely avoided the dirty corners of parasitism and degeneracy in which arthropods abound, and that their dominance is mainly a matter of power, of high organization, and finally of intelligence.

In the most primitive Vertebrata the chief hard parts are external, and though an internal skeleton is always present it was at first of organic material and rarely preserved fossil; subsequent evolution is marked in general by a steady increase in importance of the endoskeleton, which becomes a series of articulated bones hardened by calcium phosphate, and a diminution in that of the exoskeleton.

The first form taken by the exoskeleton is that still found in the sharks constituting the "shagreen": every point on this rasping surface marks a single "skin-

tooth" or *placoid scale*, the structure and development of which are essentially those of teeth (Fig. 64). Our teeth are in fact the greatly-modified survivors of what was once a general body-covering, retained on the jaws for special purposes when no longer needed on the skin.

### Water-breathing Vertebrata.

The first British Vertebrata are found near the top of the Silurian system, in the Ludlow "bone-bed." Here about the little skin-teeth of *Thelodus* (Fig. 63, a), which, as shown by a complete body (only a few inches long) found in Scotland, is a primitive member of a group, *Ostracodermi* (Fig. 62), the exact taxonomic position of which is doubtful, as it is not clear whether they possessed the biting jaws found in all other Vertebrata. In higher members of the same class, found also in the Silurian, but more abundantly in the Devonian (e.g., *Cephalaspis*) the skin-teeth became fused into large armour-plates, and (by adaptation to a similar life) many of them came to mimic closely the contemporary eurypterids. The microscopic structure of the armour is quite different in the two cases, and though much ingenuity has been wasted in trying to prove an arthropod ancestry for Vertebrata, we may feel confident that the resemblance is only a very striking case of convergence. The ostracoderms died out at the end of the Devonian.

The undoubted fishes, with typical vertebrate jaws, have an internal skeleton; but in the lower of the two grades into which fishes may be divided (*Chondrichthyes*),

this skeleton is composed of cartilage, and is therefore rarely preserved fossil. These are sharks and rays, known principally to fossil-collectors by their teeth (Fig. 63), and the bony "ichthyodorulites" which support the front margin of the fins in some cases. Ichthyodorulites (*Onchus*) accompany skin-teeth in the



FIG. 62.—LANARKIA SPINOSA, TRAQUAIR, DOWNTONIAN,  
LESMAHAGOW. ( $\times \frac{1}{2}$ .)  
(After Traquair.)

This differs from its contemporary, *Thelodus*, in having spiny skin-teeth. The head and trunk have been flattened down from above, but the tail is turned over on its side.

Ludlow bone-bed. Shark's teeth are common in some beds in most geological systems. They are usually sharp lacerating teeth, pointing inwards on the jaws, so as to prevent prey from slipping out; they are arranged in rows, new rows developing on the inside of the jaw throughout life, and moving forwards as the older teeth fall out. Thus loose teeth are commoner than

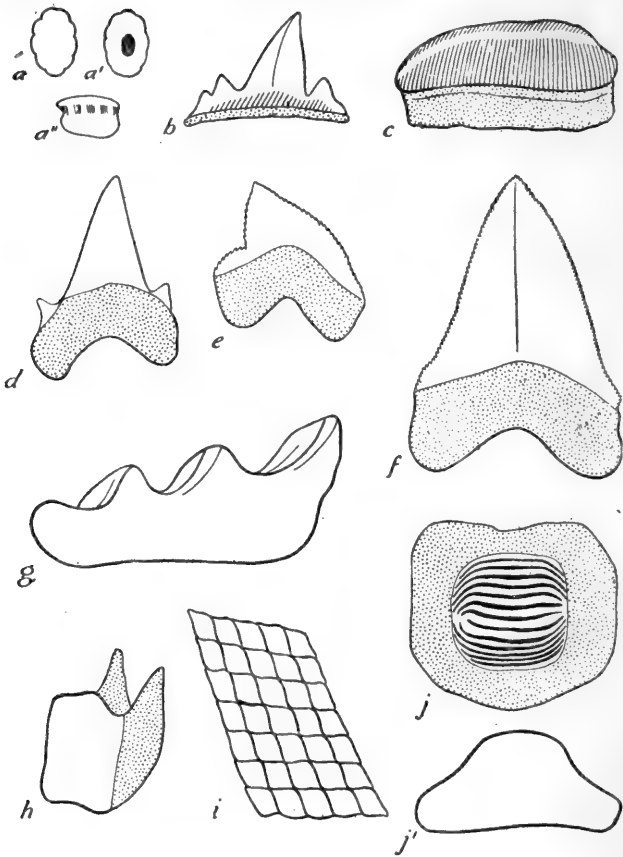


FIG. 63.—FISH TEETH AND SCALES.

*a-g, j, teeth; h, i, scales.* The dotted part in *b-f* is the root; in *h* it is the part overlapped by other scales. *a*, *Thelodus pagei* (Powrie), Devonian, skin-tooth from above; *a'*, from below, showing nutritive foramen; *a''*, from side. *b*, *Hybodus grossiconus* Agassiz, Bathonian. Tooth. (Natural size.) *c*, *Acrodus nobilis* Agassiz, Lower Jurassic. Tooth. (Natural size.) *d*, *Lamna appendiculata* Agassiz, Upper Cretaceous. Tooth. ( $\times \frac{3}{4}$ .) *e*, *Corax falcatus* Agassiz, Upper Cretaceous. Tooth. (Natural size.) *f*, *Carcharodon megalodon* Agassiz, Miocene-Pliocene. Tooth. ( $\times \frac{3}{8}$ .) *g*, *Ceratodus altus*

complete series, and it is difficult to know whether slight differences among isolated teeth are due to their belonging to different species of sharks or to different parts of the jaw of the same species.

Like other vertebrate teeth, those of the sharks consist of a *root*, buried in the soft tissues, and a *crown* which is exposed. Up to the Jurassic period, shark's teeth have shallow, undivided roots (Fig. 63, *b, c*); from the Cretaceous period onwards, forms with deep, divided roots occur (Fig. 63, *d, e, f*).

The tooth is mainly composed of *dentine*, a calcareous tissue full of fine tubules into which pass processes from the soft tissues of the central *pulp-cavity* (Fig. 64). The crown has its surface covered with a thin layer of *enamel*, a much denser material than the dentine. In the fossil state, teeth are usually highly phosphatized, and may acquire a black colour.

Sharks' teeth are among the most indestructible of fossils, and worn examples are common among derived fossils.

In one remarkable Palæozoic group (Cochliodontidæ and Edestidæ) the teeth of the middle line of the jaws do not fall out but curl in under the front of the jaw as the new teeth push them forward. In the latest

FIG. 63.—FISH TEETH AND SCALES (*continued*).

Agassiz, Rhætic. Tooth. ( $\times \frac{3}{2}$ .) *h*, *Acrolepis semigranulosus* Traquair, Lower Carboniferous. *A*, single ganoid scale,  $\times \frac{3}{2}$ , surface pattern omitted. *i*, *Lepidotus minor* Agassiz, Purbeck beds (Upper Jurassic). Part of scaly armour of trunk. ( $\times \frac{3}{2}$ .) *j*, *Ptychodus mammillaris* Agassiz, Upper Cretaceous. Tooth, surface view; *f'*, profile. ( $\times \frac{3}{2}$ .) The area shown dotted is part of the crown and should be shown with fine, more or less concentric lines. *a, h*, After Traquair; *b, c, f, g*, after Agassiz; *d, e, i, j*, after Smith Woodward.

member of this group (*Helicoprion*, Permo-Carboniferous) these old teeth are rolled up into a spiral of four or more whorls.

Some sharks and the rays, instead of swallowing their prey whole, grind it in their mouths: in these, the teeth have lost their sharp points and compressed shape, and form a mosaic with a rough surface, extending over the palate and part of the floor of the mouth as well as the jaws (Fig. 63, *j*).

No attempt can be made here to describe the details of the endoskeleton of Chondrichthyes, but a few words

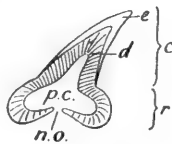


FIG. 64.—TOOTH STRUCTURE.  
(Diagrammatic vertical section.)

*d*, Dentine; *e*, enamel; *c*, crown; *p.c.*, pulp-cavity; *n.o.*, nutritive opening; *r*, root.

may be given to the general form of the body. This is elongated, tapering towards both ends, laterally compressed in the nectic (swimming) forms, depressed in the benthic (bottom-living) skates. Besides the two pairs of fins (answering to the limbs of land-vertebrates) there are a variable number of median fins, spaced out along the whole of the dorsal edge, but only on that part of the ventral edge that lies behind the paired fins. The end of the tail is bent up and combines with a median ventral fin to form the "heterocercal caudal fin," characteristic not only of all cartilaginous fishes and some



bony fishes, but also of such primitive forms as *Thelodus* (Figs. 62; 65, *a*).

The higher grade of fishes (*Osteichthyes*, bony fishes) have an endoskeleton of bone, but they retain an exoskeleton of scales of some sort. They vary greatly in shape from greatly compressed forms, whose height is nearly equal to their length, to long cylindrical eel-like forms. The latter appear to be the senile forms of a number of families, according to Dr. Smith Woodward; the former are, in part at least, highly specialized forms. Most fishes have a fusiform shape, lying between these two extremes.

Three divisions may conveniently be recognized among bony fishes.

1. The **Ganoidei**.—Though no longer admitted as a natural group by zoologists, this makes a serviceable category for palæontology.

The name refers to the possession of "ganoid" scales—*i.e.*, large thick enamel-covered scales which typically articulate together to form a coat of mail, though in some genera these scales are greatly reduced. The tail is typically heterocercal, but in some it acquires the superficial symmetry of the "homocercal" type (Fig. 65, *b*). Modern ganoids are confined to the Northern Hemisphere and to the fresh waters (except that the sturgeons migrate between river and sea). Fossil ganoids are found from the Devonian (Middle Old Red Sandstone) onwards, and in marine as well as in freshwater deposits. A familiar example is *Lepidotus* (Jur.-Cret.), of which the scales and teeth are common in the Wealden beds

(Fig. 63, *i*). The ganoids were divided by Huxley into *Crossopterygii* (fringe-finned), in which the paired fins have a central skeletal axis with a fringe of fin-rays, and *Actinopterygii*, in which the axis is wanting and the fin supported by rays only.

2. The **Teleostei**, or typical bony fishes, appear suddenly in the Upper Cretaceous. They are distinguished by their thin, overlapping scales from the typical ganoids, but some fishes reckoned as ganoids have similar scales. When preserved as fossils the skeleton is usually fairly



FIG. 65.—CAUDAL FINS.

- a*, Heterocercal fin of a shark, vertebral axis rising, second lobe of fin developed below it; *b*, homocercal fin of bony fish, vertebral axis as in *a*, but the whole fin externally symmetrical; *c*, fin of *Ichthyosaurus*, externally like *b*, but vertebral axis running into lower lobe.

complete, and the scales may also be preserved in position. Isolated vertebræ are sometimes found and are recognizable by their cylindrical bodies with very deep conical hollows at each end: this biconcave or "amphicœlous" type is, however, found also in the lower grades of nearly all branches of air-breathing Vertebrata. The neural arches which protect the spinal cord may remain attached to or be detached from the bodies; in the tail there is a similar hæmal arch below. It is impossible to give further details within the necessary limits of this chapter.

3. The **Dipnoi** are interesting as being the fishes in which there is a transition to the internal structure of air-breathing vertebrates: at least this is the case with existing survivors of the group, but many extinct forms are associated with them on account of their skeletal characters. The *Dipnoi* appear as early as the ganoids, and, like them, were both marine and freshwater, but the three surviving genera are confined to rivers and to the Southern Hemisphere (in curious contrast to the ganoids). The best-known of these modern genera is the Australian *Ceratodus* (Fig. 66, a), which has a pair of large ridged palatal teeth, formed by the fusion of many rows of small teeth. Similar palatal teeth (Fig. 63, g) were known as fossils in the Rhætic beds before the living *Ceratodus* was discovered; they occur in Triassic and (very rarely) in Jurassic strata, showing *Ceratodus* to have been marine at that time. It disappeared from the Northern Hemisphere like *Trigonia*, but somewhat earlier.

### Air-breathing Vertebrata.

These are usually divided into Amphibia, Reptiles, Birds, and Mammals, but palæontological discoveries have so extended the idea of a reptile that it is no longer logical to separate birds from that category, so that only three classes will be recognized here.

The **Amphibia** are distinguished by the fact that they retain signs of their aquatic ancestry by passing through a larval stage in which they have gills and (with a few

exceptions) live like fishes : the tadpole-stage of the frog is a familiar example. At the present day they are represented only by the primitive and somewhat degenerate newts and salamanders, the highly-specialized frogs and toads, and the equally specialized snake-like Cœcilians of the tropics. The two latter orders are unknown before the Eocene period ; the earliest newt is of Lower Cretaceous age ; and between them and the other fossil Amphibia there is at present a great gap in time, no certain remains of Amphibia being known from anywhere in the Triassic or Jurassic strata. In the Carboniferous and Permian systems there are found a series of Amphibia with complex bony skulls, which resemble those of some fishes on the one hand and those of reptiles on the other far more than those of modern newts and frogs. That they were really Amphibia is indicated by their retention of gill-arches in the throat, and by the fact that their ribs do not meet ventrally in a breast-bone, so that they must have breathed like a frog by swallowing air, not sucking it in. Unfortunately little is known of the limbs of these *Stegocephalia*, and we have no certain knowledge of the stages through which the fin of the fish, adapted to serve as a flexible oar, became transformed into a limb capable of performing the much more complex movements required by a land-living animal. The type of fin which is most easily comparable with the terrestrial limb is that of *Ceratodus*, found also in some of the Upper Palæozoic sharks (*Pleuracanthus*) and ganoids (*Holoptychius*). In this the fin is supported by a cartilaginous jointed axis, to which are articulated a series of

cartilaginous rays on both margins. If we compare this with the leg of a newt, which shows the simplest form of terrestrial limb, we see the essential changes in the latter are—(1) the lengthening of the axis; (2) the introduction in the second joint of a *pair* of elements, side by side, which makes possible a movement of rotation impossible in the fin; and (3) the great reduction in number of the rays and their separation to form five fingers or toes, capable of independent movement (Fig. 66, *a, b*).

The **Reptilia** of the present day consist of four or five small orders—the lizards and snakes, tortoises and crocodiles being the familiar forms. To these must be added, as representing a separate order, the New Zealand lizard *Hatteria*, sole survivor of an important Permian and Triassic series. The birds should also be counted as another order. These are the few scattered survivors of a series of forms so vast and varied that the Mesozoic era in which they flourished has been called the Age of Reptiles. They spread over the surface of the continents, hitherto almost devoid of animal life, and exhibited the same “radiative adaptation” to all possible methods of life that the Mammals showed afterwards in the Cainozoic era. There were herbivorous reptiles and carnivorous reptiles, aquatic, terrestrial, and aerial reptiles. We cannot here deal with the many instructive facts shown by the study of fossil reptiles, but must confine ourselves to the case of one order of reptiles, whose remains are fairly common in some of the Jurassic strata (Lias), the *Ichthyosauria*. These occupy the same position among Reptiles that the whales do among Mammals.

They underwent complete adaptation to a marine life, and approximated to fishes in shape and general structure, but in accordance with the law of irreversibility in evolution they could not lay aside all the characters they had gained during their ancestral land-life, nor could they recover certain fish-structures which their land ancestors had lost—the gills in particular. If we compare the limbs (or paddles) of an ichthyosaurus with the fin of *Ceratodus* on the one hand and the limb of the salamander

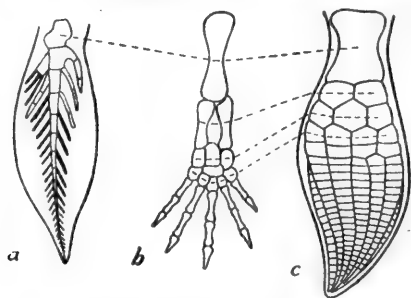


FIG. 66.—FINS AND LIMBS.

*a*, *Ceratodus*; *b*, a newt; *c*, *Ichthyosaurus*. The dotted lines connect homologous structures.

on the other, we see that while in outline, absence of separate fingers, and slight possibility of movement between the numerous small, closely-packed bones it agrees with the fish, its fundamental structure is that of a land-animal (Fig. 66, *c*). So, too, with the tail-fin: externally it resembles the homocercal tail of a bony fish, but the end of the vertebral column bends down into the lower lobe (Fig. 65, *c*). In these and other ways ichthyosaurs show *convergence* towards fishes, but the resemblances are not exact and are mainly external.

The vertebræ of *Ichthyosaurus* are common in Jurassic Clays, and easily recognized by their extreme shortness—the length of a vertebral body being only about one quarter its height or breadth; they are biconcave, and the arches are loose.

Another Mesozoic order of marine reptiles is the Sauropterygia (e.g., *Plesiosaurus*) distinguished by a long neck and small head (in contrast to the large head and very short neck of ichthyosaurs), by the vertebræ being about as long as high, with very shallow concavities at the ends, and the limbs rather less modified from the land-type. The earliest crocodiles were also marine, but the *Chelonia* (turtles) had their most striking features developed before they took to the sea.

Along two distinct lines Mesozoic reptiles adapted themselves to flight. The pterosaurs had a membranous wing, for the support of which the fifth finger was enormously lengthened, the leg and tail also helping to keep it stretched. They lived through the Jurassic and Cretaceous periods. In the birds, on the other hand, there are only a short thumb and two fingers, the latter combining to support the wing but not being greatly lengthened. (In flying Mammals—bats—yet another type of membranous wing is developed, all four fingers being lengthened to support the wing, like the ribs of an umbrella). The earliest bird (*Archæopteryx*) was found in the lithographic stone of Solnhofen, high in the Jurassic. The few known Mesozoic birds all have teeth, and *Archæopteryx* alone of all birds has a long, many-jointed tail.

The **Mammalia** are represented in a few Mesozoic rocks by lower jaws and teeth of very small forms, which appear to belong to primitive representatives of the two orders now confined to Australasia, and there represented by greatly specialized forms—the egg-laying *Monotremata* and the pouched *Marsupialia*. Why no other remains should be found than lower jaws has never been satisfactorily explained. While the Reptiles dominated the world, the Mammals seem to have been a very lowly and insignificant group, but on the extinction of most of the former at the end of the Cretaceous period the Mammals became the dominant land-animals.

The early Eocene mammals are all of small size, with the neck not flexible and the trunk passing gradually into the tail. Their limbs are not greatly removed in structure from the primitive five-toed (*pentadactyle*) type, except for the presence of a projecting elbow in the fore-limb and heel in the hind-limb: the two bones in the second limb-segment are free to move on one another so that the limbs can be rotated. There are forty-four teeth in all, in continuous series, with low crowns (*brachydont*) and a simple arrangement of conical tubercles on the surface. The brain (as shown by internal casts of the skull) is small like that of a reptile.

From these primitive forms higher forms are soon developed in a series of adaptative radiations, like those shown by the Mesozoic reptiles. All the orders of Mammalia are thus separated in the course of the Eocene period. Except for the Insectivora and Rodentia, which remain small, they all show a gradual increase in



size, the largest forms being chiefly found in the Pliocene period, after which glacial conditions exterminated the majority of them. The brain also increased greatly, and limbs and teeth underwent various specializations in accordance with the food and habitat.

The most interesting developments are perhaps shown by the Ungulata (hoofed mammals). In these the teeth become high-crowned (*hypsodont*) to stand long wear, and develop varying patterns which as they wear down show a surface partly of hard enamel, and partly of soft dentine, and therefore never wearing smooth. The limbs become longer and vertical in position, lifting the body high off the ground, while at the same time they lost the power of rotation (useless to a running animal) by the fusion of the two bones in the second limb-segment. In one branch of the Ungulata (Perissodactyla, odd-toed) the middle digit bears the weight of the body, and the others gradually shorten and finally are nearly lost in the modern horse (*Equus*), the ancestry of which has been very fully worked out. In another branch (Artiodactyla, even-toed) the weight is borne by the third and fourth digits (the "cloven" hoof), the first disappearing, as may also the second and fifth: these include the cattle, deer, and camels. In the Proboscidea, again, while the teeth undergo enormous specialization, the limbs remain comparatively primitive, all five digits persisting, and fusion of the bones of the second segment taking place in the fore-limb only. Until recently the Proboscidea were a cryptogenetic group, appearing suddenly in Europe in the Miocene period, but their earlier ancestors have

since been discovered in Eocene and Oligocene strata in Africa.

An outline classification of Vertebrata is appended which attempts to combine and harmonize those of Prof. Goodrich and Dr. Smith Woodward. Brief notes are added on some of the orders which have not been already mentioned.

### Classification of Vertebrata.

CLASS: **CYCLOSTOMATA** (without jaws: the lampreys).

Only one fossil form known: *Palæospondylus*, Devonian. (Some authorities associate the Ostracodermi with this class, instead of with the true fishes.)

CLASS: **PISCES**.

SUB-CLASS 1. **Ostracodermi** (armour-plated fishes), Sil.-Dev.

SUB-CLASS 2. **Chondrichthyes** (cartilaginous fishes).

ORDER 1. **ELASMOBRANCHII** (sharks and skates), Dev.-Rec.

2. **PLEUROPTERYGII** OR **CLADOSELACHII** (sharks with extremely primitive fins), Dev.-Carb.

3. **PLEURACANTHODII** OR **ICTHYOTOMI** (early sharks with continuous median fins and paired fins of *Ceratodus* type), Dev.-Perm.

4. **ACANTHODII** (sharks with very strong spines—ichthyodorulites—in the front of each fin), Sil.-Perm.

SUB-CLASS 3. **Osteichthyes** (bony fishes).

ORDER 1. **DIPNOI** (lung fishes), Dev.-Rec.

2. **ARTHRODIRA** (armoured fishes, e.g., *Coccosteus*), Dev.-Carb.

3. **TELEOSTOMI** (ganoids and teleosts), Dev.-Rec.

## CLASS: AMPHIBIA.

ORDER I. STEGOCEPHALIA (with armoured skulls), Carb.-Perm.

2. URODELA (newts), Lower Cret.-Rec.
3. GYMNOPIHONA OR CÆCILIA (snake-like), Recent only.
4. ANURA (frogs), Eoc.-Rec.

## CLASS: REPTILIA.

ORDER I. ANOMODONTIA OR THEROMORPHA (related to Stegocephalia on the one hand and Mammalia on the other). The dominant land-animals of the Permian period, especially in the Southern Hemisphere. Perm-Trias.

2. CHELONIA (tortoises and turtles), Trias.-Rec.
3. ICHTHYOPTERYGIA (ichthyosaurs), Trias.-Cret.
4. SAUROPTERYGIA (plesiosaurs, swimming reptiles, less fish-like in aspect than the ichthyosaurs), Trias.-Rec.
5. RHYNCHOCEPHALIA (lizard-like, with biconcave vertebræ, two rows of teeth in upper jaw, between which the single row of lower jaw bites, all teeth fused to the bones: the sole modern survivor, *Hatteria*, is confined to a few of the smaller islands of New Zealand), Perm.-Rec.
6. SQUAMATA (lizards and snakes), Upper Jur.-Rec.
7. DINOSAURIA (the dominant land-animals of the Mesozoic after the anomodonts had decayed; a very varied series, showing considerable adaptative radiation; some, as *Diplodocus* and *Iguanodon*, attained a great size; related to crocodiles and birds), Trias.-Cret.
8. CROCODILIA (crocodiles; the earlier forms were marine), Trias.-Rec.
9. AVES (birds), Upper Jur.-Rec.
10. ORNITHOSAURIA (pterodactyls), Jur.-Cret.

CLASS: **MAMMALIA**.

SUB-CLASS: **Prototheria** (egg-laying mammals).

ORDER I. **MULTITUBERCULATA** (known only by lower jaws and teeth), Trias.—Eocene.

2. **MONOTREMATA** (the egg-laying mammals of Australia), Plio.—Rec.

SUB-CLASS: **Metatheria** (pouched mammals).

ORDER. **MARSUPIALIA** (now confined to Australasia and South America), Jur.—Rec.

SUB-CLASS. **Eutheria** (placental mammals).

SUPER-ORDER I. **UNGUICULATA** (clawed mammals, including the most primitive Eutheria, Insectivores and Rodents, the Carnivora, and the two highly specialized orders, the Edentates and the Bats), Eoc.—Rec.

2. **UNGULATA** (hoofed mammals, divided by Osborn according to their geographical origin—Artiodactyla, Perissodactyla, and several extinct orders being Holarctic,\* Proboscidea, Hyracoidea, Sirenia [sea-cows], and some extinct orders African, while a number of extinct orders are South American).

3. **PRIMATES** (lemurs, monkeys, and man), Eoc.—Rec.

4. **CETACEA** (whales and dolphins, derived from primitive carnivores), Eoc.—Rec.

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\* The Holarctic Region includes the Old World north of the Himalayas and the great deserts, and North America.

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## VII

### THE ECHINODERMATA

WHEN a piece of limestone is broken with a hammer it usually shows a smooth or granular fracture, but here and there on the broken surface may often be seen distinct cleavage-surfaces of calcite: these may be few or many, and in particular cases may attain a large size. They are the fractured surfaces of fossil echinoderms. Whereas the shells of most invertebrates show on a broken surface a fibrous or laminated texture, due to the arrangement of an indefinite number of minute crystals of calcite, it is one of the essential features of echinoderms (and of no other group except the calcareous sponges) that the skeleton is composed of a series of units that may attain a large size, but of which every one is, mineralogically, a crystal of calcite—not in external shape (which is determined by organic secretion), but in molecular constitution. These units have different names, according to shape: the commonest are broad, flat structures, called *plates*. In these the normal to the surface corresponds to the vertical crystallographic axis. When the shape is long and cylindrical, as in the radioles (articulated spines) of sea-urchins, it is the long axis which is the vertical crystal-axis.

Solid crystalline calcite would be much too heavy a material for an organic skeleton. Accordingly, in the living state the plates are lightened by rounded cavities, arranged so closely as to make the whole substance spongy, and in a very definite organic pattern. This network of calcite is called the *stereom*. When the skeleton of a recent echinoderm—say, the radiole of a sea-urchin—is broken, the calcite cleavage is interrupted by these abundant cavities, and is easily overlooked, though careful observation will always show it. But the first process in fossilization is always the filling-in of these cavities with calcite in crystalline continuity with that around them. The pattern of the cavities may or may not be obliterated in the process; when not, it forms a further means of recognition (besides the crystalline character and cleavage) of echinoderm skeletons in microscopic sections of rocks. Calcite in crystalline continuity may also be deposited around the plates (or other units), if there is opportunity, concealing the organic form and replacing it, as far as circumstances permit, by the geometrical form of a crystal. Thus, on breaking open one of the sea-urchins so common in the Upper Chalk, one occasionally finds that each plate projects into the central cavity as a rhombohedron; externally the contact of the chalk has prevented such growth, and if the interior has been filled with chalk (the more usual case) the plates will preserve their original surface internally also.

There is another very general, but not universal, feature characteristic of echinoderms—a five-rayed or

pentamerous symmetry. Such a symmetry is common among flowers, but is quite unknown among animals except in the echinoderms. There is one other animal phylum with a radial symmetry—the Cœlenterata—and in Cuvier's classification, now a century old, the two were united as Radiata. But not only is the symmetry of the Cœlenterata a four-, six-, or eight-rayed symmetry, but it is in general a more perfect symmetry than that of echinoderms. The former include some forms, such as the jelly-fish, which are absolutely radial throughout their bodies; the latter include none such, though some attain almost perfect radially in their skeleton only. In some, again, radial symmetry has not yet been attained; in others it has been modified into a practically bilateral symmetry.

The skeleton of echinoderms is not truly external like that of Brachiopods or most Mollusca; there are soft living tissues outside it, but these are so thin in most cases that it may be roughly spoken of as external. Still, it is important to remember these external tissues in order to form an idea of the life of echinoderms.

The Echinodermata fall into two main divisions—Pelmatozoa or fixed forms, and Eleutherozoa or freely-moving forms. To be precise, the former are fixed at some time in their life (and usually throughout adult life), the latter never. The former were abundant in the Palæozoic era, rare afterwards; with the latter the reverse is the case. They are further divided into classes, thus:



**PELMATOZOA.**

**Cystidea.**—Extinct, Cambrian to Permian, but mainly Lower Palæozoic.

**Blastoidea.**—Extinct, Silurian to Permian, but mainly Upper Palæozoic.

**Edrioasteroidea.**—Extinct, Ordovician to Carboniferous.

**Crinoidea.**—“Sea-lilies,” Ordovician to Recent.

**ELEUTHEROZOA.**

**Echinoidea.**—“Sea-urchins,” Ordovician to Recent.

**Stelleroidea.**—“Star-fish,” Cambrian to Recent.

**Holothuroidea.**—“Sea-cucumbers,” Cambrian to Recent.

All echinoderms are marine.

It will be convenient to describe first some examples of crinoids.

1. **Cupressocrinus gracilis** (Fig. 67) is one of many crinoids found in the Middle Devonian “crinoid-bed” of Gerolstein in the Eifel (Rhenish Prussia). It consists of a *root*, *stem*, and *crown*. By the first (not often preserved) it was fixed to the sea-bottom, but this “root” had no absorbent function like the root of a plant. The stem lifted it up high above the mud: as preserved fossil it consists of a large number of squarish discs piled up into a column: these are the stem-ossicles or *columnals*. Through each of them runs a central vertical tube (axial canal) and four smaller peripheral canals. Adjacent columnals were united, in life, by organic tissues, and the surfaces of contact were roughened to give greater grip or “key”: on the articular surface of an isolated ossicle

this gives, with the canals, a pattern which is fairly characteristic of the genus *Cupressocrinus*. During life the slight amount of flexibility of the organic tissue of each joint gave a suitable degree of flexibility to the whole stem.

The *crown* contained the essential vital parts of the animal. It is divided into the *theca* or *calyx*, which is the "body" of the animal and directly articulated to the stem, and five *arms* which, when the animal was feeding were spread out widely, but in the fossil are usually found tightly closed up. The part of the calyx which is visible when the arms are closed is called the *dorsal cup*; it is the ventral surface which is hidden. The dorsal cup consists of two circlets of five plates each and a single pentagonal plate next to the stem. This last is regarded (by analogy with other crinoids) as a fused third circlet, the five plates of which if separate would be called *infrabasals*; the five plates in the circlet next to it are called *basals*; those in the upper circlet, *radials*. The straight lines along which adjacent plates meet are termed *sutures*. Radials and basals alternate in position, and if the infrabasals were separate they would alternate with the basals. Because of the presence of (fused) infrabasals as well as basals, this crinoid is said to be *dicyclic*. In many crinoids the top columnal directly joins the basals: they are *monocyclic*.

The five radii which can be drawn from the centre of the calyx through the middle of each radial plate are called *perradii*, and organs such as the arms which lie symmetrically upon them are said to be *perradial* in posi-

tion. The radii half-way between these are called *interradii*, and organs which lie upon them are said to be *interradial* (e.g., the basal plates). These alternating positions are of fundamental importance in all echinoderms, except the lowest forms in which five-rayed

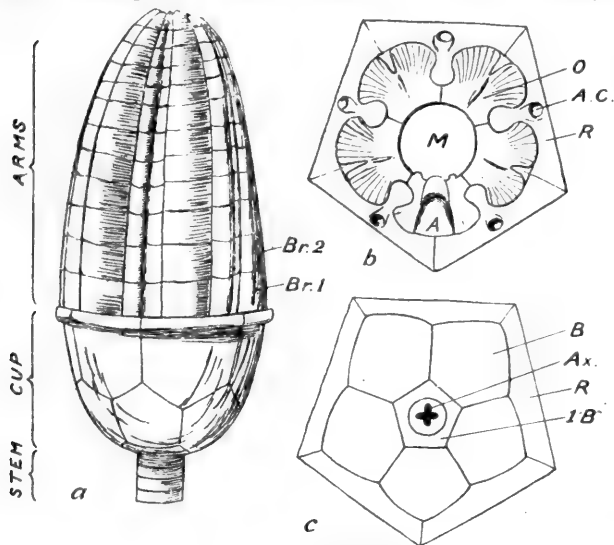


FIG. 67.—CUPRESSOCRINUS.

*a*, *C. gracilis* Goldfuss; *b*, *c*, *C. abbreviatus* Goldfuss; both Middle Devonian, Eifel. *a*, Side view of complete crown, with arms closed, and part of stem; *b*, oral view; *c*, basal view of a cup without arms or stem. (All natural size.) (Original.) *A*, Anus; *A.C.*, axial canal; *Ax.*, axial canal of stem; *B*, basal plate; *Br. 1, 2*, first and second brachial plates; *IB*, infra-basal plate; *M*, mouth; *O*, oral plate; *R.*, radial plate.

symmetry is not fully developed. It is a universal rule that the mouth and anus, unless they are central, are respectively perradial and interradial in position. With the mouth, however, the central position is the rule, with the anus it is the exception.

In the case of *Cupressocrinus* the mouth is central and appears as a large circular opening between five large plates, interradian in position. Probably the actual mouth was smaller, and other smaller plates surrounded it. The five large plates are called *orals* or *deltoids*: one of them differs from the rest in being deeply notched by the anus. This is the only disturbance of radial symmetry in the crown of *Cupressocrinus*, and it marks out the odd radial as *posterior* in position; the two adjacent to it as postero-lateral and the other two as antero-lateral. The margins of the orals that are in contact with their neighbours bear semi-oval notches, which combine into five pear-shaped perforations corresponding to the middle line of each arm. Along these were continued the five food-grooves that occupy the middle ventral line of the arms. As the edges of the five orals meet around the mouth the food-grooves must have finally entered the mouth by tunnels, and the pear-shaped openings themselves may have been converted into tunnels by small overlapping covering-plates (*ambulacrals*).

Each arm consists externally (dorsally) of a single row of large *brachial* plates, tapering to the free end. Internally (ventrally) they have a wide and deep groove, with a row of *pinnules* (like miniature arms) along each side, and a series of small plates (*ambulacrals*) arching over it and converting it into a tunnel. This groove, in life, was ciliated and constituted the *food-groove* or *ambulacrum*, along which microscopic food was wafted towards the mouth. The pinnules were similarly grooved and ciliated, and served as tributaries. Thus the method

of feeding (*microphagous*) is fundamentally the same as in brachiopods and lamellibranchs, but the structures adapted to the same ends are fundamentally different.

Not to be confused with the food-grooves are longitudinal cavities, elliptical in section, in the substance of the brachial and radial plates: these are the *axial canals* and contained a nerve-cord.

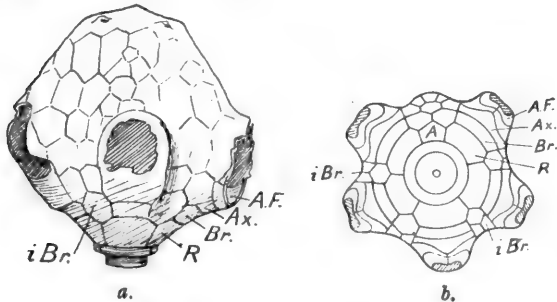


FIG. 68.—AMPHORACRINUS ATLAS (M'COY), VISEAN (CARBONIFEROUS LIMESTONE), YORKSHIRE.

*a*, Side view; *b*, base. (Natural size.) (Original.) *A*, Anal plate intercalated between radials; *A.F.*, facet to which arm is articulated; *Ax.*, axillary plate (primaxil); *Br.*, brachial plate (primibrach); *i Br.*, interbrachial plate (inter-primibrach); *R*, radial plate.

2. **Amphoracrinus atlas** (Fig. 68) is a not uncommon fossil in the Carboniferous Limestone knolls of Clitheroe and elsewhere in the North of England. Usually the calyx is found without arms or stem. The columnals are abundant, though not with certainty distinguishable from those of allied forms. Their articular surfaces show fine radiating lines and a pentagonal axial canal.

There are no infrabasals (monocyclic) and the basals are reduced to three by crowding, leading to fusion. The

radials are five in number, but when we have identified the basals and these we still have a great many plates in the dorsal cup unaccounted for. Nevertheless, we cannot have mistaken the radials, because there are plates directly above them which lead up to the arms, and that could never be the case with basals. These plates above correspond with the lower brachials of *Cupressocrinus*, but instead of forming part of free arms they are incorporated in the dorsal cup: they are called *fixed* brachials. But holding them fixed are other plates, interradial in position, arranged in bifurcating series: these are called *interbrachials*. The largest of them disturbs the five-rayed symmetry by pushing itself between the radials and meeting two of the basals: it is called the *anal*, not because it carries the anus, but because it forms the base of the interray, high up in which lies the anus.

The ventral surface, instead of being flat and of few plates, as in *Cupressocrinus*, is a lofty dome of many plates, solidly articulated together. Crinoids with this feature are confined to the Palæozoic, and are known as *Camerata*. This arrangement closes in the mouth completely and shuts it off from all possibility of the excrement from the anus fouling the food. As an additional precaution, the anus is lifted up from the level of the tegmen by a short *anal tube*.

The arms branch into two immediately they become free from the dorsal cup, and again branch repeatedly.

3. **Marsupites testudinarius** (Fig. 69) is a crinoid characteristic of a definite zone high up in the White

Chalk. It is one of the few crinoids that were not fixed in the adult stage. By analogy with the modern free crinoid *Antedon* we may infer that it was stalked in a larval stage, but of this there is no actual evidence. The top columnal, however, is apparently retained as a large pentagonal plate in the centre of the dorsal cup. Around and above this are five large pentagonal infrabasals, then

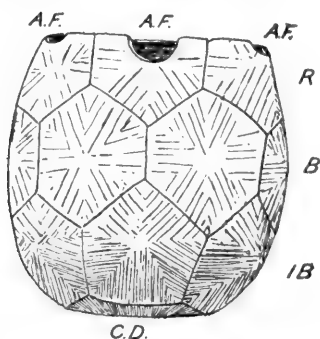


FIG. 69.—*MARSUPIITES TESTUDINARIUS* (SCHLOTHEIM), CAMPANIAN (UPPER CHALK).

(Cup without arms, natural size.) (Original.)

*A.F.*, Arm-facets; *B*, basal plates; *C.D.*, centro-dorsal plate; *IB*, infra-basals; *R*, radials.

five large hexagonal basals, and five large pentagonal radials, with facets for the arms. So far as the dorsal cup goes there is perfect five-rayed symmetry, and the dicyclic condition is shown very simply and clearly.

The arms branch repeatedly. The ventral surface is never preserved, but we may assume that, as in other post-Palæozoic crinoids, it consisted of many small plates forming a flexible surface, on which lay open food-

grooves, converging to an exposed mouth. An inter-radial anus would be the only disturbance of symmetry.

Isolated plates of *Marsupites* can easily be recognized by their curious ornament of ridges arranged in sets at right angles to the sutures. An almost identical pattern is found, however, in the Silurian *Crotalocrinus*.

There is much difference of opinion as to the classification of crinoids. Dr. Bather, of the British Museum, regards the distinction between monocyclic and dicyclic forms as fundamental, whilst most other authors treat it as of merely family value. However sound this distinction may be on morphological grounds, it has the practical difficulty that many dicyclic crinoids are "pseudo-monocyclic," so that the ordinary student does not recognize their dicyclic character.

In both monocyclic and dicyclic forms certain definite grades of structural complexity are found, which are taken as a basis for division into orders: (1) Inadunata, in which there is no incorporation of fixed brachials in the dorsal cup; (2) Camerata, with the tegmen in the form of a rigid vault covering the mouth and food-grooves (Palæozoic only); (3) Flexibilia or Articulata, in which the tegmen is composed of small plates loosely articulated, and the mouth and food-grooves exposed (almost exclusively Mesozoic and later). But authorities differ considerably as to the limits of these orders.

Among the simplest Inadunata (*Larviformia* of Wachsmuth and Springer) is the dicyclic *Cupressocrinus*, already described. *Pisocrinus* (Fig. 71, a, Sil.) is a monocyclic of equally simple structure, but much smaller sized cup, though the very slender arms attain as great a length as those of *Cupressocrinus*; the cup-plates have their symmetry disturbed by the subdivision of the right posterior radial obliquely into two plates (*r.p.* and *R'*)—a common



feature in many inadunates. *Herpetocrinus* (Sil.) is found with the stem spirally coiled, concealing the crown, but it could straighten itself when such protection was not necessary.

*Platycrinus* (Fig. 71, b, Carb.) is a monocyclic, transi-

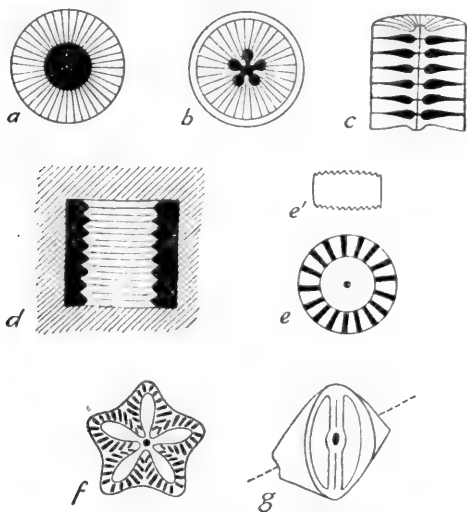


FIG. 70.—CRINOID COLUMNALS.

*a, b, e, f, g*, Views of articular surfaces; *c*, vertical section of part of stem; *d*, internal cast in place in rock-matrix; *e'*, side view. The thick black in *a-d* represents cavities. (All about natural size.) (After Goldfuss.) *a*, *Actinocrinus granulatus* Goldfuss, Devonian. *b*, *Cyathocrinus rugosus* Mill. r., Devonian. *c, d*, *Cyathocrinus pinnatus* Goldfuss, Devonian. *e, e'*, *Encrinurus moniliformis* Miller, Triassic. *f*, *Isocrinus basaltiformis* (Miller), Jurassic. *g*, *Bourgueticrinus ellipticus* (Miller), Upper Cretaceous (Upper Chalk). Dotted line=long axis of articular surface below.

tional from Inadunata to Camerata. The basals are reduced to three by fusion; the symmetry is almost perfect, there being only a slight difference between the anal interray and the others; the arms branch repeatedly, and have a large crescentic articulation on the radials. The

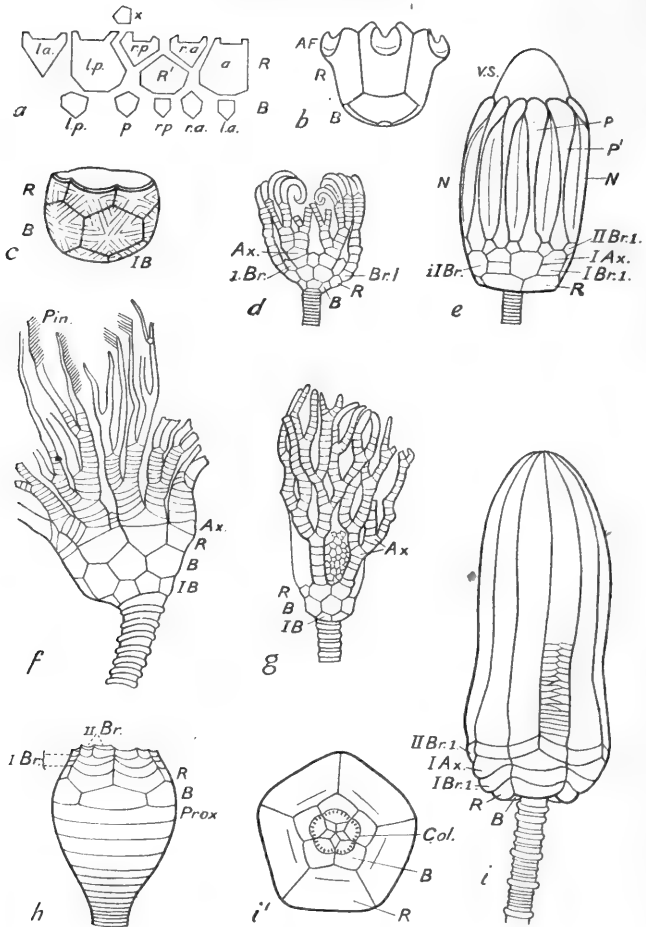


FIG. 71.—CRINOIDEA.

*IB*, Infrabasals; *B*, basals; *R*, radials; *Ax*, axillary. *a*, *Pisocrinus*, dissected. (After Bather.) *a*, Anterior; *p*, posterior; *l*, left; *r*, right; *R'*, radial; *x*, anal. *b*, *Platycrinus levis* Miller, Lower Carboniferous. Cup only. (After de Koninck.) *A.F.*, Arm-facet. *c*, *Crotaocrinus rugosus* (Miller), Silurian (Wenlock Limestone). Cup only.

columnals have elliptical surfaces, but the long axis of the ellipse on the lower surface is at an angle to that on the upper surface. Thus the axis of bending of successive joints gradually changes, enabling the stem as a whole to move in any direction in spite of the shape of the columnals. This arrangement gives the stem a curious twisted appearance. Good specimens are found in the Carboniferous Limestone of England and Ireland.

*Marsipocrinus* (Sil.) differs in the very rapid branching of each arm into four, the parts below the separation being united by single interbrachial plates, so that much more of the brachials are incorporated in the cup.

*Crotalocrinus* (Fig. 71, c, Sil.) is a dicyclic inadunate in which the arms branch with great suddenness, and all the branches of one ray are united into a sort of membrane, which was spread out horizontally when the crinoid was feeding at ease and rolled up spirally on an alarm. The stem is as broad as the crown, is composed of very wide and thin columnals, and has a very rough surface.

*Cyathocrinus* (Fig. 71, g, Ord.-Carb.) and *Gissocrinus* (Sil.) are dicyclic inadunates with very simple cup, one anal only intercalated, and much-branched arms. In the former genus the arms branch in a rather lax and irregular manner, and the anal tube is often very long; in the

FIG. 71.—CRINOIDEA (continued).

(After Murchison; restored.) *d*, *Taxocrinus tuberculatus* (Miller), Silurian (Wenlock Limestone). (After Murchison.) *Br. 1*, First brachial; *i Br.*, interbrachial. *e*, *Eucalyptocrinus decorus* (Phillips), Silurian (Wenlock Limestone). (After Murchison; restored.) *I Br. 1*, First primibrach; *I Ax.*, primaxil; *II Br. 1*, first secundibrach; *i I Br.*, inter-primibrach; *N*, niche; *V.S.*, visceral sac. *f*, *Woodocrinus expansus* de Koninck (Carboniferous Limestone), Yorkshire. (After Roberts.) *Pin.*, pinnules. *g*, *Cyathocrinus acinotubus* Angelin, Silurian (Wenlock Limestone). (After Bather.) *h*, *Apiocrinus parkinsoni* Schlothheim, Bathonian (Bradford Clay). Cup and part of stem, and of arms. (After Goldfuss.) *Prox.*, proximal columnal; *I Br.*, primibrachs; *II Br.*, secundibrachs. *i*, *Encrinus moniliformis* Miller, Ladinic (Muschelkalk). Brachials shown on lower part of one arm only. (After Goldfuss.) *i'*, base; *Col.*, proximal columnals; *II Br. 1*, first secundibrach. (After Goldfuss.) (All  $\times \frac{1}{2}$ , except *a*.)

latter the arm-branches are closely packed together, the anal tube is compressed and its plates are wider than high.

*Petalocrinus* (Sil., marking a definite zone) has the branches of each arm united into a fan-like body.

*Woodocrinus* (Fig. 71, *f*), of which beautiful examples are found in the Carboniferous Limestone of the North of England, is a dicyclic inadunate with four-branched short arms and a relatively short stem tapering to a point.

Among Camerata, *Amphoracrinus* has been described. *Actinocrinus* is similar, but with the superficial area of the tegmen not larger than that of the cup, and a longer and central anal tube. A very remarkable genus is *Eucaelyptocrinus* (Fig. 71, *e*, Sil.-Dev.), with the base deeply concave, the visible part of the cup being mainly composed of brachials and interbrachials: the arms bifurcate within the cup, and from the ten sets of interbrachials there grow up vertical pillars which arch out and meet at their upper ends, forming ten niches in which the arms lie when not spread out. There are a few dicyclic camerates, of which *Rhipidocrinus* (Dev.) and *Rhodocrinus* (Carb.) may be mentioned.

The few Palæozoic Flexibilia are dicyclic and impinnate (*i.e.*, arms have no pinnules): *Taxocrinus* (Fig. 71, *d*, Sil.-Carb.) is the commonest. The best-known Triassic crinoid is *Encrinus* (Figs. 70, *e*; 71, *i*), which seems to be related to Carboniferous inadunates such as *Woodocrinus*. It is dicyclic, but the infrabasals are minute and difficult to find.

*Isocrinus* (Fig. 70, *f*, Trias.-Rec.) and *Pentacrinus* (Jur.) not only have minute infrabasals, but the basals are very small, and the radials intervene between them and come into contact with the stem, so that the whole cup, lying between a large stem and large, much-branched and pinnulate arms, is reduced to insignificance. The stem

is five-sided, and the columnals show a very striking pattern. *Apiocrinus* (Fig. 71, *h*, Jur.) has a cylindrical stem, which expands at its upper end, so that its outline passes imperceptibly into that of the crown; the infra-basals are not recognizable (pseudo-monocyclic or cryptodicyclic), the arms branch into two very quickly, and their lower part is incorporated in the cup. Beautiful specimens have been found, and fragments are common, in the Bradford Clay of Bradford-on-Avon. In *Bourgueticrinus* (Fig. 70, *g*, Cret.) most of the columnals have the same peculiarity as in *Platycrinus* (*ante*, p. 251), but are longer and more barrel-shaped; towards the crown they are round and the proximal one is as wide as the cup, which shows five basals and five radials: the arms are rarely preserved. *Antedon* or *Comatula* (Jur.—Rec.) is fixed by a stem in its earliest youth, but afterwards becomes free-swimming. Another free-swimming form is *Saccocoma*, in which the radials form nearly the whole cup; the arms are bifurcated and the ten branches often spirally coiled, the brachials bearing wing-like expansions. This is abundant in the Upper Jurassic lithographic stone of Solnhofen, Bavaria, and pyritized plates are found at the same horizon in the English Kimmeridge Clay, recognizable by the coarse meshwork of stereom.

The **Cystidea** are a somewhat heterogeneous group, consisting of the most primitive forms, in which gradual development of five-rayed symmetry can to some extent be traced.

**Echinosphæra aurantium** (Fig. 72) is very abundant in the Cystid Limestone of the Ordovician of Sweden, erratics of which, carried by ice, are common on the plains of North Germany. It is an almost spherical

body, a slight projection at one point forming a rudimentary stem, while almost opposite it is the slightly-raised rim of a circular opening, presumably the mouth. About one-third the distance from the mouth to the stem is a third projection—a low pyramid of five triangular plates, the *anal pyramid*. Between this and the mouth, but nearer the latter, is a very small round opening, interpreted as a *hydropore*, that is an opening by which water is taken into the system of water-vessels.

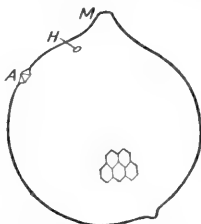


FIG. 72.—ECHINOSPHERA AURANTIUM, GYLLENHALL, ORDOVICIAN, SWEDEN.

(Natural size. Original.) (Only a few of the plates are indicated.)

*A*, Anal pyramid; *H*, hydropore; *M*, mouth.

The spherical theca is made up of a very large number of polygonal (mostly hexagonal) *thecal plates*, which when closely examined show a pattern somewhat resembling that on the infrabasals of *Marsupites*, though due, not as in that to external ornament, but to the internal structure of the plates. The stereom of each plate is thrown into folds perpendicular to the adjacent suture, so that the whole surface appears divided up into a series of rhombs, each belonging half to one plate and half to another, the folds in each rhomb forming a parallel series. The

cystids showing this structure form an order Rhombifera.

In specimens much better preserved than usual small

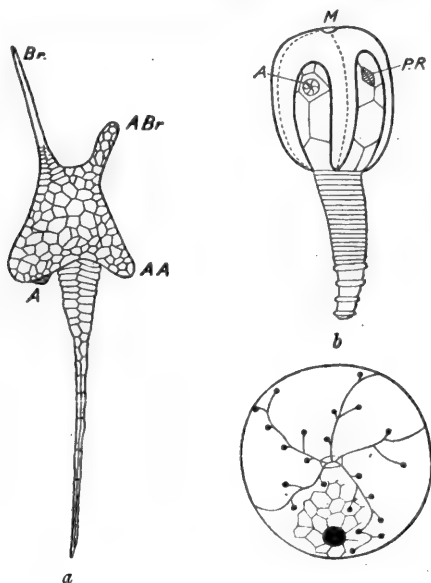


FIG. 73.—CYSTOIDEA.

*a*, *Dendrocystis scotica* Bather, Ordovician, Girvan. ( $\times \frac{1}{2}$ .) Details of plates omitted from brachiole. (After Bather.) *b*, *Lepadocrinus quadri-fasciatus* (Pearce), Silurian (Wenlock Limestone). Slightly enlarged; details of plates on arms omitted. (After Forbes.) *c*, *Glyptosphara leuchtenbergi* Volborth, Ordovician, Pulkowa (Russia). ( $\times \frac{1}{2}$ .) Mouth in centre, with five radiating grooves, irregularly branched, each branch ending in articulation of a brachiole (represented by black spots: where plate-sutures are shown, each of these is seen to be in the centre of a plate). Anus below, black (plates of pyramid missing). Thecal plates only shown around anus. (After Jaekel.) *A*, Anal pyramid; *AA*, anti-anal process; *ABr*, anti-brachial process; *Br.*, brachiole; *M*, mouth; *P.R.*, pectinirhomb.

arms have been found arising from the mouth, composed of grooved brachial and smaller ambulacral plates.

These are usually three in number, but may be two or four. Thus there is nothing in *Echinosphæra* showing pentamerous symmetry, unless it be the anal pyramid. Certain other cystids, however, give a hint of how the pentamerous condition arose: they have also three food-grooves, but while the anterior one (opposite the anus) remains unbranched, the other two branches soon divide into two, giving five grooves with an imperfect radial symmetry (Fig. 73, *c*).

The Cystidea are divided into four orders:

1. **Amphoridea**, with no trace of radial symmetry, varying from simple sacs like *Aristocystis* (Ord. of Bohemia) to forms with well-developed stem, flattened theca and more or less bilateral symmetry. *Dendrocystis* (Fig. 73, *a*, Ord.) has one long arm, with the mouth at its base, the anus at the opposite end near the stem, both on the same side, while on the other side are outgrowths (*ABr* and *AA*) which served to balance them. There are still more specialized bilateral forms like *Placocystis* (Sil.) with a curious mimicry of Branchiopod Crustaceans, which suggests that they were actively moving animals.

2. **Rhombifera**, showing the rhomb-foldings of stereom described above. *Echinosphæra* is about the simplest of these. Others like *Macrocystella* (Tremadoc) show stem, circlets of thecal plates, and arms almost like crinoids. Others like *Lepadocrinus* (Fig. 73, *b*, Sil.) show a remarkable specialization of a few (usually three) of the rhombs into large *pectinirhombs* with all the appearance of respiratory organs (gills), while the food-grooves are on the crests of ridges which might be described as arms sessile on the theca.

3. **Aporita**, a small group with fair pentamerous symmetry and no special stereom-structures, e.g. *Cryptocrinus* (Ord.)



4. **Diploporita**, in which the stereom-cavities are normal to the surface and grouped in pairs, giving rise to an appearance which must by no means be confused with the very different "pore-pairs" of Echinoidea. There is fair pentamerous symmetry, and the food-grooves radiate on the surface of the theca. *Sphaeronites* (Ord.) and *Glyptosphaera* (Fig. 73, *c*, Ord.) are spheroidal contemporaries of *Echinospheera*.

The **Blastoidea** may be illustrated by *Pentremites pyriformis* (Fig. 74), of the Lower Carboniferous of North

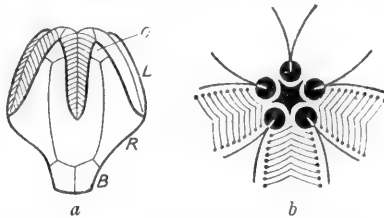


FIG. 74.—*PENTREMITES PYRIFORMIS*, SAY, MISSISSIPPIAN (CHESTER GROUP), ALABAMA, U.S.A.

*a*, Side view. (Natural size.) *b*, Oral region. ( $\times 2$ .) (Original.) *B*, Basals; *R*, radials; *L*, lancet-plates; *O*, orals or deltoids. In *b*, the mouth is in the centre, the five spiracles around it, and beyond and alternating with these the five ambulacra.

America. The shape suggests a flower-bud just opening. There is no true stem, but the base is drawn out into a stem-like stump. It would consist of five lozenge-shaped basals, but two pairs are fused, so that only three basals are counted. The five radials are much larger and would be hexagonal but for a very deep notch which almost cuts each in two. Five small orals or deltoids alternate with the radials above. Between these, and in the notches of the radials, lie five *lancet-plates*, each with a central food-groove into which run numerous oblique

grooves from right and left alternately. Between the margins of the lancet-plates and the radials are *side-plates*, which in exceptionally preserved specimens bear each a pinnule. From their position in relation to other structures it is obvious that a lancet-plate with its side-plates (sometimes termed an *ambulacrum*) answers to the arm of a crinoid—an arm which is sessile upon and forms part of the calyx. The side-plates bear pores, which open into internal gill-like organs, the *hydrospires*. The mouth is in the centre of the upper surface: around it are five openings, interradial in position, divided into two internally, the *spiracles*, which also communicate with the hydrospires. Each spiracle is roofed by the halves of two lancet-plates and their side-plates. The anus is probably confluent with one of the spiracles.

In another common American species, *P. godoni*, the base is flattened at the level of the lower end of the lancet-plates. In *Orbitremites*, found in the Carboniferous Limestone of England, but not common, the calyx is ellipsoidal, and the ambulacra very narrow and extending very far down towards the base.

The **Eleutherozoa** are always freely-moving benthic animals, sometimes carnivorous, sometimes mud-eaters, but never microphagous as are all Pelmatozoa (even the few nectic forms).

**Hemicidaris intermedia** (Fig. 75) is a sea-urchin of which many very perfect specimens have been found in the Coral Rag of Calne in Wiltshire. The general characters and symmetry of the skeleton suggest at once

an affinity to crinoids, but there are no stalk and no arms. The skeleton (or *test*) has somewhat the appearance of a globe with poles flattened, but one (the *oral* pole) so much more so than the other (*aboral*) that the flattened surface is but little way below the equator (or *ambitus*). A full-grown specimen is about 36 mm. in diameter at the ambitus and 25 mm. high. Sometimes the fossil is found with the movable spines (or *radioles*) which characterize the sea-urchins still in their natural position; but as a rule they fell off before burial, and the test only shows the tubercles with which they were articulated. Some of these are large and prominent, and carried thick cylindrical radioles, up to 95 mm. in length. These large (or *primary*) tubercles are arranged in five double rows, between which are narrower areas each with a double row of much smaller tubercles. The difference between these alternate areas is most striking near the aboral pole, and becomes much less so near the oral pole by the increase in width of the narrower areas and in the size of their tubercles. But there is a more important distinction that persists throughout: the narrower areas carry a series of fine pores, always arranged in pairs, and in each area there are two vertical columns of pore-pairs. These pores, in life, transmitted finger-like muscular tubes kept tense by the pressure of water in them from an internal system of water-vessels (analogous to blood-vessels): these are the tube-feet (or *podia*), the organs of locomotion of sea-urchins. In life they extend out beyond the long radioles, and their sucker-like ends can adhere firmly to any foreign body.

The five areas containing pores are called the *ambulacral* areas, or, briefly, the *amb*s; the alternate areas are the *interambulacral* areas or *interamb*s. The *amb*s are perradial, and the *interamb*s interradial. Together they form the *corona*, which is the greater part, but not the whole, of the test.

It is not always easy to see the sutures of the plates

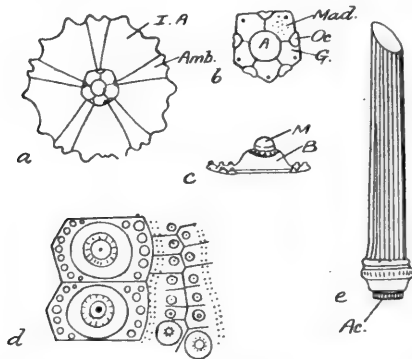


FIG. 75.—HEMICIDARIS INTERMEDIA, FLEMING, ARGOVIAN  
(CORAL RAG), CALNE (WILTS).

- a*, Aboral view. ( $\times \frac{1}{2}$ .) All details of *amb*s and *interamb*s omitted.  
*b*, Apical disc. (Natural size.) *c*, An *interamb* plate in profile. ( $\times 2$ .)  
*d*, Two *interamb* plates with adjacent part of *amb*. ( $\times 2$ .) *e*, Large radiole. ( $\times \frac{2}{3}$ .) (After Wright.) *A*, Periproct; *Ac.*, acetabulum (articular socket for mamelon); *Amb.*, ambulacral area; *B*, boss; *G*, genital plate; *I.A.*, interambulacral area; *M*, mamelon; *Mad.*, madreporite; *Oc.*, ocular plate.

which build up the ten areas, especially on the external surface. On the internal surface they are plainer. Each area consists of two vertical columns of plates, the sutures down the middle of an area being zigzag, while those between adjacent areas are nearly straight. In the *interamb*s there is a plate to each large tubercle. In the *amb*s there is, near the aboral pole, one pore-pair to each

plate, and each plate extends across half the width of the amb. Such plates are called *simple primaries*. Lower down *compound* plates appear, each with several pore-pairs. The development of living forms shows that such plates arise by the fusion of simple plates, and sometimes the fused sutures can be traced in a fossil. When this can be done in *Hemicidaris*, it is found that three plates fuse together: the middle one carries most of the large tubercle and may be the only one that occupies the full width of its column (*primary plate*), the other two only covering about two-thirds of that width (*demi-plates*).

Growth of the corona takes place (1) by intercalation of new plates at the aboral end of the ambcs and inter-ambcs, and (2) by increase of size (if necessary, with alteration of shape) of existing plates. The early-formed coronal plates thus get thrust farther from the apical system as growth proceeds. Sometimes plates next the peristome may undergo resorption. Thus, though individual plates grow by accretion, the corona as a whole does not, but grows by a more complex process of intussusception. Consequently the way in which the adult corona illustrates its own development is the reverse of that seen in molluscs and brachiopods. In echinoids the earliest-formed coronal plates, instead of illustrating the earliest stage of growth, are the most highly developed; while those which have been latest formed show the simplest characters. Thus it is that in *Hemicidaris* the ambulacral plates next to the apical disc are simple, while those near the peristome are compound.

The ambcs and interambcs end orally around a large

space, the outline of which has ten notches, which mark the position of external gills. This space in fossils is colloquially termed the mouth, but that is not strictly correct, the real mouth being smaller, and surrounded by a membrane (*peristome*), the plates in which are loose and on its decay fall away, leaving a large space. The mouth was furnished in life with a complex series of biting organs (jaws and teeth) forming the *lantern* of Aristotle. This is rarely preserved, but its existence is shown by the presence of the *perignathic girdle*, a series of internal arches arising from the lowest plates of the corona, and serving as an origin for the muscles inserted on the lantern.

Towards the aboral pole the corona is surmounted by a flat series of ten plates called the *apical disc* (or better, *apical system*), in the centre of which is a space, colloquially called the anus, but more correctly the *periproct* (for a similar reason to that of the peristome). Of the ten plates, the five smaller are at the ends of the ambæ and are called the *ocular* plates; the five larger interradial plates are termed *genital*, because they bear the apertures of the genital ducts. One of the genital plates, in addition to the genital pore, is perforated by a great number of smaller pores, through which water filters into the water-vessels: this plate, called the *madreporite*, constitutes the only imperfection of five-rayed symmetry in the test of *Hemicidaris*. The ocular plates have been termed radials, and the genital, basals; but they are certainly not strictly homologous with the plates so named in crinoids, which do not encircle

the anus: they seem more comparable with the plates of the anal pyramid in cystids.

The radioles of *Hemicidaris* articulate with the tubercles by a ball-and-socket joint. They are moved by muscles in the skin, which lies *outside* the test. The tubercles are distinguished according to size into primary, secondary, and miliary. The primary tubercles consist of a boss and a mamelon (Fig. 75, *c*): in *Hemicidaris* the inner

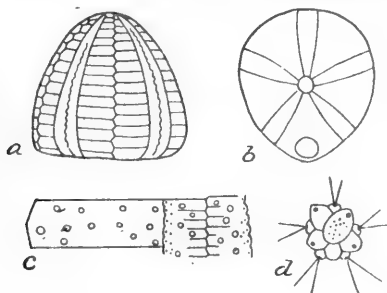


FIG. 76.—*CONULUS ALBOGALERUS*, LESKE, EMSCHERIAN  
(UPPER CHALK).

*a*, Side view. ( $\times \frac{1}{2}$ .) *b*, Oral view. ( $\times \frac{1}{2}$ .) *c*, One interambulacral plate and adjacent ambulacral plates. ( $\times 2$ .) *d*, Apical disc. ( $\times 2$ .) (After Wright.) Sutures of ambulacral plates omitted in *a*; of all plates in *b*; madreporite dotted in *d*.

part of the boss shows a ring of radial *crenulations*, and the centre of the mamelon has a perforation; so the tubercles are described as *crenulate* and *perforate*.

**Conulus albogalerus** (Fig. 76) is a common sea-urchin of the White Chalk. The first obvious differences from *Hemicidaris* are its more conical shape and much smoother surface. Next we notice that the symmetry is not strictly radial, but is bilateral, the base being a pentagon of which one side is highly convex, while the

others are flat: in the middle of this side is a large opening, the periproct. The mouth, however, is still in the centre of the oral surface, and the very small apical disc is equal central at the aboral apex.

The smoothness of the surface enables the sutures of the plates to be traced easily. The interambes are broad and composed of large, nearly oblong plates, with from one to twelve or more larger flat tubercles and numerous, much smaller tubercles (granules). The ambes are narrow; their plates are much smaller and more irregular, including simple primaries, simple demi-plates, and some compound plates; each has one or sometimes two larger flat tubercles, and a number of granules.

The peristome is small; the lantern and perignathic girdle are in a vestigial condition. The apical disc is not very different from that of *Hemicidaris*, except that the madreporite is larger than the other genital plates and extends into the space vacated by the periproct.

**Micraster cor-anguinum** (Fig. 77) is another sea-urchin from the Upper Chalk. Viewed from above or below its outline is heart-shaped, the anterior amb being deeply depressed so as to notch the outline. The other ambes are also sunk in a similar way for some distance from the apical disc, but not far enough to affect the outline. The posterior interamb is raised into an obtuse ridge, the keel or *carina*, which runs almost horizontally back from the apical disc to the hind margin which drops perpendicularly. Sometimes the carina projects slightly above this vertical end, forming a *rostrum*. The anus lies near the top of this vertical face.



The mouth lies far forward (four-fifths of the whole length) and faces forwards instead of downwards, as a distinct lower lip (*labrum*) projects on its under side.

In the apical disc the two posterior ocular plates are in contact, the genital plates between them being crowded out; the madreporite is large and extends into the centre of the disc, taking a flask-like shape and in contact with

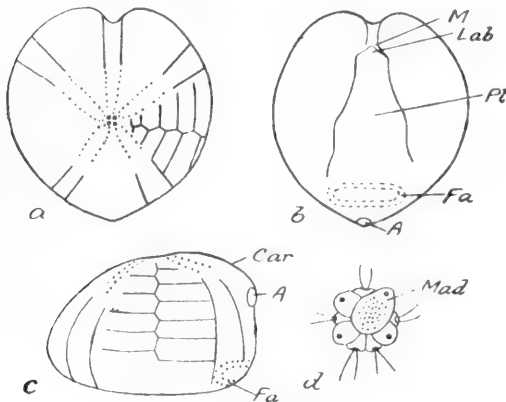


FIG. 77.—MICRASTER COR-ANGUINUM, LESKE, EMSCHERIAN  
(UPPER CHALK).

*a*, Aboral view. ( $\times \frac{1}{2}$ .) *b*, Oral view. ( $\times \frac{1}{2}$ .) *c*, Side view. ( $\times \frac{1}{2}$ .)  
*d*, Apical disc. ( $\times 4$ .) (After Wright.) Some of the interamb sutures are indicated in *a* and *b*. *A*, anus; *Car*, carina; *Fa*, sub-anal fasciole; *Lab*, labrum; *M*, mouth; *Mad*, madreporite; *Pl*, plastron.

all the other plates except the left posterior ocular. Otherwise the plates retain a fairly regular arrangement.

The ambis are composed, near the apical disc, of close-set plates, very short and broad, with uniserial pore-pairs. At about half-way towards the ambitus a sudden change takes place: the plates become much larger and squarer, and their pore-pairs become much less notice-

able. The three anterior ambs can be traced directly down to the mouth; the two posterior extend to the posterior end of the plastron, whence they can be traced with some difficulty along either side of the plastron. It is evident that the abundant tube-feet of the dorsal surface cannot serve to convey food to the mouth, since they are separated from it by a wide space with very scanty tube-feet: probably they serve as gills. These aboral regions of abundant pore-pairs are called the petals, from a resemblance to an open five-petalled flower; but *Micraster* is not typically "petaloid," only *sub-petaloid*, because the two series of pores in each petal are nearly parallel, instead of widening out and closing in again.

The interamb plates, having to occupy all the space between the ambs, are for the most part very large. Their regular double-row becomes rather confused on the under side. The posterior interamb on the under side constitutes the plastron.

All plates except those of the petals bear tubercles and granules. On the upper surface the tubercles are small, not very prominent, and scattered, with abundant small granules between. On the under surface they are larger, with more deeply excavated areola, and are much more closely set; the granules, though fewer in number, being also coarser and more close-set. Running round the lower corner of the vertical posterior end there is a narrow ring which at first sight appears smooth, but under magnification is seen to be covered with extremely fine granules. This is a *fasciole*, and from its position is called a sub-anal fasciole.

The micrasters of the White Chalk, of which *M. coranguinum* is the latest, are famous from the work of Dr. Rowe, who showed in 1899, from the study of large numbers of specimens collected and arranged with care according to their exact zones, that they went through a gradual series of changes which did not bear a close relation to the accepted distinctions of species. These changes, in fact, run on parallel lines in separate stocks, so that they may serve as zonal indices. The chief changes may be summarized thus:

(1) In general form they tend with the lapse of time to become slightly broader and very distinctly higher, while the ambital outline tends to change from wedge-shape to ovate.

(2) The carina appears and becomes more marked, the highest point which was at first at the apical disc shifting backwards; finally a rostrum appears.

(3) The anterior groove becomes deeper.

(4) The mouth shifts forward and the labrum makes its appearance; at first smooth at the tip, it becomes more and more granulated; the labral plate changes from triangular to oblong, and its tubercles from irregular to linear in arrangement.

(5) The amb-petals become longer and shallower.

(6) The sub-anal fasciole, from being weak, becomes very strong, and loses a slight tendency towards an 8-shape which it had at first.

(7) The periplastral area (the two posterior ambps on the under surface) from smooth passes to granulated and finally to very coarsely granulated (mammillated).

(8) Perhaps the most easily observed change of all is that in the *interporiferous areas* (*i.e.*, the middle strip of the petals, between the pore-pairs). These pass through a series of stages (*a*) "smooth"; (*b*) "sutured," *i.e.* the sutures of the plates are clearly marked; (*c*) "inflated," *i.e.* instead of being gently concave, they rise in a double convexity; (*d*) "subdivided," *i.e.* the middle line between these convexities becomes a distinct groove; and (*e*) "divided," *i.e.* this groove becomes very deep and narrow.

The main division in the classification of Echinoidea is between those with radial and bilateral symmetry, or Regularia and Irregularia. The great differences between these two sub-classes may be tabulated thus:

REGULARIA.	IRREGULARIA.
Radial symmetry, perfect except for madreporite.	Bilateral symmetry, perfect except for apical system.
Anus within apical system, which is symmetrical and large.	Anus in posterior interamb. Apical system usually asymmetric; small and compact, or elongated.
Mouth central, with well-developed jaws.	Mouth either central (when jaws may be well-developed or reduced), or in anterior amb (when jaws are lost).
Corona usually bearing large, prominent tubercles (as well as smaller ones) with long stout radioles.	Corona hardly ever with large, conspicuous tubercles. Radioles small.

The Palæozoic echinoids are distinguished from all later forms (except one Triassic and one Barremian genus) by the inconstancy in the number of coronal columns of plates, which may be more or less than twenty, but never that exact number, which is the invariable number among later forms (with the one excep-

tion named). This has been made the basis of a classification into "Palechinoidea" and "Euechinoidea," but as a morphological classification this leaves *Tetracidaris* in an anomalous position; as a genetic classification it is unsatisfactory, as it unites a number of divergent Palæozoic stocks, of which one was apparently more closely related to Mesozoic regular echinoids than the others. The following classification is based on that of Martin Duncan, with modifications taken from the classifications of Professor J. W. Gregory and Dr. R. T. Jackson, neither of which is fully adopted.

## CLASS: ECHINOIDEA.

### SUB-CLASS: Regularia (Endocyclica).

Order I. BOTHRIOCIDAROIDA. With a single column of interamb plates. Only genus *Bothriocidaris* (Fig. 78, a), Ordovician of Baltic Provinces, the only known Ordovician echinoid.

2. ECHINOCYSTOIDA. Two aberrant forms, morphologically exocyclic, though not related to the Irregulares. *Echinocystis* and *Palæodiscus*, Silurian of Shropshire.

3. MELONECHINOIDA. A series in which both amb and interamb columns tend to increase in numbers; no large tubercles, only granules with small radioles. Silurian to Permian. *Palæechinus* (Sil.-Carb., Fig. 78, b), *Melonechinus* (Carb., Fig. 78, d).

4. CIDAROIDA. A series in which the amb have never more than two columns, but in Palæozoic genera and in the Barremian (*Tetracidaris*) the interamb have more than two. Even where there are only two interamb columns the interamb are many times wider than the amb. Large tubercles and radioles on the interamb

only. Amb plates simple. Devonian to Recent. *Archæocidaris* (Carb.-Perm.), *Cidaris* (Trias.-Rec., Fig. 78, c, e).

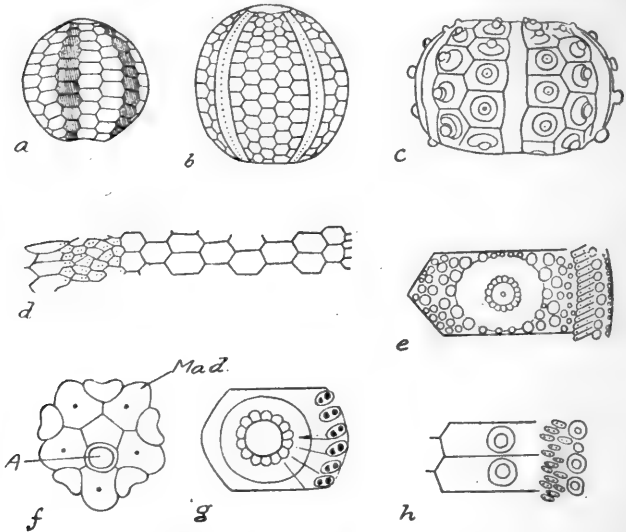


FIG. 78.—REGULAR ECHINOIDS.

- a, *Bothriocidaris pahleri* Schmidt, Ordovician, Russia. (Natural size.) Interambis shaded. b, *Palæechinus elegans* M'Coy, Lower Carboniferous. ( $\times \frac{1}{2}$ .) Details of ambis omitted. c, *Cidaris florigemina* Phillips, Argovian (Coral Rag). ( $\times \frac{1}{2}$ .) Details of ambis omitted. d, *Melonechinus liratus* Jackson, Lower Carboniferous. Portion of one amb and one interamb (full breadth). ( $\times \frac{2}{3}$ .) e, *Cidaris smithi* Wright, Argovian (Coral Rag). One interamb plate, with perforate tubercle, and the amb plates of the adjacent single column. Slightly enlarged. f, *Peltastes wrighti* Desor, Aptian, Faringdon (Berks). Apical disc. (Natural size.) (After Wright.) A, periproct; Mad., madreporite. Between these is the pentagonal sur-anal plate. g, *Cyphosoma königi* Mantell, Emscherian (Upper Chalk). Compound amb plate. ( $\times 3$ .) Traces of the sutures between the original six plates are seen. Tubercle imperforate. h, *Stomechinus germinans* (Phillips), Aalenian (Pea Grit). Two interamb plates and the adjacent amb plates. ( $\times \frac{2}{3}$ .) Showing triserial character of ambis, and imperforate tubercles. a, d, after R. T. Jackson; b, after Bailly; remainder after Wright.

5. PLESIOCIDAROIDA.—An aberrant Triassic group, with very large apical disc, and only three plates in the interambis. *Tiarechinus* (Carnic.).

6. CENTRECHINOIDA [DIADEMOIDA].—Regular echi-noids in which there is a tendency to form compound plates in the ambcs, which are not much narrower than the interambcs. *Peltastes* (Jur.—Cret.), *Salenia* (Cret.—Rec.), and *Acrosalenia* (Jur.—Cret.) have a large apical disc with an extra suranal plate (Fig. 78, *f*). *Hemicidaris* (Jur.) has been described. In *Pseudodiadema* (Jur.—Cret.) three primaries are fused, but the pores remain uniserial except close to the peristome. In *Diplopodia* (Jur.—Cret.), with the same type of compound plate, the pores are *biserial*—*i.e.*, they form two vertical columns within each column of plates; while in *Stomechinus* (Jur.—Cret., Fig. 78, *h*) they are *triserial*.

In *Cyphosoma* (Jur.—Cret., Fig. 78, *g*) as many as six plates, three primary and three demi-, may fuse into a compound plate to carry the big tubercles, which are imperforate (the last three genera having them perforate).

*Echinus* (Cret.—Rec.), the common sea-urchin, has plates compounded of two primaries and one demi-; pores triserial; poriferous zone narrow; tubercles and radioles numerous and not very large.

*Pelanechinus* (Jur.) and *Echinothuria* (Cret.) form a remarkable group, of which there are living survivors, in which the whole corona is flexible, the plates being movably articulated by bevelled edges.

-SUB-CLASS: **Irregularia (Exocyclia)**.—Sea-urchins of this sub-class appear first near the top of the Lower Jurassic (Aalenian stage), and the simplest of them, *Pygaster* (Fig. 79, *a*), is very little removed from some simple member of the Regular Centrechinoida, the periproct having shifted to a position only just outside the apical system. With this, however, are others with much stronger irregularity (*Hyboclypeus*), the mouth having also shifted forwards from its central position and having

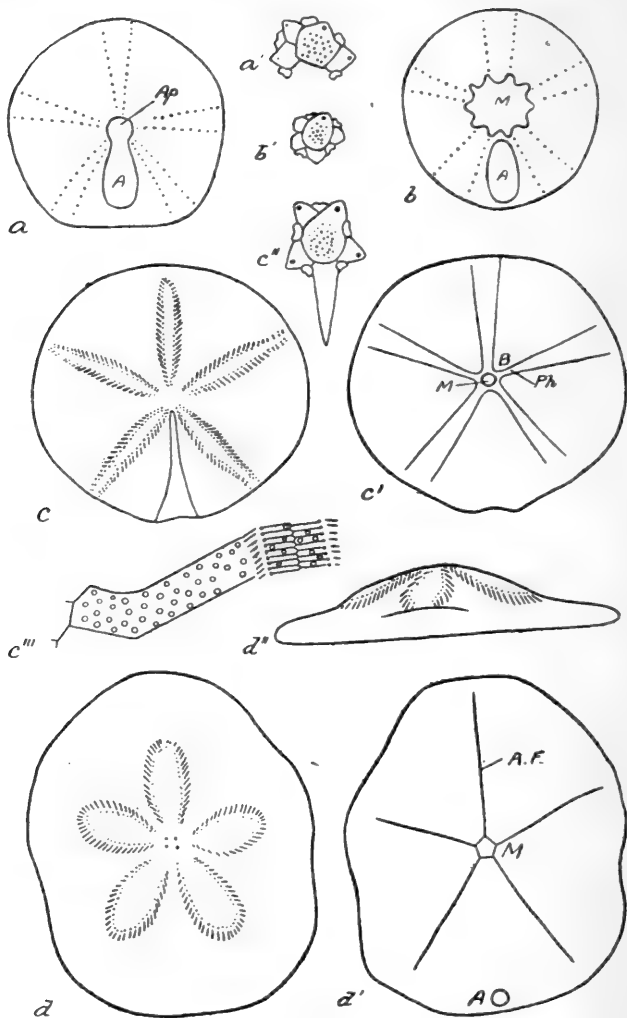


FIG. 79.—(For description see p. 275.)



lost its jaws and teeth. From the beginning we thus find two well-marked and divergent orders.

ORDER I: GNATHOSTOMATA.—Mouth central, with girdle and lantern (the latter sometimes vestigial). All amb. similar. Symmetry bilateral, but with strong radial tendency.

Two divergent sub-orders are found: (1) *Holectypina*, in which the jaws are reduced in size and strength, the pores of the amb. extend in unbroken series from apex to base, and some of the amb-plates may be compound; and (2) *Clypeastrina*, in which the jaws are very powerful, and the amb. tend to be petaloid, but there are no compound plates.

The chief genera of (1) are *Pygaster* (Jur.-Cret., Fig. 79, *a*), with periproct close behind apical disc; *Holectypus* (Jur.-Cret., Fig. 79, *b*), in which it has shifted to the under side; *Discoidea* (Cret.), hemispherical, periproct marginal, with ten radiating ridges internally around mouth, well seen on internal casts; and *Conulus* (Cret.), already described.

In (2) the tendency is for the shape to become very flat (cake-urchins): this diminishes the strength of the corona against vertical pressure, and two methods are adopted to strengthen it. The more usual is for vertical pillars or

FIG. 79.—IRREGULAR ECHINOIDS.

- a*, *Pygaster morrisoni* Wright, Bathonian. Aboral view. ( $\times \frac{1}{2}$ .) *a'*, Apical disc of *P. umbrella* Agassiz. ( $\times \frac{1}{2}$ .) *b*, *Holectypus depressus* Leske, Bathonian. Oral view. ( $\times \frac{1}{2}$ .) *b'*, Apical disc. ( $\times \frac{1}{2}$ .) *c*, *Clypeus altus* M'Coy, Vesulian. Aboral view. ( $\times \frac{1}{2}$ .) *c'*, Oral view. ( $\times \frac{1}{2}$ .) *c''*, Apical disc. ( $\times \frac{1}{2}$ .) *c'''*, Interamb plate and adjacent part of amb. ( $\times 2$ .) *d*, *Clypeaster suffarcinatus* Duncan and Sladen. Aboral view. *d'*, Oral view. *d''*, Side view. (All  $\times \frac{1}{2}$ .) *a*, *b*, *c*, After Wright; *d*, after Duncan and Sladen. In all, except the apical discs, the sutures between the plates are omitted; in *a* and *b*, pore-pairs are indicated by single dots. In the apical discs the madreporite is dotted; the ocular plates are distinguished by smaller size and absence of genital pores; in *b'*, the left anterior ocular plate and pores on four genital plates are accidentally omitted. *A*, periproct; *A.F.*, actinal furrow; *A.p.*, apical disc; *B*, bourrelet; *M*, peristome; *Ph.*, phyllode

radiating partitions to be developed internally to support the roof. The other is for the margin to be notched in the interamb, the plates in the sides of these notches serving as supports of the roof: further growth may reunite the plates at the margin, converting notches into perforations ("lunules"). In all but the more primitive genera some of the amb plates widen out and pinch the interamb across until they meet the plates of the next amb (*discontinuous* interamb), and there are furrows (actinal furrows) radiating from the mouth along the amb.

Chief genera: *Echinocyamus* (Cret.-Rec.) and *Fibularia* (Cret.-Rec.) are very small primitive forms with petaloid

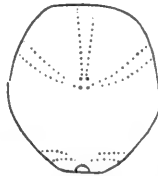


FIG. 80.—COLLYRITES RINGENS, AGASSIZ, VESULIAN.

Aboral view. ( $\times \frac{3}{4}$ .) Periproct seen at lower end. The four black spots near centre are the genital pores of the apical disc; from here the "trivium" radiates, while the "bivium" is far behind. (After Wright.)

amb, but none of the other special features of the sub-order. *Scutella* (Eoc.-Rec.) is very flat, circular, with bifurcating actinal furrows; *Mellita* and *Rotula* (Plio.-Rec.) have lunules; *Clypeaster* (Fig. 79, *d*, Olig.-Rec.) is oval to pentagonal in plan, with straight actinal furrows. In some species advantage is taken of the strengthening pillars to raise the central part of the roof, including the respiratory petals, into a dome. Such species are the largest and most massive of all sea-urchins. All but the most primitive genera of this sub-order are confined to warm seas.

ORDER 2: ATELOSTOMATA.—Mouth shifted forward; lantern and jaws lost. Anterior amb somewhat different

from the other amb. Symmetry strongly bilateral. Tendency to separate the three anterior amb. (*trivium*) from the two posterior (*bivium*).

There are two sub-orders—(1) Cassiduloidea, in which the mouth, though slightly forward, still opens downwards; and (2) Spatangoidea, in which the mouth opens forwards, with more or less of an underlip, and between it and the anus the posterior interamb plates form a strong convex *plastron*.

Chief genera of (1) are *Nucleolites* [*Echinobrissus*] (Jur.—

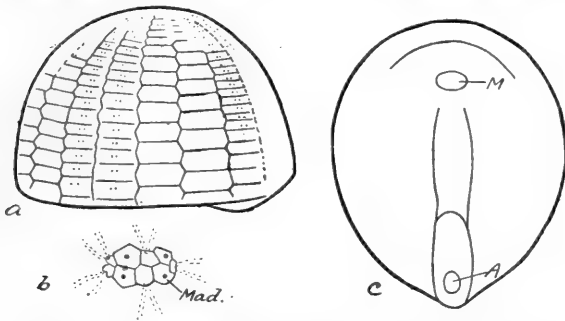


FIG. 81.—ECHINOCORYS SCUTATUS, LESKE, EMSCHERIAN (UPPER CHALK).

*a*, Side view; *b*, apical disc; *c*, oral view. (All  $\times \frac{1}{2}$ .) (After Wright.)

Cainozoic), with oval outline, broader and rather truncated behind, with deep anal groove on upper surface, amb. sub-petaloid, the outer pore of each pair elongated; *Clypeus* (Fig. 79, *c*, Jur.), flat, circular, anal groove as in the last, amb. petaloid, elongation of outer pores very great, mouth surrounded by a *floscelle*—five ambulacral grooves (*phylloides*), with protuberances (*bourrelets*) on the interamb.; *Echinolampas* (Eoc.—Rec.), ovoid, somewhat conical, amb. petaloid, anus sub-marginal, *floscelle* present; *Collyrites* (Fig. 80, Jur.—Cret.), oval, with rounded base, with strong separation of *bivium* and *trivium*.

Chief genera of (2) are *Echinocorys* [*Ananchytes*] (Fig. 81, Cret.), oval, with flat base, periproct sub-marginal; *Holaster* (Fig. 82, Cret.-Mio.), heart-shaped with anterior groove, slight separation of bivium and trivium; *Micraster* (Cret.-Mio.), already described; *Hemiaster* (Cret.-Rec.) and *Schizaster* (Eoc.-Rec.) differ from *Micraster* in not having a sub-anal fasciole, but have a *peripetalous* fasciole running round the petaloid ambcs, which are deeply sunk, especially in *Schizaster*, which has also a *lateral* fasciole branching off from the main fasciole on each side.

The Echinoidea are by far the most important, geologically, of the Eleutherozoa. Of the Stelleroidea it is

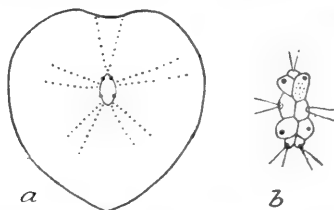


FIG. 82.—*HOLASTER SUBGLOBOSUS*, LESKE, CENOMANIAN.

*a*, Aboral view. ( $\times \frac{1}{2}$ .) *b*, Apical disc. ( $\times \frac{2}{3}$ .) (After Wright.)

only necessary to say that they are known from the Cambrian upwards, and where they do occur it is frequently in "starfish-beds" (*e.g.*, where representatives of one or a few species are extremely abundant), yet between such beds there are enormous thicknesses of rock destitute of any trace of them. A knowledge of them is, therefore, far less needed by the geologist than that of echinoids or crinoids.

The Holothurians have their skeleton reduced to microscopic spicules, so that special search has to be made for them. They are found, here and there, from the Cambrian upwards.

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## VIII

### THE GRAPTOLITES AND CORALS

THE Graptolites are an extinct group, found only in the Older Palæozoic rocks, and most abundantly preserved in black shales. Their habit of growth is more suggestive of plants than animals, consisting as they do of numerous similar parts borne on a stem which may be branched. Such a habit is, however, known in living aquatic forms which are undoubtedly animals: it is easily arrived at when very simple structure is associated with a fixed habit. So far as this feature goes the graptolites might be assigned to any one of several animal phyla, but the balance of opinion is in favour of regarding them as hydrozoa (see later, p. 296). The names given to the parts of the graptolite are chosen on this assumption.

The skeleton of graptolites is composed of some organic material. When preserved in shales it is usually crushed flat, and appears as a thin film, sometimes of a whitish material, more often of graphite. More rarely the material was replaced by pyrite before being crushed, and still more rarely it has been preserved uncrushed and unaltered in limestone from which it can be extracted by treatment with acid.

1. **Didymograptus murchisoni** (Fig. 83) is an abundant graptolite in the black shales of Middle Ordovician age of Aberiddy Bay, Pembrokeshire (and elsewhere). Its shape is well described by the name "tuning fork graptolite." Corresponding to the stem of the fork is an acutely conical body (crushed flat in the shale) called the *sicula*, its apex drawn out into a short thread called the *nema*. There is reason to believe that by



FIG. 83.—**DIDYMOGRAPTUS MURCHISONI** (BECK), UPPER LLANVIRNIAN.  
(Natural size.) (After Elles and Wood.)  
*S*, Sicula.

the *nema* the graptolite was attached to floating seaweed, from which it hung downwards, and we will describe the fossil as if in this position. In this description many statements cannot be fully verified on ordinary specimens, the facts having been demonstrated by Dr. Holm and other Swedish palæontologists on specimens preserved uncrushed in limestone.

The *sicula* probably lodged the original polyp, from which other polyps afterwards were formed by a process



of budding (Fig. 84). These are arranged along two branches, or *stipes*, hanging down almost vertically but slightly divergent. Each stipe consists of a series of somewhat cylindrical cups, or *thecæ* (hydrothecæ), which lodged a polyp each, and a *common canal* uniting their inner ends. The sicula and stipes constitute the *polypany*, or complete skeleton, of the colony of polyps. The end at

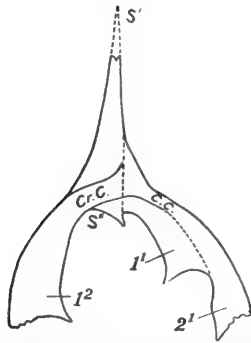


FIG. 84.—*DIDYMOGRAPTUS MINUTUS*, TÖRNQVIST, LOWER ORDOVICIAN (ORTHO CERAS LIMESTONE), OLAND.

Initial portion, reverse side ( $\times 19$ ). (After Holm.)  $S'$ , Apical part of sicula;  $S''$ , aperture of sicula; *Cr. C.*, crossing canal; *c.c.*, common canal;  $1^1$ ,  $2^1$ , first and second thecæ of first stipe;  $1^2$ , first sicula of second stipe.

which is the sicula is called the *proximal* end, the opposite end the *distal*.

The two stipes are not, however, absolutely symmetrical. The first theca of one stipe arises directly from the sicula, and successive thecæ, with the common canal pertaining thereto, are budded off in turn; but the first theca of the other stipe is budded off from the first theca of the first stipe, so that its portion of common canal has

to cross from one side of the sicula to the other. This is called the *crossing canal*, and the side on which it lies is called the *reverse*, while the side on which the sicula is in front is the *obverse*. After thecæ have thus been formed for each stipe, further thecæ are developed alike on each. Each theca is straight, and being at an acute angle to the direction of the stipe, overlaps the adjacent theca considerably. If tangents are drawn to the outer face of the first theca on each side, the angle enclosed by them is the *angle of divergence*, which in this species is less than  $45^{\circ}$ . This angle is not maintained by the stipes, as lower down they become sub-parallel: a polypary so disposed is described as *dependent*. Seven British species of *Didymograptus* have this dependent form: they are distinguished from one another by differences of detail in the thecæ.

There are other species which begin their growth like *D. murchisoni* and form two stipes, but with a different angle of divergence or different final direction.

Thus if the angle of divergence is about  $90^{\circ}$  and the stipes continue at that angle, the polypary is said to be *declined*; if starting at less than  $90^{\circ}$  they gradually spread out almost horizontally, *deflexed*; if with an angle of divergence less than  $180^{\circ}$ , they quickly become *horizontal*; if curved upwards, *reclined*; if curved upwards and then downwards, *reflexed* (Fig. 85). Even in these last two cases (known only in one species each) the original angle of divergence is less than  $180^{\circ}$ . The constancy of these angles and curvatures, as well as the frequent abrupt bends in stipes that have been














DEPENDENT SERIES	DECLINED SERIES	HORIZONTAL SERIES	RECLINED SERIES	REFLEXED SERIES
 <p><i>Bryograptus ramosus</i>, Tremadocian.</p>	 <p><i>Clonograptus callavei</i>, Tremadocian.</p>	 <p><i>Loganograptus logani</i>, Lower Skiddavian.</p>	 <p><i>Bryograptus retroflexus</i>, Tremadocian.</p>	
 <p><i>Tetragraptus fruticosus</i>, Middle Skiddavian.</p>		 <p><i>Tetragraptus quadribrechiatus</i>, Skiddavian.</p>	 <p><i>Tetragraptus ligshyti</i>, Middle and Upper U Skiddavian.</p>	 <p><i>Tetragraptus denticulatus</i>, Skiddavian.</p>
 <p><i>Didymograptus murchisoni</i>, Upper Llanvirnian.</p>	 <p><i>Didymograptus affinis</i>, Skiddavian - Llanvirnian</p>	 <p><i>Didymograptus extensus</i>, Middle and Upper Skiddavian.</p>	 <p><i>Didymograptus gibberulus</i>, Middle and Upper Skiddavian</p>	 <p><i>Didymograptus fasciculatus</i>, Lower Llanvirnian.</p>

FIG. 85.—EVOLUTION OF THE DICHOGRAPTIDÆ.

Five parallel series, of which two are incomplete. It will be noted that the evolution is most rapid in the case of the horizontal forms and slowest in that of the dependent. (After Marr and Nicholson, with alterations in accordance with the later conclusions of Elles.)

snapped by too great strain (as in Fig. 88, *c*) shows that the polypary was a fairly stiff structure.

All these forms, covering twenty-seven British species alone, are habitually included in the one genus *Didymograptus*. But the modern conception of a genus is that of a number of species connected together and separated from species of other genera by an immediate common descent. That *Didymograptus*, in its accepted extent, is a true genus has been rendered very doubtful by certain observations made in 1895 by Marr and Nicholson.

The genus *Didymograptus* is found in the Lower and Middle Ordovician. In the Lower Ordovician only are found graptolites which start growth like *Didymograptus*, but branch again, forming four or eight stipes, and in the Tremadoc beds (transitional between Cambrian and Ordovician) are still more complexly branched forms. Marr and Nicholson pointed out that similarities of stipe-disposition and thecal form can be traced through the morphological genera *Bryograptus* (or *Clonograptus* or *Loganograptus*), *Tetragraptus* and *Didymograptus* in these successive periods, and they suggested that these indicate the true lines of descent, while the number of stipes underwent reduction from many to four, and at last to two, in at least five independent lines of descent (Fig. 85).

The reader may have been struck with the fact, which has puzzled many geologists, that the earliest graptolites (Tremadoc) are more complex than their descendants in the Ordovician. Further, that in individual growth a *Tetragraptus* must pass through a *Didymograptus* stage, while a *Clonograptus* must pass through first a *Didymo-*

*graptus* and afterwards a *Tetragraptus* stage; and he may ask whether this does not contradict all that has been deduced from other animal phyla as to the relation of ontogeny to phylogeny.

To this it must be replied, in the first place, that in the graptolites we know very little of actual ontogeny. The development of the sicula is ontogeny; all that follows is not the development of an individual, but of a colony, by budding—*astogeny*. However, students of other colonial animals (as the Bryozoa) have shown grounds for the view that astogeny is also, like ontogeny, a recapitulation of phylogeny. Apparently, then, the graptolites contradict this conclusion. But we must not stop short at the Tremadoc graptolites in tracing their descent. It is inconceivable that these complexly branched forms should have been derived abruptly from non-colonial ancestors. They must have had intermediate ancestors (quite unknown) in which the branching gradually became more and more complex. The known graptolites of this family must illustrate the catagenetic stages of branching from an acme in the Tremadoc epoch.

However the extent of the "genera" so far mentioned may have to be altered, they appear to form a natural family—the *Dichograptidae*, of which the five series mentioned would be sub-families. The family is distinguished by the simple structure of its thecæ, and by the fact that the first-formed thecæ always grow downwards from the sicula. It ranges from Tremadocian to Llandeilian.

Another "genus" which should find a place here is

*Phyllograptus* (Fig. 85), which in a purely morphological classification has been made into a separate family or even sub-order, since it has four rows of thecæ on one stipe, while all other graptolites have two or one. It consists of species closely allied to the reclined *Tetragrapti*, but with the four stipes confluent.

2. ***Climacograptus wilsoni*** (Fig. 86) is a graptolite which occurs in such abundance at the base of the Hartfell Shales in the Southern Uplands of Scotland that it has been chosen as a zone-fossil. It has an unbranched stipe with a double column of thecæ (*biserial* polypany), and may reach a length of six centimetres or more. When complete, the proximal end shows the sicula, having at its base a very large vesicle (a specific character, not found in other *Climacograpti*); and passing at its apex into a rod, the *virgula*. This answers to the nema of *Didymograptus*, but serves an additional function. The first theca budded from the sicula begins to grow downwards as in *Didymograptus*, but soon makes a sharp bend and grows upwards, and all subsequent thecæ grow in this way. Consequently the *virgula* comes to be imbedded between the two columns of thecæ and serves as a support to them. In many species of *Climacograptus* (though apparently not in *C. wilsoni*) the *virgula* extends for some distance beyond the most distal thecæ, and probably served to suspend the polypany from floating weed.

The thecæ near the proximal end have a simple form, but higher up they acquire a double right-angled bend, which gives the polypany the appearance of a double row of square bodies with narrow spaces (*excavations*) between.

Each square is the distal portion of a theca, with its aperture horizontal and opening upwards into the excavation above it. The middle portion of each theca is bent horizontally, and the proximal portion is again vertical.

Specimens of *Climacograptus* are usually flattened in the plane which bisects both columns of thecae, and thus give a *profile* view; but occasionally they are flattened in the plane separating the two columns: they

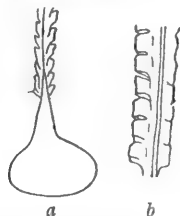


FIG. 86.—CLIMACOGRAPTUS WILSONI, LAPWORTH, LOWER CARADOCIAN.

*a*, Initial part of polyary ( $\times \frac{2}{3}$ ), showing sicula with large vesicle, and six thecae of each column; *b*, distal part of polyary ( $\times \frac{5}{8}$ ), showing form of thecae and "excavations" clearly on the left side. (After Elles and Wood.)

then show one set of thecae only in full face, and from its ladder-like appearance this is called the *scalariform* view.

3. **Monograptus priodon** (Fig. 87) is a very abundant graptolite in the lower part of the Wenlock Shale, though not restricted to that horizon. Its polyary is unbranched and attains a considerable length—up to a foot (25 c.m.) and more. The sicula lies on one side of the proximal end, and from its apex arises a stout virgula which supports a single column of

thecæ on the opposite side to the sicula. These thecæ lie obliquely and overlap one another for about half their length; the free portion is bent first outwards and then downwards, so as to have a hook-like appearance. The curvature of the theca and the direction of the aperture are thus the opposite to those of *Climacograptus*. The first theca grows upwards from the sicula: the first stage of downward growth, corresponding to the permanent direction of *Didymograptus*, and still preserved in *Climacograptus*, is skipped altogether in *Monograptus*.

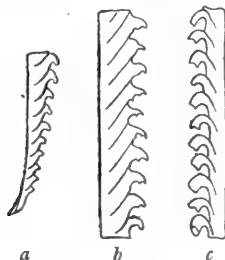


FIG. 87.—*MONOGRAPTUS PRIODON* (BRONN), WENLOCK SHALE.

*a*, Initial part of polypary, showing sicula, with virgula arising from its apex; *b*, distal thecæ, reverse aspect, apertures partly embedded in rock; *c*, distal thecæ in low-relief, obverse aspect, showing apertural margins. ( $\times \frac{5}{2}$ .) (After Elles and Wood.)

It is very probable that *Monograptus* was not a floating organism, but was fixed to the sea-bottom.

The following classification of the graptolites is that given in the monograph by Elles, Wood, and Lapworth. Professor Frech of Breslau unites the three first families as **Axonolipa** (without a virgula), and the rest as **Axonophora** (with virgula).

Family **DICHOGRAPTIDÆ**.—Uniserial Graptoloidea, with bilateral polyparies, bearing simple subcylindrical thecæ.



Branching usually dichotomous, but occasionally irregular. Primary angle of divergence generally  $180^\circ$  or less. Tremadocian to Middle Llandeilian.

Chief genera are those mentioned on Fig. 85. Of these only *Didymograptus* ranges above the Lower Llanvirnian (*bifidus* zone).

Family LEPTOGRAPTIDÆ.—Uniserial, with slender flexuous polyparies; primary angle of divergence approximately  $180^\circ$ ; branching usually lateral; thecæ elongated, with slight sigmoid curvature, apertures inclined, situated partly within depressions (excavations), somewhat introverted (turned inwards), but not introverted (twisted inwards). Range in Europe: Middle Llanvirnian to Middle Ashgillian, but in Australia a species of *Leptograptus* is associated with other graptolites of Skidavian facies.

Chief genera: *Leptograptus* (Fig. 88, *b*), without lateral branching (range of family); *Nemagraptus* (Fig. 88, *c*), S-shaped polypary with numerous lateral branches (Middle Llandeilian); *Pleurograptus*, with compound lateral branches (one zone in Hartfell Shales, Ashgillian).

Family DICRANOGRAPTIDÆ.—Uni- or uni-biserial, angle of divergence always exceeding  $180^\circ$ ; thecæ with strong sigmoid curvature; apertures horizontal or inclined, situated within well-defined "excavations" and frequently introverted and introverted. Llanvirnian to Ashgillian.

There are two genera: *Dicellograptus* (Fig. 88, *d*), in which the two branches rise up somewhat as in the reclined dichograptids, and *Dicranograptus* (Fig. 88, *e*), in which they are united at first (as in *Phyllograptus* or *Climacograptus*), but afterwards separate. This family appears to be transitional between Leptograptidæ and Diplograptidæ, but *Dicranograptus* in its life-history shows apparently catagenesis from the

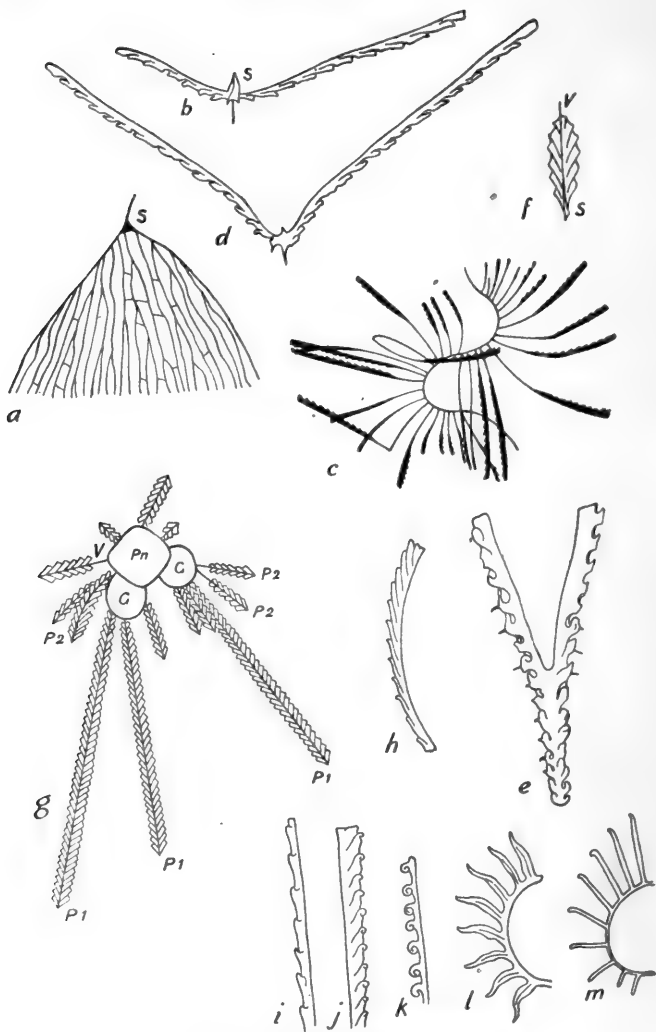


FIG. 88.—(For description see p. 293.)

higher diplograptid stage and may be compared with those early nautiloids (*Lituities*, etc.), which show uncoiling before coiled forms had become well established; while *Dicellograptus* shows only an intermediate stage without any anagenesis. The latter has the range of the family, while the former is Llandeilian and Caradocian only.

Family DIPLOGRAPTIDÆ.—Biserial, with straight unbranched stipes. Thecæ tubular, usually in contact for a large part of their length. Range: Middle Skiddavian to Upper Valentian, with acme from Caradocian to Middle Valentian.

Two genera are usually recognized. *Climacograptus* (Fig. 86) is characterized by the sigmoid curvature of the thecæ, and its "excavations"; *Diplograptus* (Fig. 88, *f, g*) has straight or nearly straight thecæ, overlapping and with aperture everted (turned outwards). The latter has been subdivided into several sub-genera. Dr. Ruedemann of the New York Geological Survey has discovered specimens showing that *Diplograptus* lived in clusters hanging from

FIG. 88.—VARIOUS GRAPTOLITES.

- a*, *Dictyonema flabelliforme* (Eichwald), Tremadocian. Part of polyrapy, with sicula and nema. (Natural size.) (Full length over 80 mm., maximum width 75 mm.) *b*, *Leptograptus flaccidus* (Hall), Caradocian. ( $\times \frac{1}{2}$ .) *S*, Sicula. *c*, *Nemagraptus gracilis* (Hall), Llandeilian. ( $\times \frac{1}{2}$ .) *d*, *Dicellograptus gurleyi* Lapworth, Llandeilian, New York. ( $\times \frac{1}{2}$ .) *e*, *Dicranograptus nicholsoni* Hopkinson, Llandeilian-Caradocian. ( $\frac{3}{4}$ .) *f*, *Diplograptus* (*Petalograptus*) *palmeus* var. *tenuis* (Barrande), Valentian. *S*, Sicula; *V*, virgula. *g*, *Diplograptus foliaceus* M'Coy, Llandeilian, New York. Floating colony. (Natural size.) (After Ruedemann.) *Pn*, Pneumatophore (float); *G*, gonangia (reproductive vesicles); *P*<sub>1</sub>, first generation of polyparies; *P*<sub>2</sub>, second generation; *V*, virgula. *h*, *Monograptus cyphus* Lapworth, Lower Valentian. Thecæ near proximal end. *i*, *M. sandersoni* Lapworth, Valentian. Distal thecæ. *j*, *M. vomerinus* (Nicholson), Salopian. Thecæ near proximal end; in full relief, showing torsion of thecal axis. *k*, *M. lobiferus* (M'Coy), Valentian. Distal thecæ. *l*, *M. convolutus* (Hisinger), Valentian. *m*, *M. (Kastrites) longispinus* Perner, Valentian. (All  $\times \frac{1}{2}$ , unless otherwise stated.) *a*, *e*, *g*, After Ruedemann; *b*, *d*, from Ruedemann, after Lapworth; *c*, from Ruedemann, after Hall; remainder after Elles and Wood.

a float, and that numerous siculæ were developed in reproductive vesicles under the float and grew out from these as a second generation of polyparies (Fig. 88, *g*).

Families GLOSSOGRAPTIDÆ and RETIOLITIDÆ are allied to the last, but show peculiar developments of the test—firstly, in a change from a membrane of uniform thickness to one with strengthening ribs, at last becoming a complex network, in the meshes of which is left a membrane so delicate that it is lost in the fossil state; secondly, in a great development of projecting spines. The latter form the special feature of the *Glossograptidæ* (extending through nearly the whole Ordovician), the network being most highly developed in *Retiolitidæ* (almost confined to Silurian).

Family DIMORPHOGRAPTIDÆ is a small group generally spoken of as transitional between *Diplograptidæ* and *Monograptidæ*. They may either be regarded as monograptids which revert to a diplograptid stage, or as diplograptids in which the formation of the second column is delayed, as they are uniserial only in the early part of the polypary and biserial afterwards. The only genus, *Dimorphograptus*, is confined to the Lower Valentian, being contemporaneous with the earliest monograptids.

Family MONOGRAPTIDÆ.—Uniserial and unilateral. The characteristic Silurian family, ranging from bottom to top of that system.

The chief genus, *Monograptus* (Figs. 87; 88, *h-m*), is divided by Miss Elles and Miss Wood into the following seven groups, characterized by differences in the thecæ, and named after a type-species:

1. *M. cyphus*: thecæ simple, straight, overlapping tubes, with even apertural margins (Middle Valentian to top Salopian; Fig. 88, *h*.)

2. *M. sandersoni*: thecæ with flowing sigmoid curvature and oblique apertural margins (Lower and Middle Valentian; Fig. 88, *i*).

3. *M. vomerinus*: thecæ short tubes with abrupt sigmoid curvature and some torsion of axis (Middle Valentinian to Lower Salopian; Fig. 88, *j*).

4. *M. priodon*: thecæ with apertural region more or less isolated and retroverted (Middle Valentinian to Upper Salopian; Fig. 87).

5. *M. lobiferus*: thecæ with apertural region coiled into a definite lobe (Middle Valentinian to Lower Salopian; Fig. 88, *k*).

6. *M. convolutus*: thecæ triangular or conical, with reflexed apertural margins (Middle and Upper Valentinian; Fig. 88, *l*).

7. Usually taken as a distinct genus, *Rastrites*: thecæ more or less linear and isolate, with reflexed terminations (Middle and Upper Valentinian; Fig. 88, *m*).

The polypary of *Monograptus* is usually straight or slightly curved, but increased curvature resulting finally in a spiral is found in all groups except the second and third, and is the invariable case in the last two.

The name *Cyrtograptus* is applied to monograptids in which branches grow out from certain thecæ, at regular or irregular intervals; the main stipe is more or less spiral. Whether this is justifiably taken as a generic character may be doubted; but the species with this character all occur within a narrow time range (practically Lower Salopian), and although some of them are almost identical in other characters with particular species of *Monograptus*, they are not contemporary with them.

In addition to these well-defined families, there are a number of other genera, with abundant irregular branching, classified loosely as "dendroid graptolites." Some of these may not be graptolites at all, but plants or colonial animals of some other phylum. One genus, however, *Dictyonema* (Fig. 88, *a*), has thecæ of simple type, like those of dichograptids. Its abundant branches are

arranged in the form of a hollow cone, and are connected at intervals by cross-pieces. This genus ranges from Cambrian to Devonian, but it is only common in one well-defined zone in the Lower Tremadoc.

The graptolites have proved of the greatest value as zone-fossils. Thanks to them alone, Professor Lapworth was able to unravel the complexities of structure of the Southern Uplands of Scotland, which had been entirely misinterpreted before. Apart from detailed zoning they provide any geologist with the means of recognizing broad divisions: the complex Dichograptidæ are easily recognized as marking the lowest Ordovician, the Monograptidæ as distinctive of the Silurian, and so on. Their zonal distribution appears to be the same in the Ordovician in Europe and North America, though in the latter region Silurian graptolites (other than Dendroidea) are very rare: it is only in Australia that an important difference in range has been found (see under *Leptograptidæ*, p. 291).

The graptolites have been assumed to be hydrozoa—that is to say, that the individual animal which occupied each theca is supposed to have been a *hydroid polyp*, all the polyps in a polypary being united by a living cord in the common canal. A polyp is essentially a cylindrical sac with an opening (the mouth) at one end, and around the mouth a circlet of tentacles; in a *hydroid* polyp, the internal cavity is undivided.

There are other fossil hydrozoa besides the graptolites: they form calcareous skeletons and may be spoken of as *hydrocorallines* (using that term in a less exact zoological

sense than Moseley's *Hydrocorallinæ*). Chief of these are the *Stromatoporoïds* which form an important constituent of some of the Ordovician, Silurian, and Devonian limestones. Their skeleton consists of close-set, wavy, concentric laminæ traversed by abundant vertical pillars, and the masses of this structure may attain a considerable diameter and thickness.

Similar structures are found here and there in later systems—*e.g.*, the spheroidal bodies, about 25 mm. in diameter, found in the Cambridge Greensand, called *Parkeria*. Some fossils of this kind may, however, be calcareous Algæ.

A modification of the hydroid polyp adapted to a nectic life is the *Medusa*, or jelly-fish. These most delicate of living organisms would appear to be the most hopeless to look for among fossils, yet remains of such have been preserved in such fine-grained sediments as the lithographic Limestone of Solnhofen and the Middle Cambrian Shale of Mount Stephen, British Columbia.

A more advanced type of polyp than the hydroid is the *coral polyp*, in which the internal cavity comes to be divided into a central throat, leading down from the mouth, and a series of peripheral chambers separated by radiating partitions (mesenteries). This characterizes the Actinozoa, which is one of the classes of the phylum Cœlenterata, the Hydrozoa being another class. The common sea-anemone is an example of a polyp of this advanced type, but it secretes no hard parts (*stereom*). Those Actinozoa which do are spoken of as *corals*, a term which has no

exact taxonomic value, but is a very useful one, especially in palæontology.

1. **Zaphrentis** (Fig. 89) is a genus of which there are several species common in the Carboniferous Limestone. Though the following description applies essentially to *Z. konincki*, much of it is true of other species.

The shape is that of a drinking-horn—that is, a cone with its axis more or less curved. An ordinary specimen is about an inch (25 mm.) in height, and about 12 mm. in diameter at the broad end. The external surface is marked with concentric rings, obviously lines of growth, and in some species there are also fine vertical ribbings.\* The curvature of the cone may be in part the effect of the conditions of growth: a cone fixed by its apex and growing larger upwards is in unstable equilibrium. If not firmly fixed it will topple over towards one side, and, fixing itself in that position, will become curved in the effort to grow straight upwards. The direction of curvature is always determined by the internal structure to be described next.

At the broad (distal) end the cone is hollowed out into a depression (the *calyx*) about 6 mm. deep, with steep sides and a nearly flat floor. A well-marked groove, the *fossula*, extends from the centre of this floor to that side which

\* In specimens from Tournai, Belgium, otherwise very well preserved the surface-ornament is largely obliterated by chemical alteration of the substance of the coral. The original aragonite has been replaced by chalcedonic silica, not uniformly (as is often the case in other fossils), but in a series of rings, alternately thick and thin. This is known as "beekite"-structure (see Chap. XI.). It is found also in brachiopods, lamellibranchs, etc., in strata of various ages.



corresponds to the convex curve of the horn (Fig. 89, *b*). The sides and floor of the calyx bear a radiating series of ridges, the *septa*, which are the most distinctive character of corals in general. In this species they are over sixty in number and arranged in an alternation of two series. One series, the *major septa* (or *entosepta*), extend from the margin of the calyx to the centre of its floor. The

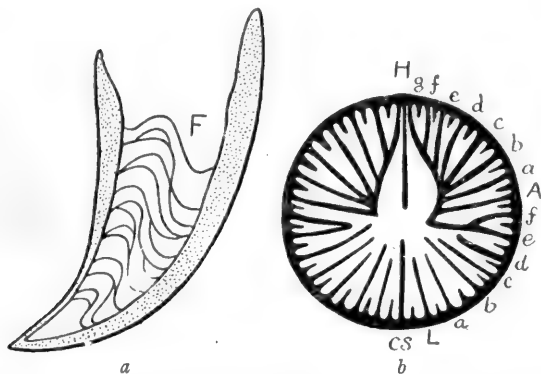


FIG. 89.—ZAPHRENTIS KONINCKI, MILNE-EDWARDS AND HAIME.

Diagrams of vertical and transverse sections. (After Carruthers, simplified.)  
*a*, Vertical section. ( $\times 2$ .) Cardinal and counter septa dotted.  
*F*, fossula. *b*, Transverse section. ( $\times 5$ .) *H*, Cardinal; *CS*, counter;  
*A*, alar septa; *a-g*, metasepta, lettered in order of development. The short unlettered septa are minor septa.

alternate *minor septa* (or *exosepta*) are thinner, less prominent, and confined to the calyx sides. Although the septa are, in a general way, radial, the presence of the fossula makes the whole calyx very distinctly bilateral, and there cannot be said to be more than an approximation to radial symmetry. The major septum which corresponds to the middle line of the fossula is shorter

and less prominent than the others: it is called the *cardinal septum*. The next major septa on either side are nearly parallel, converging very slightly downwards on the calyx-sides, and diverging slightly on the floor, where they form the boundaries of the fossula. It is not easy to make out any further characters of the septa in the

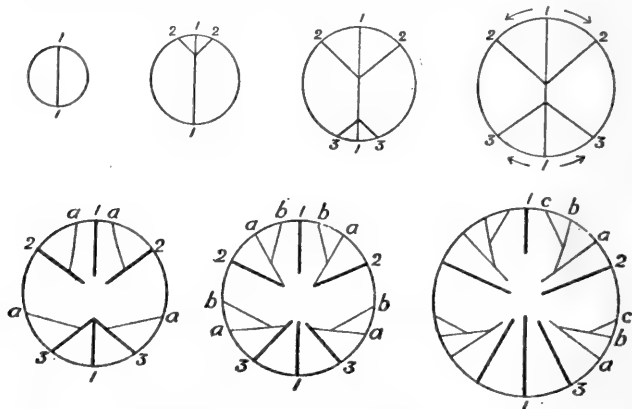


FIG. 90.—DEVELOPMENT OF MAJOR SEPTA IN A RUGOSE CORAL.

1, 2, 3, Protosepta; *a*, *b*, *c*, metasepta; 1, cardinal and counter septa; 2, alar septa; 3, counter-lateral septa. Seven successive transverse sections, giving ontogenetic stages, are shown. The numbering and lettering denote the order of development of the septa. (After Caruthers and Duerden.)

calyx, but by taking transverse and longitudinal sections through the coral more may be learned.

If a section were taken very near the apex of a well-preserved specimen, it is probable (from what is known in allied corals) that at the very early stage of growth here preserved, six septa only would be present. Owing to the destruction of the actual apex in most specimens it is not possible to prove this, but these six primary

septa can easily be recognized in slightly later stages, and by means of a series of transverse sections the method by which additional septa are intercalated can be recognized: this method shows that the symmetry of the coral is bilateral, not radial (Fig. 90). One of the six primary septa is the cardinal septum, already noted; another which is and remains exactly opposite to this is called the *counter-septum*. The two on either side of this are the *counter-lateral* septa; the two between them and the cardinal are the *alar* septa.

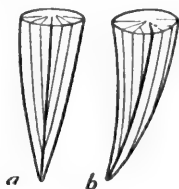


FIG. 91.—SEPTAL DEVELOPMENT IN RUGOSA.

Diagrammatic side views of apex. *a*, Showing cardinal septum in centre, metaseptum arising on both sides of it; *b*, showing alar septum in centre, cardinal on right margin, counter on left, metaseptum arising on only one side of alar septum, away from cardinal.

Professor Duerden distinguishes the six first septa as *protosepta*, and the major septa that arise later as *metasepta*. As growth proceeds, additional major septa appear between the cardinal and alar septa, and between the alar and counter-lateral, but none between the counter-lateral and counter-septum (Fig. 91). There are thus four spaces only in which new septa appear, and the newest septum in each space is always that nearest the cardinal septum. The minor septa, on the other hand, appear simultaneously after the full number of major septa has been formed.

The transverse sections also show that the cone is hollow, consisting of a *visceral cavity* with a comparatively thin wall (the *theca*), and divided by the septa into *loculi*. Near the theca there may be seen a few curved calcareous plates crossing some of the loculi: these are called dissepiments.

A vertical section shows that the floor of the calyx is the last of a series of horizontal partitions (*tabulæ*) across the visceral cavity, which must be formed, as growth proceeds, in somewhat the same way as the septa are formed in a cephalopod-shell. They do not, however, serve the same function, as all corals are fixed animals; they are much less regular in arrangement, and have no perforation like a siphuncle. Each tabula is convex upwards, and in addition to the cardinal fossula there can sometimes be recognized three other similar, but much slighter, fossulæ, in the position of the two alar and counter-septa. The counter-lateral septa have no fossulæ. The septa are continuous through the tabulæ. In those species of *Zaphrentis* which have external ribbing, the ribs alternate with the septa.

The general facts of the development of the septa stated for *Zaphrentis* apply to a very large series of Palæozoic corals, which constitute the extinct order Rugosa. By the late Professor Haeckel they were called the "Tetracoralla," because of the four principal septa and fossulæ, and in distinction from the Mesozoic and modern "Hexacoralla," in which the septa are arranged by sixes. But the recent discovery of the early appearance of the counter-lateral septa makes this numerical distinction inaccurate.

When a *Zaphrentis* grows large it may pass from conical to cylindrical in shape, and then a change takes place in the septa: instead of continuing as vertical plates through the later-formed tabulæ, they retain the form seen in the calyx, of low ridges on the upper surface of the tabula rising up on the inner face of the theca as low vertical ridges. Such a condition is described as the "amplexoid habit," because it attains its fullest development in the genus *Amplexus*. In this form, the tabulæ are so horizontal and far apart, and the septa reduced to such feeble ridges, that J. Sowerby, who first described it a century ago, mistook it for a cephalopod-shell, and, thinking the resemblance to a coral was accidental, called the species he described *Amplexus coralloides*. The same habit is seen, rather less pronounced, in the genus *Caninia*, species of which may attain a gigantic size. This is distinguished from *Zaphrentis* by the far greater abundance of dissepiments between the septa for some distance in from the theca. These two genera occur, like *Zaphrentis*, in the Carboniferous Limestone of England and Belgium.

If we now try to form an idea of the animal of which the skeleton has just been described, we can only do so by analogy with living corals. The main living part of the body of *Zaphrentis* must have lain within and beyond the calyx, and perhaps it could shrink up within the calyx completely when safety required it. In structure it was essentially a polyp, but more complex than a hydroid polyp. From the tentacle-surrounded mouth a short tube projected down into the general cavity, and

from this tube to the outer wall there radiate a series of vertical partitions (mesenteries), which also extend down to the base of the general cavity, which is thus incompletely divided into radiating chambers. It might easily be supposed that the septa are the skeleton of the mesenteries, but this is not the case: the mesenteries occupy the centre of the interseptal loculi; and where the septa come the wall and floor of the polyp are, as it were, indented by them, for the whole skeleton is a secretion of the external layer of the polyp.

2. **Lithostrotion irregulare** (Fig. 92) is a coral very abundant in some of the uppermost beds of the Carboniferous Limestone (zone D<sub>2</sub>). At Wrington, Somerset, for instance, it occurs in great masses, red-stained by iron oxide. It is a *compound* coral, consisting of a mass of vertical cylindrical *corallites* (each secreted by a single polyp), loosely in contact or slightly separated, and originating one from another by lateral branching. Only near the base of the *corallum* (as the whole compound skeleton is termed) is branching abundant, but it occurs occasionally at higher levels. Externally each corallite is marked by slight horizontal wrinkles, closely set. The calyx of a full-grown specimen shows twenty-four major septa and as many minor, the former reaching nearly to the centre, the latter scarcely projecting through a narrow marginal zone of dissepiments; but in young specimens or cross-sections of the early parts of the colony, eighteen major only can be found, and there may be fewer. In the centre of the calyx there projects a laterally compressed structure, the *columella*. In a vertical

median section of a corallite this is seen to be a vertical pillar extending the whole length. It is crossed by numerous very regular tabulæ, which are very slightly convex upwards except near the columella, where each is lifted up into a cone, and towards the margin, where it falls steeply into the marginal zone of dissepiments. In the calyx of an adult corallite the septa appear very

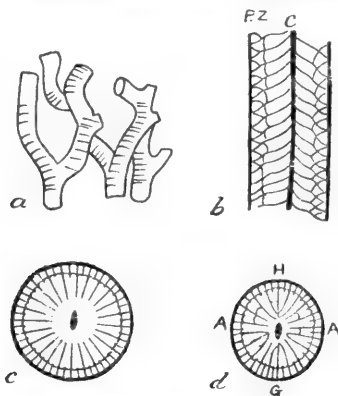


FIG. 92.—LITHOSTROTION IRREGULARE (PHILLIPS), VISEAN (CARBONIFEROUS LIMESTONE).

- a*, Small portion of a young corallum. ( $\times \frac{1}{2}$ .) *b*, Vertical section of a corallite. ( $\times 2$ .) *c*, Columella; *P.Z.*, peripheral zone of dissepiments. *c*, Transverse section of a full-grown corallite. ( $\times 3$ .) *d*, Transverse section of a young corallite. ( $\times \frac{5}{2}$ .) *H*, Cardinal; *G*, counter; *A, A*, alar septa. *a, b, c*, After Milne-Edwards and Haime; *d*, original.

perfectly radial. The compression of the columella, however, indicates a median plane, and on examining a cross-section of the younger part of a corallite, a distinctly bilateral arrangement can be recognized, and the same proto-septa as in *Zaphrentis* can be made out (Fig. 92, *d*).

In other species of *Lithostrotion* (e.g., *L. martini*, which

has twenty-eight major septa) the proto-septa are better defined: in these species, however, the much greater abundance of dissepiments tends to confuse the appearance of a cross-section.

Some species of *Lithostrotion* have cylindrical corallites in a loose bundle, like *L. irregularis*; in others (*L. basaltiforme*) they are tightly packed together and become polygonal (mostly hexagonal) in section.

The essential feature of the genus is the laterally compressed columella. Its species are confined to, and very abundant in, the upper stage (Visean) of the Carboniferous Limestone.

3. **Parasmilia centralis** is a simple coral found in the White Chalk of England. It is attached to molluscan or echinoid shells by a spreading base, from which rises a short cylindrical peduncular portion, soon expanding into a conical form which may attain a length of 25 mm. and a diameter of 12 mm. If further growth takes place, the form becomes cylindrical; a total length of 75 mm. or more may be attained. The calyx is nearly circular, and shows a prominent columella (which in a section is seen to be spongy in texture), and forty-eight septa showing almost perfect radial symmetry. Instead of being in two series, major and minor, there are four series (*cycles*) of unequal length. The first cycle consists of six long septa, reaching the columella; the second, of six, slightly shorter, alternating with the first six; the third, of twelve, decidedly shorter, alternating with those of both first and second cycles; and the fourth of twenty-four, still shorter, and alternating with all the others. This arrangement



differs altogether from that of *Zaphrentis* and *Lithostrotion*, and as it is generally characteristic of Mesozoic and later corals, they are often united as Hexacoralla in contrast to the Palæozoic Tetracoralla.

A vertical section shows the visceral chamber to be

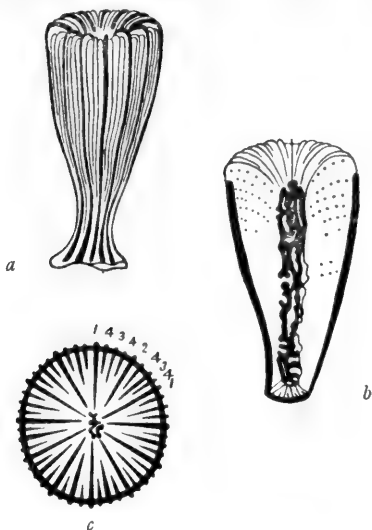


FIG. 93.—PARASMILIA CENTRALIS (MANTELL).

*a*, Young specimen. ( $\times \frac{3}{2}$ .) *b*, Vertical section. ( $\times \frac{3}{2}$ .) Trabecular columella in centre, black; dots represent granulations on septa; thick marginal lines represent theca in section; edges of half the septa seen at the top and (broken section) at the bottom. *c*, Calyx. ( $\times 2$ .) Numbers denote septa of the four cycles. (After Milne-Edwards and Haime.)

free from tabulæ and dissepiments; the surfaces of the septa bear little tubercles. At the edge of the calyx the septa project and extend across the theca into continuity with a series of vertical ridges (*costæ*) on its outer surface. These *costæ* show by their varying strength an arrange-

ment in the same cycles as the septa, except that the first and second cycles are not distinguishable.

Dr. W. D. Lang, of the British Museum, has shown that these costæ pass through a series of stages in ontogeny. On the peduncle the costæ are low and faint (they are also only twelve in number, the last cycle of septa not being yet developed); as growth proceeds they become stronger, but remain quite smooth. This anagenesis of costæ continues for a distance, and is followed by a sudden catagenesis, the costæ almost disappearing. A second long period of anagenesis follows, but this time the costæ are not smooth, but have a roughened or etched appearance. This is as far as the development goes in *P. centralis*, though if it continues to grow in cylindrical form there will be several temporary stoppages of growth, followed by a *rejuvenation*—a fresh start being made from a lower stage of anagenesis than had been reached before the stoppage.

In other species of *Parasmilia*, the anagenesis of etched costæ is followed by another sudden catagenesis, and that by a third period of anagenesis in which the costæ have a granulate appearance. There are thus three types of costæ, and if we recognize three stages in each (low, medium, and high), altogether nine stages. No species shows all nine. Those which come earliest in time show the first four (*P. serpentina*) or six (*P. centralis*); later species skip the first three stages (tachygenesis), and show the next five (*P. granulata*) or six (*P. gravesi*); still later forms (*P. cylindrica*, *P. mantelli*) start straight away with granulate costæ, and show the last three

stages only. Rejuvenation may also occur to lengthen out the life-history, but that is an independent phenomenon that may intervene at any stage.

The classification of the corals is in a state of flux at present, and the following scheme is really out-of-date, but in the absence of any complete modern scheme it must be retained provisionally. Also the classification of corals cannot be separated from that of their non-calcareous allies, which are here distinguished by an asterisk as of little importance or none to the palæontologist.

CLASS : **ACTINOZOA** (or **Anthozoa**).

SUB-CLASS : **Zoantharia**.

ORDER : **ACTINIARIA** \* (sea-anemones).

**ANTIPATHARIA** \* (with horny skeleton).

**MADREPORARIA** (with calcareous skeleton : the true corals).

SUB-ORDER : **Rugosa**.—These are the Palæozoic Madreporaria, often termed *Tetracoralla*, because characterized by four principal septa (cardinal, counter, and two alar), Mesozoic and later corals being termed *Hexacoralla*, because their symmetry is based on six main septa. (The recognition of the early development of the counter-lateral septa, making six, in the Rugosa has weakened, but not destroyed, this distinction.) The usual abundance of tabulæ is another general point of distinction in the Rugosa.

GROUP : **Inexpleta**.—This includes a few simple corals, in which the interseptal loculi are almost entirely undivided, tabulæ and dissepiments being very rare. Common genera : *Turbinolopsis*, conical, with occasional tabulæ, found as casts in Llandovery Sandstone ; *Palæocyclus* (Fig. 94, a), of which the commonest species is discoidal—*i.e.*, the angle of the cone is increased to 180°

and the theca no longer encloses the visceral chamber, common in the Wenlock Limestone; *Cyathaxonia*, acutely conical, with strong columella, Carboniferous Limestone.

GROUP: **Zaphrentoidea**.—Simple corals; septa and tabulæ well developed, but few dissepiments. Includes *Zaphrentis*, *Caninia*, and *Amplexus*, already mentioned. *Streptelasma* (Ord.-Sil.) is usually associated with them, but although earlier in time it has a more elaborate structure.

GROUP: **Cyathophylloidea**.—Simple or compound, with a marginal zone of vesicular tissue; tabulæ usually less extensive than in Zaphrentoidea.

Family *Cyathophyllidæ*.—Septa with smooth surfaces, the primary lamella of each septum being thickened uniformly on each face with a layer of stereoplasma; primary septa not strongly marked, symmetry approaching radial. A large family, with chief genera: *Cyathophyllum* (Sil.—Carb., Fig. 94, *c*), simple or compound, with major septa reaching almost to centre, and minor septa not very much shorter; *Acervularia*, compound, massive, the septa swelling out at a certain distance from the centre so as to unite to form a circular "inner wall"; *Lithostrotion*, already described; *Omphyma*, simple, top-shaped, with root-like outgrowths, the four main septa often very conspicuous.

Family *Heliophyllidæ*.—Septa with stereoplasma deposited in vertical ridges, otherwise much like *Cyathophyllidæ*. Genera: *Heliophyllum* (Sil.—Dev.), simple; *Phillipsastræa* (Dev.—Carb.), compound.

Family *Clisiophyllidæ*.—With a large "false columella" (not a solid rod, but made up of twisted lamellæ, having a "spider's web" appearance in transverse section, and making a large protuberance in the calyx). Genera: *Clisiophyllum* (Sil.—Carb.), simple; *Lonsdaleia* (Carb., Visean, Fig. 94, *b*), compound; *Dibunophyllum* (Visean),

simple, with a lamina from cardinal to counter-septum running through the false columella.

GROUP: **Cystiphyloidea**.—Simple; with great development of dissepiments, replacing tabulæ and leading to degeneration of the septa. Includes the only corals with an operculum to the calyx. Genera: *Cystiphyllum* (Sil.–Dev.), cylindro-conical, no operculum; *Goniophyllum* (Sil.), four-sided pyramidal, with an operculum of four pieces; *Calceola* (Dev., Fig. 94, *d*), slipper shaped, with an operculum of one piece.

The post-Palæozoic Madreporaria are sometimes united as Hexacoralla. The order of development of the septa in them differs greatly from that of Rugosa. They are usually divided into three orders (or sub-orders), though it is now very doubtful if these express natural affinities.

SUB-ORDERS: **Aporosa**.—Theca and septa compact. Include two principal families.

Family *Turbinolidæ*.—Without dissepiments. Simple. Genera: *Turbinolia* (Eoc.–Rec.), conical, with projecting lamella and very prominent costæ; *Smilotrochus*, similar but no columella; *Flabellum* (Eoc.–Rec.), compressed, calyx elliptical, costæ weak.

Family *Astræidæ*.—With dissepiments; simple or compound. Includes the chief reef-building corals. Genera: (1) Simple—*Parasmilia* (Cret.), already described; *Montlivaltia*, (Jur.–Cainozoic), conical, turbinate or discoidal, no columella, dissepiments abundant, covered externally by a perishable calcareous skin (*epitheca*). (2) Compound—*Thecosmilia* (Jur.–Cain., Fig. 94, *e*), essentially a *Montlivaltia*, which becomes compound by equal fission; *Isastræa* (Trias.–Cret., Fig. 94, *f*), massive, with prismatic corallites; *Holocystis* (Lower Cret., Fig. 94, *g*), massive, remarkable for superficial resemblance to some Rugosa, there being four septa longer than the others, and tabulæ being well developed.

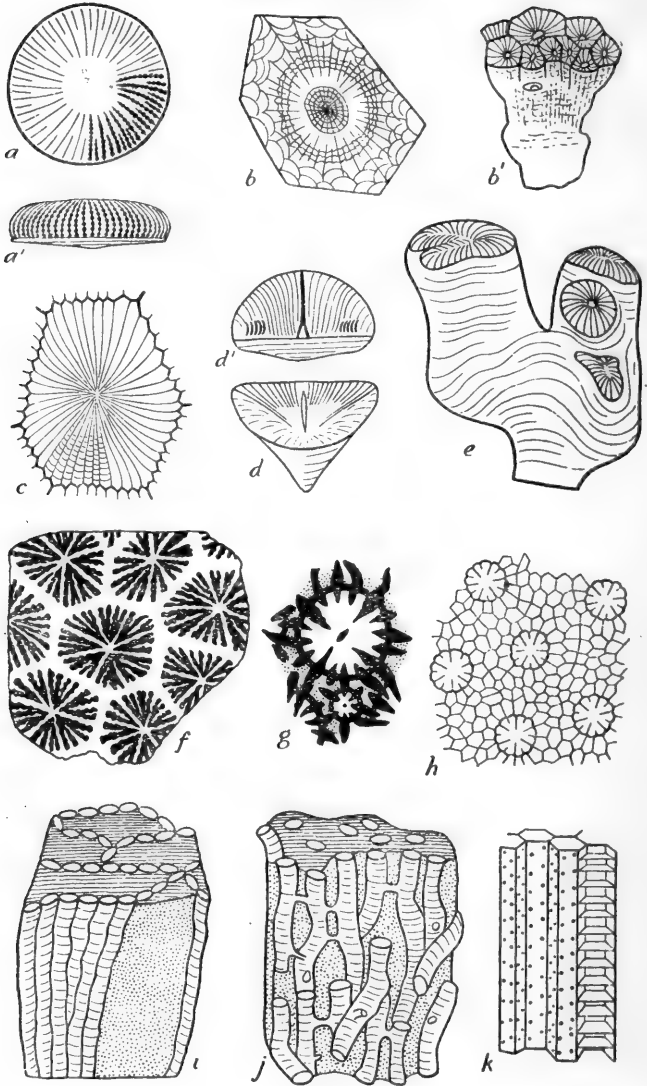


FIG. 94.—(For description see p. 313.)

**SUB-ORDER: Fungida.**—Dissepiments replaced by calcareous rods (*synapticulæ*) crossing the interseptal loculi. Genera: *Anabacia* (Jur.), simple, discoidal; *Cyclolites* (Jur.-Eoc.), similar, but septa are thin and perforate, thus approaching the next sub-order; *Thamnastræa* (Jur.), compound, massive, septa continuous from one corallite to its neighbours.

**SUB-ORDER: Perforata.**—All parts of the skeleton traversed by pores, which may reduce it to a spongy network. Genera: *Stephanophyllia* (Cret.-Rec.), simple, discoidal; *Dendrophyllia* (Eoc.-Rec.), compound, tree-like (dendroid); *Goniopora* [*Litharæa*] (Eoc.-Mio.), compound, massive.

**SUB-CLASS: Alcyonaria.**—Skeletons of very variable character. Many extinct forms are doubtfully placed here. Septa usually feeble or absent, and never showing either a tetracorallan or hexacorallan plan; tabulæ well developed. All compound. Genera: *Favosites* (Sil.-Carb., Fig. 94, *k*), massive, corallites polygonal, septa vestigial, tabulæ horizontal and regularly spaced,

FIG. 94.—FOSSIL CORALS.

- a*, *Palæocyclus porpita* (Linné), Wenlock Limestone. Plan of calyx, detail omitted from three quadrants. *a'*, Side view. ( $\times \frac{3}{4}$ .) *b*, *Lonsdaleia floriformis* (Fleming), Visean (Carboniferous Limestone). Cross-section of single corallite. ( $\times 2$ .) *b'*, Side of young corallum. ( $\times \frac{1}{2}$ .) *c*, *Cyathophyllum hexagonum* Goldfuss, Middle Devonian. Cross-section of single corallite. ( $\times \frac{3}{2}$ .) Dissepiments omitted from greater part. *d*, *Calceola sandalina* Lamarck, Middle Devonian. ( $\times \frac{1}{2}$ .) *d'*, Operculum. (After Goldfuss.) *e*, *Thecosmilæ annularis* (Fleming), Argovian (Coral Rag). ( $\times \frac{1}{2}$ .) *f*, *Isastræa oblonga* (Fleming), Portlandian. Section of silicified corallum. ( $\times 3$ .) Thecæ and septa white. *g*, *Holocystis elegans* (Fitton), Aptian (Atherfield Clay). Surface of part of corallum. ( $\times 6$ .) Septa and columella, black; theca, dotted. *h*, *Heliolites porosa* (Goldfuss), Middle Devonian. Transverse section. ( $\times \frac{1}{2}$ .) *i*, *Halysites catenularia* (Linné), Silurian. Diagrammatic view of portion of a corallum. ( $\times \frac{3}{4}$ .) *j*, *Syringopora ramulosa* Goldfuss, Lower Carboniferous. (Natural size.) *k*, *Favosites gothlandica* Lamarck, Wenlock Limestone. Diagrammatic view of four corallites. ( $\times 4$ .) The exterior of three is seen, with mural pores, the fourth is split vertically in half, showing tabulæ. *d*, After Goldfuss; *i* and *k*, original; the rest after Edwards and Haime.

*mural pores perforating the thecæ; Pachypora (Dev.), similar but branching, with thickened walls; Alveolites (Sil.-Dev.), similar to the last, but calyces cusped-triangular; Michelinia (Carb.), with tabulæ strongly arched, corallum with thick epitheca bearing root-like out-growths; Syringopora (Sil.-Carb., Fig. 94, j), corallites cylindrical, spaced out and connected by horizontal tubes, tabulæ funnel-like; Aulopora (Sil.-Carb.), an encrusting network of tubular corallites, with raised trumpet-like apertures; Halysites (Ord.-Sil., Fig. 94, i), like the last, but corallites rise up vertically, forming linear series—the "chain-coral"; Heliolites (Sil.-Dev., Fig. 94, h), massive, two kinds of corallites, abundant small polygonal and scattered larger cylindrical, both with tabulæ, the latter with apparent septa.*

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## IX

### THE PORIFERA AND PROTOZOA

BELOW the Cœlenterata there are two grades of animal structure, both of importance in palæontology—the Porifera or Sponges, and the Protozoa, simplest of all animals.

The **Porifera** are so named because they take in their food, not by a single mouth as do all animals from Cœlenterates upwards, but by innumerable pores scattered over the surface of the body. As a consequence of this, and of their fixed mode of life, the form of the body is much more variable than in any phylum yet considered, and is sometimes very indefinite indeed. The skeleton in the more primitive forms is composed of great numbers of separate *spicules* usually of amorphous silica (opal), but of calcite in one class. These spicules form a support to all parts of the body, but are only united by soft tissues, so that on the death of the sponge they fall apart and are scattered on the sea-floor. In many cases two kinds of spicules may exist in the same sponge—*body spicules*, elongated and often branched, and *dermal spicules*, flat or rounded. A simple spicule in the fresh state, when seen under the microscope, has the appearance of a fragment of thermometer-tube, being glassy and with a

fine central canal. Some of the most characteristic forms of spicule are shown in Fig. 95. Loose siliceous spicules of this kind accumulate in such amounts on the sea-floor to-day as to form a "spicular ooze," as, for instance, off Kerguelen, at a depth of 120 fathoms. Similar deposits among the stratified rocks have passed

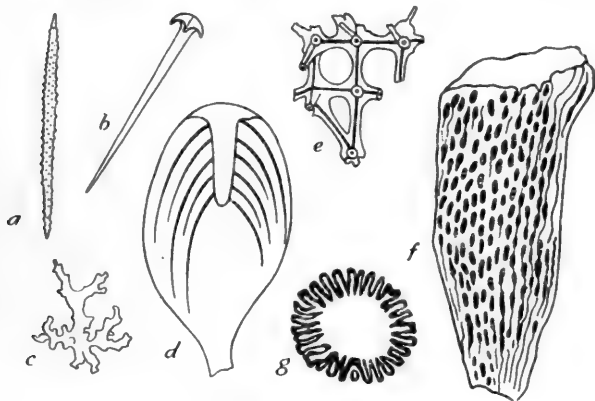


FIG. 95.—PORIFERA.

- a*, Monactinellid ( $\times 15$ ), and *b*, Tetractinellid ( $\times 10$ ) spicules from interior of hollow flint. *c*, Dermal spicule of a Lithistid, Upper Chalk. ( $\times 32$ .) *d*, *Siphonia tulipa* Zittel, Cenomanian (Upper Greensand), Warminster (Wilts). Vertical median section (stalk broken off) showing vertical canals opening into central cloaca. *e*, Fragment of hexactinellid meshwork, showing central canals (black), Neocomian. ( $\times 30$ .) *f*, *g*, *Ventriculites infundibuliformis* S. P. Woodward, Upper Chalk. *f*, Side view of imperfect specimen; *g*, cross-section. (Both  $\times \frac{1}{2}$ .) (All after Hinde.)

into *cherts*, the spicules becoming cemented by a secondary deposit of chalcedony into a very hard rock. Such sponge-cherts are found in Britain in the Carboniferous Limestone, at several Jurassic horizons, and particularly in the Lower and Upper Greensands of the Cretaceous.

In the higher orders of sponges the spicules are united

into a meshwork, and in such cases the form of the body is preserved in the fossil. The substance never persists as unaltered opal; it may simply change into chalcedony, or may be replaced by pyrites, marcasite (passing into limonite), or calcite.

The common bath-sponge belongs to a class having a continuous skeleton of a horny organic substance, but such forms are not preserved as fossils, and palæontologists are only concerned with two classes, distinguished by the chemical composition of the skeleton.

CLASS : **SILICISPONGIÆ**. \*—Skeleton of silica.

ORDER 1 : **Monaxonida**.—Spicules one-rayed (Fig. 95, *a*). Only known fossil by loose spicules, except one genus *Cliona*, a boring sponge in lamellibranch shells and belemnite-guards, known by its borings, often preserved as internal casts in flint.

ORDER 2 : **Tetragonida**.—Spicules four-rayed (Fig. 95 *b, c*).

SUB-ORDER : **CHORISTIDA**.—Spicules not united.

SUB-ORDER : **LITHISTIDA**.—Spicules united into a continuous skeleton (Fig. 95, *c*). Genera : *Siphonia* (Cret., Fig. 95, *d*), pear-shaped, stalked; *Doryderma* (Cret.), cylindrical, branched; *Verruculina* (Cret.), cup-shaped or irregular, with short stalk.

ORDER 3 : **Hexactinellida**.—Spicules of six rays, intersecting at right angles (Fig. 95, *e*). In the earliest genus *Protospongia* (Camb.) the spicules were very feebly united, as they are found only a few together, the form of the body being unknown. The same is the case with

\* Zoologists do not admit this as a natural group: they make Hexactinellida a class in itself, and unite the remainder with the horny sponges as a class, Demospongiæ.

other Palæozoic genera, but from the Trias onwards a continuous skeleton is found. Genera: *Ventriculites* (Cret., Fig. 95, *f, g*), more or less inverted conical, with roots, wall of cone folded; *Plocoscyphia* (Cret.), frilled laminae uniting into a coarse net-work; *Cæloptychium* (Cret.), mushroom-shaped, with folded wall. Siliceous sponges attain their greatest abundance in Europe in the Cretaceous system.

CLASS: **CALCISPONGIÆ**.—With calcareous skeleton. There are several orders, with three-rayed spicules, not forming a continuous skeleton, but little is known of them in the fossil state.

ORDER: **Pharetrones**.—Spicules united into a fibrous meshwork. Genera: *Barroisia* (Cret.), clusters of double cylinders, the space between the inner and outer cylinder being crossed by partitions much coarser than the tabulæ of a coral; *Peronidella* (Trias.-Cret.), hollow, cylindrical; *Raphidonema* (Cret.), more or less cup-shaped. Calcareous sponges are locally very abundant in the Upper Jurassic of South Germany, the Lower Cretaceous of Faringdon in Wiltshire and Upware in Cambridgeshire, and the Upper Cretaceous (Cenomanian) of Westphalia, but are rare in general.

The **Protozoa** are animals composed of a single cell, or a small number of undifferentiated cells. Only two orders leave fossil remains—the Radiolaria, which form a beautiful lattice-work skeleton of silica, and the Foraminifera, which have one of calcite, aragonite, or of agglutinated foreign bodies. The majority of forms in both orders are very small, ranging from 1 mm. diameter downwards, but some of them occur in such abundance at certain horizons as to be quite important rock-forming

organisms. A few genera of Foraminifera attain a much greater size, up to a maximum of perhaps 80 mm., and these giant forms are of value as indices of age, though unfortunately their geographical range is limited.

The Radiolaria range from possibly pre-Cambrian to the present day: they are divided into two main sub-orders—*Spumellaria*, spherical or discoïdal, with the range of the order, and *Nassellaria*, of various forms, but always with dissimilar ends, dating from the Devonian only. Beds of Radiolarian chert are known in the Ordovician of South Scotland, the Devonian of New South Wales, the Carboniferous of Devon and Cornwall, and the Mesozoic of the Alps. These beds have very generally been taken as analogous to the modern Radiolarian ooze of the greatest depths of the oceans; but in the case of the British Lower Carboniferous cherts their shallow-water character seems now decisively proved. On the other hand, the Miocene Radiolarian earths (not consolidated into chert) of Barbados and other West Indian islands are probably of deep-sea origin.

The Foraminifera form a shell which is nearly always chambered, the chambers being arranged sometimes in a straight line, sometimes in a zig-zag, but most frequently in some sort of spiral. They were at one time taken for cephalopods, but the resemblance in the shells of the two groups is only homœomorphy of the most general sort. There are no gas-chambers in a foraminifer, the cell-protoplasm filling all the chambers as well as extending to a greater or less extent outside the shell; this it does through a well-defined aperture (much smaller

than the diameter of the chamber) in the last-formed chamber, and (in one sub-order) through numerous perforations of the whole surface. Moreover, the foraminifer does not cut off new chambers by secreting septa—each “septum” formed the terminal part of the outer shell before it was converted into an internal structure by the building of a new chamber in front of it. The ontogeny reveals in many cases a striking *dimorphism*: in the same species growth may begin by a very



FIG. 96.—DIMORPHISM IN A FORAMINIFER, *Biloculina bulloides*, D'ORBIGNY, RECENT.

*a*, Exterior showing aperture with T-shaped partition. ( $\times \frac{3}{2}$ .) *b*, Cross-section of microspheric and *c*, of megalospheric form. ( $\times 125$ .) Only the early chambers are shown, up to the attainment of the regular alternation of chambers. Chambers numbered in order of development. (After Schlumberger.)

small chamber (*microspheric* form) or by a much larger one (*megalospheric* form). The study of living forms has shown that this is due to an alternation of generations.

The microspheric form is produced by a sexual process, and its ontogeny is complete; the megalospheric is produced asexually, and the early stages are skipped altogether, just as they are in a rejuvenated coral (Fig. 96, *b*, *c*). The microspheric form in some species attains

a much larger size than the megalospheric; in others there is no difference in size. Both forms occur together in the same strata, the megalospheric forms being more abundant than the microspheric—a natural result of the fact that a number of megalospheric generations intervene between one microspheric and the next. The late Robert Douvillé noticed that in the last beds in which a given species occurred, megalospheric individuals might be exclusively present—an indication of near approach to extinction.

The Foraminifera have been divided into three orders, based on the structure and composition of the test: (1) *Perforata* or *Hyalina*, with test of calcite, transparent (at least in the more primitive forms) and with abundant small perforations in addition to (rarely without) a main aperture in the last formed chamber; (2) *Imperforata* or *Porcellanea*, with shell of aragonite, less translucent and of a brown colour by transmitted light, and without perforations; (3) *Arenacea*, in which the test is formed of foreign bodies, such as sand-grains, sponge-spicules, or the small tests of other Foraminifera, held together by an organic secretion. The first two orders are well defined, but the third is probably a rather mixed assemblage of forms which have been led by special circumstances to adopt this curious way of protecting themselves in place of secreting a shell.

The five principal families of the *Perforata* are as follows:

1. **Lagenidæ**, the simplest forms, with thin transparent shell. Genera: *Lagena*, single-chambered, flask-shaped; *Nodosaria*, a straight row of chambers (orthocone); *Cristellaria*, spiral (ophiocone to sphærocone). These all appear to range from Lower Cambrian to



Recent; *Webbina* (*Vitriwebbina*), an irregular row of elliptical chambers, encrusting shells (Jur.-Rec.).

2. **Textularidæ**, with a zig-zag alternation of chambers. Chief genus: *Textularia* (Camb.-Rec.).

3. **Globigerinidæ**, with chambers globose, usually in a somewhat irregular spiral, perforations coarse. Chief genus: *Globigerina* (Camb.-Rec.), a most abundant pelagic form at the present day. Associated with it is the perfectly spherical *Orbulina*, of which most specimens when broken open are found quite hollow, but occasionally a *Globigerina* is found inside: this suggests that *Orbulina* is the final stage of *Globigerina*, the majority of specimens being megalospheric and omitting the *Globigerina*-stage in ontogeny.

4. **Rotalidæ**, with chambers coiled in an asymmetric spiral, all the whorls being visible on one face, and only the last whorl on the other. In this family first appears the *supplemental skeleton*, an outer calcareous layer plastered over the surface of the ordinary perforate wall, penetrating between the two folds of the latter which here form the septa, and sometimes forming a surface ornament (even long spines in some) which quite obscures the arrangement of the chambers.

Chief genera: *Discorbina* (Cret.-Rec.); *Planorbulina* (Carb.-Rec.); *Truncatulina* (Carb.-Rec.); *Anomalina* (Cret.-Rec.); *Pulvinulina* (Jur.-Rec.), with the form described above, but differing in the relative convexity of the two faces, without supplemental skeleton; *Rotalia* (Jur.-Rec.), with supplemental skeleton, but recognizably spiral; *Calcarina*, discoidal with peripheral spines, spiral internally (Cret.-Rec., chiefly in Maestrichtian); *Tinoporos*, similar shape but chambers irregularly arranged, and surface with pattern of tubercles (Eoc.-Rec., abundant on modern coral-reefs).

5. **Nummulinidæ**, spiral or cyclical, with subdivided chambers, and great development of supplemental skeleton, surface generally smooth, never spinose. This family includes most of the giant Foraminifera, and most of those useful as time-indices. Genera: *Fusulina* (Carb.—Perm.), spindle-shaped, spirally coiled about the long axis; *Polystomella* (Cret.—Rec.), lenticular, last whorl only visible externally, its chambers and their subdivisions recognizable on the surface; *Nummulites* or *Nummulina* (Carb.? Eoc.—Rec.), discoidal or lenticular (Fig. 97);

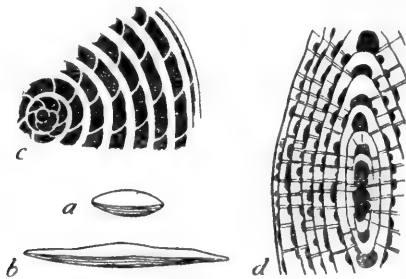


FIG. 97.—NUMMULITES.

*a*, *N. vicaryi* d'Archiac and Haime. Edge view. ( $\times \frac{1}{2}$ .) *b*, *N. complanatus* Lamarck. Edge view. ( $\times \frac{1}{3}$ .) *c*, *d*, *N. garansensis* Joly et Leymerie. *c*, Part of horizontal section. ( $\times 8$ .) *d*, Part of vertical section. ( $\times 12$ .) (All after d'Archiac and Haime.)

*Assilina* (Eoc.), similar, but the later whorls only partially overlap the earlier. These and other genera are spiral, but in one sub-family, generally known as the Orbitoides, the spiral mode of growth is abandoned (except in the early stages of ontogeny in microspheric individuals) for a cyclical growth, chambers being added in concentric rings, which more or less overlap the sides: a medium horizontal section shows the structure in its simplest form, and enables the genera to be distinguished easily. Thus the "equatorial" chamberlets of *Orbitoides* (Cret., Upper Campanian) are rounded; those of *Orthophragmina*

(Eoc., Fig. 98) rectangular; of *Lepidocyclina* (Oligo., Fig. 99) more or less hexagonal; while in *Miogypsina* (Mio.) there is a more distinct spiral "nucleus." The generic distinctions given above are those most readily made out in thin sections of Limestones, but are not the only ones.

The Imperforata are regarded as all belonging to one family, **Miliolidæ**. The simplest example is *Biloculina* (Trias.—Rec., Fig. 96), in which the adult chambers are hemispheroidal, the aperture with a T-shaped central septum, alternately at one end and the other as new

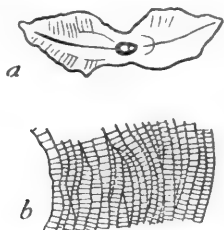


FIG. 98.—*ORTHOPHRAGMINA UMBILICATA*, DEPRAT, EOCENE, NEW CALEDONIA.

*a*, Vertical section. ( $\times \frac{1}{2}$ ) *b*, Portion of a horizontal section. ( $\times 10$ ) (After Deprat.)

chambers are added. The early chambers of the microspheric form show an arrangement found in the adults of other genera, as *Spivoloculina* and *Miliolina*. The family also includes some large, though scarcely giant, forms—*Alveolina* is a homœomorph of *Fusulina*, but very different in age (Cret.—Rec., maximum in Eocene), and *Orbitolites* (Eoc.), and *Marginopora* (Cret.—Rec.) resembles the large discoidal genera of the Nummulinidæ: the chambers, except in the initial stages, are arranged in cycles with a very regular "engine-turned" pattern, visible externally owing to absence of overlapping. This

last genus is very abundantly represented on modern coral beaches.

Of the Arenacea the most important are *Saccammina* (Carb.—Rec.) of one or several spheroidal chambers; *Endothyra* (Carb.—Trias.) resembling some of the Rotalidæ in form; and *Orbitolina* (Cret.) conical, the chambers cyclical in arrangement. *Textularia* is commonly in-

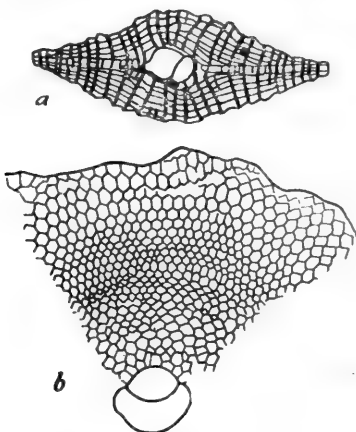


FIG. 99.—LEPIDOCYCLINA TOURNOUERI, DOUVILLÉ AND LEMOINE,  
OLIGOCENE.  
(Megalospheric form.)

*a*, Vertical section. ( $\times 13$ .) *b*, Part of horizontal section. ( $\times 18$ .)  
(After R. Douvillé and Lemoine.)

cluded among Arenacea, but is always perforate and hyaline, at least in early life.

The Perforata are usually well-preserved fossils, whether in Limestone or Clay, or even in sands in some of the latest formations. The Imperforata, having aragonite tests, are less frequently preserved. A very special mode of preservation is that of internal casts in

glauconite. The formation of these goes on at the present day on certain areas of the ocean floor. By some means not yet fully explained this complex hydrated silicate of iron, aluminium, and potassium is precipitated in the interior of these minute tests, which themselves may afterwards undergo solution. The resulting casts form "green sands," or on a muddy bottom "green muds." Similar deposits are found at many geological horizons, but most abundantly in the Cambrian and Cretaceous systems.

As rock-forming organisms the Foraminifera are important. A local example is the "spotted post" in the Carboniferous Limestone of the north of England, full of the arenaceous *Saccamina carteri*. Of far greater importance are the *Fusulina*-limestones of the Upper Carboniferous, found in the Eastern Alps, Russia, China and Japan, the East Indies, and the southern United States. The arenaceous *Orbitolina* [*Patellina*] gives its name to a limestone in the Aptian of Switzerland. The White Chalk is made up in great measure of the remains of *Globigerina* and *Textularia*. The Eocene *Calcaire grossier* of the Paris basin (the Paris building-stone) is full of Miliolidæ, and an *Alveolina*-limestone occurs in the Hampshire Basin. Far more important are the Eocene Nummulitic limestones, found throughout the area of the great ocean (Tethys) of that period, *i.e.* in the Atlas, Pyrenees, Alps, Carpathians, Balkans, Egypt, Persia, the Himalayas, the East Indies and New Caledonia. In many of these limestones *Orthophragmina* is associated with *Nummulites*. The Oligocene *Lepido-*

*cyclina* limestones (commonly known as orbitoidal) have a similar distribution and are found in the West Indies also. Although the accumulation of these giānt Foraminifera to a sufficient extent to form masses of limestone is confined to the site of this great tropical and sub-tropical ocean, the genera are occasionally found beyond its limits. Thus *Nummulites* spread as far as Hampshire in the latter part of the Eocene period, and *Lepidocyclina* into Bavaria in the Oligocene.

This completes the survey of the Animal Kingdom as known in the fossil state, but for a few minor groups that have been omitted and may briefly be mentioned here.

The **Bryozoa** (or **Polyzoa**) are a phylum or sub-phylum of fixed compound animals, having some superficial likeness to the corals, but belong to a decidedly higher grade. They are often united with the brachiopods under the name *Molluscoidea*. Their skeleton (*zoarium*) is made up of many more or less tubular individual skeletons (*zoæcia*), which are much smaller in size than most corallites, and have no septa. In a few simple cases the zoarium is like a branching thread; very often it forms a flat lamina, either spreading freely in the water or encrusting other organisms; sometimes it is massive, in which case it may become difficult to draw the line between this phylum and the Alcyonaria, especially as structures analogous to tabulæ may be present. Certain Palæozoic forms have been referred to the one phylum by some investigators, and to the other by others. The Bryozoa are almost exclusively marine, and range from the Ordovician to the Recent period. Occasionally they occur in such abundance as to form

bryozoal deposits, for instance the Coralline Crag (Lower Pliocene) of East Anglia.

The **Annelida** (segmented worms) are for the most soft-bodied and rarely preserved; but one order, Tubicola, is characterized by a fixed habit and the secretion of a tube. These tubes may be nearly straight, regularly curved, spiral or irregularly twisted. The curved tubes might be confused with *Dentalium*, the irregular for an uncoiled, and the spiral for an ordinary gastropod, and there are cases where the proper placing of such a fossil is still doubtful; but in general there is a roughness and want of regularity about annelid tubes that prevents confusion between them and molluscan tests.

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## X

### THE VEGETABLE KINGDOM

PLANTS are divided by botanists into four grades, corresponding broadly to an advance from an entirely aquatic to an entirely terrestrial life. From what we have learned from fossil animals we may expect that such an advance would not take place along one line but along several parallel lines, and that there would be occasional reversions to an aquatic life on the part of plants whose ancestors had become adapted to the land. Both these expectations are justified.

1. **Thallophyta.**—This, the lowest grade, corresponds in a general way to the Protozoa among animals, its members being composed of cells only, though they may form aggregates of much greater size and more differentiation than do the Protozoa. An alternation of sexual and asexual generations (as in the Foraminifera and other Protozoa) exists, and is important for its bearing on the life-history of the higher plants. The Thallophyta include the Algæ (the great majority of all aquatic plants) and the Fungi.

2. **Bryophyta.**—In this grade (mosses and liverworts) the alternation of generations is much more regular than in the Thallophyta, the sexual generation (*gama*

*tophyte*) being the larger and more important plant, the asexual (*sporophyte*) being short-lived and always attached to the gametophyte: hence it is commonly taken for a mere fruit of the latter. The male and female reproductive cells can only function in a liquid environment, hence the gametophyte can only live in damp situations; but the asexual spores produced by the sporophyte are adapted to resist drought and to be disseminated by the wind. The plant-body of the Bryophyta shows greater differentiation in its cells than the Algæ, and the beginning of formation of vessels, but it never attains a truly woody structure and is hence almost unknown in the fossil state.

3. **Pteridophyta**.—In this grade (Ferns, etc.) there is a reversal of the relative importance of sporophyte and gametophyte. The former is now the larger and longer-lived, it is well differentiated into root, stem, and leaf, and has woody and other tissues capable of preservation in the rocks. It can live in dry soils, but must not be far from water. The spores are borne in spore-cases (*sporangia*) usually on the ordinary leaves, sometimes on special leaves (*sporophylls*), and are wind-scattered, germinating into gametophytes in damp places.

The gametophyte is very small, delicate, as simple in structure as any of the Bryophyta, and short-lived. Sometimes the sporangia and spores are of two kinds, large *megaspores* from which female gametophytes grow, and small *microspores* which produce males.

4. **Spermaphyta** (Seed-Bearing Plants).—In these, the highest plants, the megaspore germinates, forms a

female gametophyte, which is fertilized and produces an embryo of a new sporophyte—all without ever being shed from the megasporangium, which, when all these developments have taken place within it, is called the *seed*. The microspores are called pollen, and germinate on the megasporangium. Thus the dependence of the gametophyte on an aquatic (or even a damp) environment is entirely avoided, and adaptation to the driest conditions becomes possible.

**Algæ.**—Most of the Algæ leave no trace in the rocks except indefinite carbonaceous remains. There are two groups which form exceptions to this rule.

1. The *Diatomaceæ* (diatoms), microscopic forms with a siliceous skeleton, with a very fine network-structure, resembling that of Radiolaria but much finer. These occur in immense numbers in fresh and salt waters, and their remains accumulate to form masses of diatomaceous ooze, in the cold Arctic and Antarctic seas especially. Similar deposits occur in Tertiary and Cretaceous rocks, and are worked for polishing powder and as the inactive basis of dynamite. The deposits of Bilin (Bohemia) and Richmond (Virginia) are examples. Sometimes the deposit becomes a chert. Below the Cretaceous rocks they are practically unknown.

2. Among the red and green seaweeds there are a number of families in which calcium carbonate is deposited in the cell-walls. These forms are collectively known as “calcareous algæ,” and some of them have been shown to play a large part in the building of modern coral-reefs, and they were no less important as

rock-builders in the past. Their remains have often been misunderstood and attributed to Foraminifera, Sponges or Hydrozoa. The calcareous green seaweeds (Chlorophyceæ) form in general branching tubular structures, which often break up into segments of characteristic appearance. Such are *Gyroporella* (Perm.-Trias.) and *Diplopora* (Trias.), which play a part in the building of the Alpine dolomites, and *Ovulites* (Eocene), of which the segments, common in the *calcaire grossier* of Paris, are egg-shaped with a central tubular cavity.

The calcareous red seaweeds, on the other hand, are more often massive or encrusting. Important are *Solenopora* (Camb.-Jur., Fig. 100, *a*), which contributes to the substance of many British Palæozoic Limestones, and *Lithothamnion* (Cret.-Rec.), a rock-former in the Miocene of the Vienna basin.

An interesting group, which attains a higher grade than the true Algæ, though on different lines from other plants, is the *Characeæ*, of freshwater habitat and secreting a calcareous skeleton. It is best known by its spirally-marked fruits, found in the Purbeck and Oligocene beds of the South of England (Fig. 100, *b*).

**Pteridophyta** (Vascular Cryptogams).—Three distinct lines of descent may be recognized, in all three of which two sub-grades are passed through (a lower *homosporous*, with only one kind of spore and sporangium, and a higher *heterosporous*, with mega and micro-sporangia and spores), while two of them evolve independently into the higher seed-bearing grade. These three lines are the *Lycopodiales* (represented to-day by the creeping,

moss-like *Lycopodium* and *Selaginella*) the *Equisetales* (by the marsh-loving "horse-tails") and the *Filicales* (ferns). The two first, at least, existed in the earliest known land flora (Devonian) and attained their highest development in the newer Palæozoic, and alongside them are found both undoubted ferns and another group, *Sphenophyllales*, which appears to represent the common stock from which they sprang. The extensive working of coal in the Carboniferous rocks has enabled the flora to be collected very extensively and studied very thoroughly, and some explanation is necessary of the conditions of preservation of these fossils.

The remains of land-plants are of two kinds—*impressions* of leaves, bark, etc., which show in a carbonaceous film the outward form and surface-markings, often very perfectly, but preserve no internal structure; and *petrifications*, either in silica or calcite, which preserve internal structure often as perfectly as in a recent plant kept in methylated spirit, but may often fail to show outward form. Further, the various parts of a complete plant—root, stem, leaves, sporophylls, seeds—are rarely found in organic continuity, and even such a single part as the stem may present very different appearances according as the outer cortex is preserved or not, etc. It is evident therefore that the palæobotanist has to reconstruct his plants out of very scattered and fragmentary evidence. Great difficulties of nomenclature arise: leaf impressions receive one set of names, stems another, roots another, and even when leaf, stem, and root have been pieced together it may be found that leaves whose forms differ



FIG. 100.—(For description see p. 337.)

so much that they have been put into distinct genera belong to stems which cannot be distinguished, and again stems which seem justifiably to be divided into two or more genera have indistinguishable roots. A triplicate nomenclature at least is therefore inevitable, and palæobotanists speak of "leaf-genera," etc. In the case of the most fully investigated Coal-Measure plant, it is known that at least five generic and five trivial names had been given to its separate parts.

**Sphenophyllales.**—Only one genus is known, *Sphenophyllum* (Dev.? Carb.—L. Perm.), which seems to have been a climbing plant, very much like the modern bed-straws in appearance. The leaves are in whorls round the stem, and are wedge-shaped, narrow at the attachment, widening out and ending abruptly at their broadest.

**Equisetales.**—This group attained its highest development in the Carboniferous period, when it was represented

FIG. 100.—FOSSIL PLANTS.

*a*, *Solenopora compacta* (Billings), Ordovician. *a*, Vertical section ( $\times 25$ ), showing part of three concentric layers of cells. *a'*, Horizontal section. ( $\times 50$ .) (After Brown.) *b*, *Chara lyelli* Forbes, Oligocene. Fruit. ( $\times 10$ .) (After Forbes.) *c*, *Sphenophyllum schlotheimi* Brongniart, Coal Measures. *c*, Stem with whorls of leaves. ( $\times \frac{1}{2}$ .) *c'*, single leaf. (Natural size.) *d*, *Lepidodendron sternbergi* Brongniart, Coal Measures. ( $\times \frac{1}{2}$ .) *d'*, Leaf-traces of *L. gracile* Lindley. ( $\times \frac{1}{2}$ .) *e*, *Sigillaria tessellata* Brongniart, Coal Measures. *e*, Part of trunk ( $\times \frac{1}{2}$ .) *e'*, Leaf-traces. ( $\times \frac{1}{2}$ .) *f*, *Calamites mougeoti* Brongniart, Coal Measures. Trunk. ( $\times \frac{1}{3}$ .) *f'*, *C. decoratus* Brongniart, Coal Measures. Bark. ( $\times \frac{1}{2}$ .) *g*, *Neuropteris heterophylla* Brongniart, Coal Measures. Part of leaf. ( $\times \frac{1}{2}$ .) *g'*, Venation of *N. blissi* Lesquereux. ( $\times \frac{1}{2}$ .) (After Kidston.) *h*, *Alethopteris lonchitica* (Schlotheim), Coal Measures. Leaf. ( $\times \frac{1}{2}$ .) *h'*, Leaflet. (Natural size.) To show venation. *i*, *Glossopteris browniana* Brongniart, Permo-Carboniferous, New South Wales. Leaf. ( $\times \frac{1}{2}$ .) *i'*, Venation. ( $\times \frac{1}{2}$ .) (After Seward.) *j*, *Williamsonia pecten* (Phillips), Lower Estuarine beds (Aalenian), Scarborough. ( $\times \frac{1}{2}$ .) (After Seward.) *k*, *Ginkgo digitata* (Brongniart), Middle Estuarine beds (Bajocian), Scarborough. ( $\times \frac{1}{2}$ .) (After Seward.) (After Brongniart or Lindley, where not otherwise stated.)

by trees which attained a height of fifty feet or more and a thickness of several feet, the latter attained by a process of secondary thickening like that of modern trees. Like the little *Equisetum* of to-day, they had a hollow stem, and are most frequently represented by internal casts (pith-casts), the markings on which are very like those of the exterior of *Equisetum*—vertical flutings, alternating in position at the nodes (where leaf-whorls arose). Chief genera: *Archæocalamites* (U. Dev.—L. Carb.), *Calamites* (U. Carb., Fig. 100, *f*, leaves known as *Annularia*, *Asterophyllites*, *Calamocladus*, reproductive cones as *Calamostachys*, etc.), *Schizoneura* (Perm.—Trias.), *Equisetites* (Rhætic-Wealden).

**Lycopodiales.**—The post-Carboniferous members of this group are all herbaceous plants, of little geological importance, but in the Devonian and Carboniferous periods it was also represented by forest-trees of great size and with secondary thickening. Genera: *Lepidodendron* (Dev.—Carb., Fig. 100, *d*), *Sigillaria* (U. Carb., Fig. 100, *e*). These two genera are readily distinguished by the leaf-scar pattern on the bark—the former having large rhomboidal scars covering the whole surface, the latter having small scars of varying shape in vertical rows: in both, the full pattern is only shown on the exterior of the bark, its internal surface or the decorticated stem showing a ghost of the same pattern. The roots of both are alike, branching dichotomously (*Stigmara*); the reproductive cones of *Lepidodendron* are known as *Lepidostrobus*, those of *Sigillaria* as *Sigillariostrobus*. In some species of *Lepidodendron* the megasporangium



seems to have become a true seed, the microspores germinating on it and fertilization taking place inside it.

**Filicales.**—The modern ferns are divided into three groups, (1) Eufilicinæ, which includes all the familiar ferns: they are described as homosporous (producing one kind of spores only) and leptosporangiate (the sporangia developing from a single cell); (2) Hydropteridæ, a small group of water-ferns, which are leptosporangiate but heterosporous (with mega- and micro-sporangia); (3) Marattiales, a very small group which are eusporangiate (sporangia developed from a group of cells) and homosporous.

Fossil Eufilicinæ, related to the recent *Osmunda*, are known from Upper Permian upwards, and representatives of other families from the Upper Triassic upwards. In the various estuarine beds of the Jurassic of Yorkshire, for instance, there are found fern-leaves closely similar to those of ferns now found only in the Malayan region. Hydropteridæ are known from the Eocene upwards, but from earlier times the only records are very doubtful.

The Marattiales, however, are very well represented, from the Carboniferous onwards. Some at least of the species placed in the leaf-genus *Pecopteris* (Carb.-Jur.) seem to belong to the tree-fern stem *Psaronius* (U. Carb.-L. Perm.). Other forms are known from Mesozoic and Cainozoic rocks.

But the great majority of what have been called ferns in the Carboniferous flora have proved to belong to a higher grade. They may be related to the Marattiales

as the Hydropteridæ are to the Eufilicinae, but they had advanced much beyond merely being heterosporous, and form the first division of the Spermaphyta.

**SPERMAPHYTA.**—The seed plants again fall into two sub-grades, according to whether the seed is borne on the surface of a sporophyll (Gymnosperms) or in a closed ovary formed by the folding over of one or more sporophylls (Angiosperms). The Gymnosperms include the following five groups.

**1. Pteridospermeæ.**—This extinct group is intermediate between the eusporangiate ferns (Marattiales) and the cycads. It is confined to the Upper Palæozoic, and best known from the fern-like leaves of the Coal Measures. Only of recent years, by the piecing together of evidence from the microscopical structure of petrifications with that from leaf-impressions, has it been possible to discover its true position. Common leaf-genera are *Alethopteris* and *Neuropteris* (Fig. 100, *g, h*), corresponding to the stem genus *Medullosa* and the seed *Trigonocarpum*; *Sphenopteris*, to the stem *Lyginodendron* and the seed *Lagenostoma*. Other leaves probably belonging here are *Glossopteris* (Permo-Carb.—Rhætic, Fig. 100, *i*) with its rhizome *Vertebraria*, and the allied *Gangamopteris* (Permo-Carb.)

**2. Cycadophyta.**—The modern cycads are a group of plants with palm-like foliage, but much more primitive in their sporophylls than the palms (which are angiosperms). They are confined to tropical regions, but extend all round the world. Their Mesozoic allies had

no such restriction in latitude, being common in England for instance, and some of them attained a far higher grade of floral structure, which makes it probable that from them sprang the Angiosperms (typical flowering plants with seeds enclosed in a fruit). They are doubtfully represented in the Coal Measures, but undoubtedly from the Rhætic, Jurassic, and Lower Cretaceous. The Jurassic period has been termed the "age of cycads."

Their remains are abundant in the Jurassic estuarine beds of the North of England, in some of the Purbeck beds, where they occur in the position of growth in the "fossil forest" of Dorset cliffs, and in the Wealden beds. But the most famous locality for them is the Black Hills of Dakota, where wonderfully preserved specimens of Upper Jurassic age have enabled Dr. Wieland to determine the full details of the floral organs. Leaf-genera: *Pterophyllum* (Trias.), *Cycadeoidea*, *Williamsonia* (Fig. 100, *j*), *Ptilophyllum* (all Jur.), *Otozamites* (Trias.-L. Cret.), *Nils-sonia* (Jur.-L. Cret.), *Zamites* (L. Cret.)

3. **Cordaitales.**—The genus *Cordaites* (Dev.-Rhætic) was a forest tree resembling in habit the Australian Kauri pine, to which it may have been not very distantly related. Its leaves were long, narrow, thick and parallel veined; its seeds (*Cardiocarpus*) were borne on a cone.

4. **Ginkgoales.**—The maiden-hair tree, *Ginkgo*, with its bifid wedge-shaped leaves (Fig. 100, *k*), is now confined to parts of China and Japan; but closely allied forms had a world-wide distribution in Jurassic times, ranging from Greenland to Tasmania. Its time-range in Europe is Rhætic to Eocene.

5. **Coniferales**.—These include the familiar firs and pines, the yew and monkey-puzzle (*Araucaria*). This last is now native only in South America and Australasia, but it also had an almost world-wide distribution in the Jurassic and Lower Cretaceous. Allied forms are *Walchia* (Perm., rare in U. Carb.) and *Voltzia* (Perm.—Trias.). Coniferous wood is a common object in many Jurassic and Cretaceous rocks, both marine and freshwater.

**Angiospermæ**.—A few rare remains of angiosperms occur in Lower Cretaceous strata, but at the beginning of the Upper Cretaceous period there was such a sudden appearance of an extensive angiosperm flora in Europe, that it is obvious that such a cryptogenetic flora must have migrated from some other part of the world, as yet unknown. Its fossil remains are found, not in England, which was then covered by a fairly deep sea, but in regions like Saxony, which were close to a shore-line and where sandy deposits occur in place of chalk. From this time onwards, the angiosperms are the dominant members of the flora everywhere. Their natural orders and genera are far too numerous to be mentioned in detail here.

The possible existence of marine life provinces in past times has been referred to in Chapter V. Fossil plants have provided the most unquestionable example of terrestrial life provinces. The flora of Devonian and Lower Carboniferous times is practically the same all over the world, but in the Upper Carboniferous there were two sharply contrasted floras—a northern flora, including *Lepidodendron*, *Sigillaria*, *Calamites*, and many

pteridosperms, and a southern flora, without any large trees, but chiefly characterized by *Glossopteris* and *Gangamopteris*. The former is found over most of the northern hemisphere, both in the Old and New Worlds, the latter is principally found in the southern hemisphere and India. So entirely different are the two, that for a long time many geologists would not admit them to be contemporaneous, but held the *Glossopteris* flora as Mesozoic, it having in fact nearer affinities to the European Mesozoic than to the European Carboniferous flora. The discovery of marine strata having an unmistakable Upper Carboniferous or Lower Permian fauna, alternating with beds containing the *Glossopteris* flora, at length gave conclusive proof of the Permo-Carboniferous age of the latter. It appeared, therefore, that there were two continental masses, a northern on which the descendants of the Lower Carboniferous plants continued their evolution, and a southern on which that flora had been exterminated (possibly by glacial conditions of which there is good evidence), and a new and much less rich flora developed. Later discoveries have shown that there was some geographical overlap of the two floras, *Sigillaria* having been found in South Africa, and *Glossopteris* in Russia; but the exact nature of this overlap remains to be explained. By the Rhætic epoch a uniform flora had once again established itself over the land-surfaces of the world.

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## XI

### THE COLLECTION AND PRESERVATION OF FOSSILS

REFERENCE has incidentally been made in previous chapters to some of the conditions of preservation of fossils. They may here be summarized:

1. Very rarely is an animal or plant body preserved whole: the case of insects in amber—a fossil resin which enveloped them as it trickled down the bark, preserved them by its antiseptic character, and became hardened by loss of its volatile constituents—is perhaps the only case. The frozen mammoths of Siberia are not true fossils, as they are not entombed in sediments.

2. While the soft parts decay, the hard parts—mainly of mineral substance, but sometimes organic—may be preserved without any chemical change. This is a very common case among animals, if we interpret the term “chemical change” rather broadly. Some amount of chemical change is almost inevitable—the filling-up of minute cavities with secondary mineral matter, as in echinoderm skeletons and vertebrate bones, is rarely escaped. Among plants, where the hard parts are organic, some carbonization nearly always takes place; but in the paper-coal of Tula, in Russia, the cuticles of the plants are said to be absolutely unchanged.

3. The hard parts may be preserved, but with more or less complete chemical change. If the original skeleton was of calcite this may be replaced by silica, dolomite,

chalybite, limonite, calcium phosphate, pyrite or selenite. Aragonite may be replaced by any of the same, or may undergo a paramorphic change into calcite. The extent to which these changes may alter the minute structure of the skeleton varies very much: when any recrystallization takes place the minute structure is usually destroyed, wholly or in part. Amorphous silica (opal) may preserve the finest details, but if it passes into chalcedony it will often produce a structure due to imperfect crystallization in rings (*beekite* structure), which will not only destroy minute structure but even obscure the outward form. So, too, with the formation of selenite (gypsum), few fossils but belemnites can survive it in recognizable form; but this chemical change differs from most others, as it is probably quite a recent result of weathering near the surface, while most others took place soon after the entombment of the fossil.

Originally siliceous skeletons may be altered to calcite, pyrite or marcasite, the last in turn passing into limonite under conditions of weathering. Sponges in the chalk may sometimes be found, partly silica, partly limonite.

Hard organic tissues generally undergo some degree of carbonization, but they may be replaced by pyrite (as with graptolites), or by calcite or silica (as in plant petrifications).

Phosphatic skeletons are the most stable of all, and beyond having their minute cavities filled with secondary phosphate they undergo no change. Very rarely they may be changed to vivianite (a blue iron phosphate).

4. An organism may be represented by casts of its skeleton—external casts or moulds, and (if a hollow skeleton) internal casts. External casts are composed of the matrix of the rock, that is to say the sediment in which the organism was buried: in hard enough rocks they are always produced when a fossil is extracted, but



they may be found naturally produced through the removal of the fossil in solution. Infillings of the interior may also consist of the matrix, when that had free access to the interior; when it had no access, they consist of some material deposited from solution, or partly the one and partly the other, when the sediment could only penetrate into part of the interior. Very rarely does a hollow skeleton remain really empty, though infilling may often be incomplete. In limestones, the material deposited from solution will be calcite, or chalcedony (as in the chalk-flints); in clays it is usually pyrite, or marcasite (the two forms of  $\text{FeS}_2$ ). In cases where deposit on the sea-floor was extremely slow, calcium phosphate is a usual infilling, or for minute cavities glauconite: these two substances being deposited before burial is complete.

In any of these cases it is only by subsequent removal of the shell that the infilling appears as an actual internal cast. Such removal may be by solution on the sea-bottom or within the rock, or it may be artificially produced, either accidentally during extraction, or deliberately for the purpose of investigating internal structure. When naturally produced, the external and internal casts together are often described as "hollow casts": by pouring melted wax or gutta-percha, etc., into the cavity, a mould of the fossil can be produced.

5. There are other traces of living organisms in rocks that may rank as fossils, though even less definite than casts. Such are footprints and other impressions of moving animals in sand or mud (preserved by being covered by a lamina of a different kind of sediment), burrows in sand or mud (preserved by being filled with slightly different material) and borings in hard rocks or in fossils. Among boring organisms are minute algæ, sponges (*Cliona*), some echinoids, many lamellibranchs

(*Lithodomus*, *Pholas*, *Teredo*). Sometimes when a shell is bored into, the material filling the boring may resist subsequent solution better than the shell itself, and a cast of the boring may result.

All these various ways of preservation must be borne in mind by the intelligent collector when at work on cliffs and quarries. While the spoil-heap of a quarry will often provide the choicest specimens, he should never neglect to search for fossils *in situ* in the undisturbed rock. Only by so doing can he know whether all the fossils belong to one fauna, or whether there are several, and through what thickness a single fauna persists; only so can he see whether lamellibranchs, for instance, are in the vertical position of living burrowers or in the horizontal position of drifted shells; only so can he distinguish with certainty the presence of *derived* fossils, whose original home was in some older bed and whose worn and rounded surface distinguishes them from the contemporaneous fossils with which they may be mixed.

The collector would be well-advised not to attempt to clean or select his fossils on the spot where he obtains them, except when their weight is serious. Many a good specimen has been spoiled by the attempt to clean it on the spot. Even broken specimens may often prove to show special features not seen in perfect examples. The writer once picked up seventy-three specimens of *Chonetes laguessiana* from the Carboniferous shales of Fourstones (Northumberland). They all looked alike at the time, but on cleaning and sorting them at leisure afterwards, fifty-eight were found to be complete specimens but with the dorsal valve crushed in; fourteen were ventral valves, and *one* was a dorsal valve showing both external and internal features. That one dorsal valve would probably have been lost had any attempt to clean or select been made on the spot.

Care must be taken to pack up specimens so that they do not get broken in transit home: heavy fossils must not be placed on top of fragile small ones, for instance. They must be so labelled that there will be no mistake as to the exposure and the particular bed from which they came. At the time it may seem quite safe to trust to memory, but a week afterwards an unlabelled specimen will prove a serious worry to the conscientious collector.

The extracting and cleaning of fossils—the removal of fossil from matrix or matrix from fossil—is an art in itself. In extracting large specimens from hard rocks, such as tough limestones, the latter must be subjected to great stress—the blow of a sledge-hammer may make a fossil jump out quite clean. A screw-movement stone-breaking machine may be effectively used in the same way. At other times when the fossils are fragile and firmly cemented to the matrix, their violent extraction may be almost hopeless, but heating the rock and cooling it by plunging it into cold water may have the required effect. In the extraction of small fossils, such as foraminifera and ostracods, from sands and friable rocks, the rock is first broken up and then passed through a series of sieves: the great majority of fossils will be found between a mesh of 32 to the inch and one of 64 to the inch. In the case of stiff clays, another method must be used: the clays are broken up into small pieces, about the size of a pea or larger, and heated on a metal plate over a flame until thoroughly dry, when they are dropped while still hot into cold water in a circular dish. The clay quickly disintegrates into mud, and by keeping up a swirling of the water by constant movement of the dish, decanting the muddy water and adding fresh over and over again, all the argillaceous material is at length removed and a concentrate left, consisting of sand-grains and small fossils. This is dried and then spread out, a

little at a time on black paper, examined with a lens and fossils picked out with a moistened sable brush, or in the case of heavy ones with a fine forceps. Siftings of friable rocks are picked over in the same way.

Chalk may be scrubbed under water with a stiff brush, and a concentrate obtained by the method just described: the chalk from the interior of large fossils (such as echinoids) is often the most fruitful, because the small shells have been more protected from destructive movements in the ooze on the sea-bottom.

The methods of removing of matrix from a fossil depend greatly on their respective toughness. When the fossils are strong and the matrix friable, washing with or without the help of a brush (a tooth-brush is very convenient) may be enough; but some fossils (many lamellibranchs) will break into pieces if wetted, and must be cleaned dry with the help of some tool. A shoemaker's awl mounted in a handle is very useful for tough matrix; in other cases a mounted needle, pin, or steel pen, or even a common pocket-knife may be serviceable. The golden rule about all such tools is that they should never be used to scrape the matrix away from the fossil (with a possible exception for silicified and pyritized fossils, where the fossil is harder than the steel of the tool). The aim should always be to put such a strain on the matrix by means of a tool, that it breaks away from the fossil without the tool touching the latter. The application of this rule to particular cases must be very varied.

As an example, take the case of a graptolite, part of which is exposed on the lamination surface of a shale, partly buried under other laminæ. The natural first idea is to push a knife-blade between the laminæ and separate them, but the probable result of this will be that the laminæ break away anywhere except where the

graptolite lies, and in the end the hidden part may be broken before it is exposed. If, however, we press the knife-blade vertically downwards along a line parallel to the hidden part but a quarter-inch or more away, the strain on the concealing laminæ of shale will very likely cause them to split off just where wanted.

Brushes, the bristles though stiff being softer than most fossils, can be applied directly to the surface of fossils. The dental drill used by dentists for the filing of teeth can be adapted to the cleaning of fossils: it enables a rapidly rotating brush to be applied to any point on the surface of a fossil, with much more concentrated and rapid effect than that of a hand-brush. Wire brushes can even be used to clean pyritic fossils embedded in hard slates.

Where mechanical means fail, chemical methods may be used. The simplest of these is ordinary weathering, which in many cases disintegrates matrix without injuring fossils (though in other cases the reverse is the case). Very weak acids may effect the same result more rapidly. In general acids must be resorted to with great care, since most fossils are calcareous and at once attacked by them. Where it is desired to expose more fully a fossil partly embedded in tough limestone, the exposed surface may be varnished to protect it and acid poured on: careful watch must be kept so that as soon as any more is exposed it may be washed and varnished.

A generally safer reagent is caustic potash. This is applied dry, small pieces being scattered over the surface of matrix which it is desired to remove: as the potash deliquesces it penetrates into the matrix and disintegrates it, while it does no harm to the fossil if it be an echinoderm or a mollusc. (It must not be used, however, for brachiopods, their laminated shell being easily penetrated and flaking away in consequence.) The fossil is then

thoroughly washed and scrubbed, and it is well to preserve the washings and evaporate them to a more concentrated solution of potash, to be used for another purpose mentioned below.

Many fossils, though stable enough in their long home, are physically or chemically unstable as soon as extracted, and need special treatment to save them from disintegration or the risk of it. If they are simply fragile they must be impregnated with some binding material. The most usual one is gelatine, applied as a hot, strong solution with a soft brush: it penetrates the shell and as it hardens it binds the parts together and prevents decay. It has the disadvantage of requiring very rapid treatment lest it harden before penetrating. Another material is a solution of collodion in amyl acetate: this has the advantage that it hardens much more slowly by evaporation. It can be brushed over the shell at intervals of a day or more until no more is absorbed, or small specimens can be dropped into the solution and left there indefinitely. Care must be taken not to inhale the amyl acetate.

The chief case of chemical disintegration is that of fossils or casts in marcasite. This is an unstable sulphide of iron which absorbs moisture and oxygen, and gives a crystalline efflorescence of ferrous sulphate. As soon as such an efflorescence is noticed, it must be brushed away and the fossil soaked in hot, but not boiling, potash solution to neutralize any free sulphuric acid. It is then washed thoroughly in distilled water to remove the potash, and thoroughly dried on a hot plate, after which it is painted all over with shellac varnish (or if not too large soaked in the varnish). In this way further access of oxygen and moisture is prevented.

When a fossil is represented only by a cavity in a rock, it becomes necessary to take a cast of it. For this purpose many substances may be used—paraffin wax,

sealing wax, gutta-percha and the various compositions used by dentists for moulding the teeth and palate.

The various methods so far described give some idea of the most frequent and general forms of palæontological technique. Other special methods can only be mentioned, such as the delicate methods employed by Norman Glass and others for exposing the brachial spirals of brachiopods, the methods of exposing, tracing, and reproducing the suture-lines of ammonoids (see Frontispiece), the making of serial sections of solid fossils at regular intervals and constructing from them enlarged models of the internal structure. The accurate measurement of fossils by means of sliding callipers is a very necessary process in the identification of species and the tracing of gradual evolution.

## XII

### THE RULES OF NOMENCLATURE

THE subject of the nomenclature, or naming of fossils, is one productive of much irritation and of many sarcastic utterances among geologists, to whom the time spent by many palæontologists on the accurate determination of the names of fossils appears as sheer waste. The attitude of mind of many critics of these palæontologists is expressed by a rather hackneyed quotation from Shakespeare, of which it is sufficient to say that if Juliet had ordered a rose from her gardener by the name of garlic, the rose would not have smelled as sweet as she desired. The whole purpose of giving names to things is that persons may be able to speak to one another about them without danger of misunderstanding.

In proportion as we wish to discriminate more and more minutely between things, we require more and more exact names for them. There are purposes for which roses and lilies and buttercups may be spoken of without discrimination as "flowers"; there are others for which they require distinct names; there are yet others for which the need is felt of finer discrimination, by means of qualifying adjectives as "red rose" and "white rose"; while a modern gardener requires separate names for a great number of different kinds in each of these categories.

The naming of fossils is only a part of the naming of animals and plants in general. Leaving plants aside



for the moment, the Animal Kingdom is divided into a number of *phyla*, each of which is divided into *classes*, these again being divided into *orders*, these into *families*, these into *genera*, and these into *species*. To define a *species* is difficult enough among living animals, where the test of inter-breeding is available; among fossils there is only one really scientific way of delimiting species, and that is by determining whether variation is continuous or discontinuous. To do this a large number of individuals from the same bed must be taken, note made of those measurable characters in which they show variation, and a series of accurate measurements taken. The results for each character are plotted as a graph, the horizontal coordinates being the measurements and the vertical coordinates the number of individuals giving each particular measurement. If the plotted curve is a simple one with a single maximum, that is evidence for treating all the individuals as one species; but if it shows two or more maxima with very decided minima between, then there is ground for regarding them as two or more species. Confirmation must be sought in the curves for the other measurable characters.\*

This method is only practicable when large numbers of individuals from the same bed are available, and when their variations are expressible in simple numerical form. In the absence of such conditions no better definition of a species than this can be suggested for the purposes of palæontology: *A species is a collection of individuals so nearly alike that they may conveniently be denoted by the same name.* This definition leaves the decision as to whether there is sufficient likeness to the judgment of every palæontologist, and judgments will

\* For a good illustration of this method see Hickling, G., "Variation of *Planorbis multiformis* Bronn," *Mem. Proc. Manchester Lit. Phil. Soc.*, vol. lvii., pt. 3 (1913).

inevitably differ: as such differences constantly occur, this definition recognizes the facts of the case.

A *genus* may be defined either as a *collection of species having certain features in common* (the morphological definition) or as a *collection of species believed to be derived from the same immediate ancestral stock* (the genetic definition). The difference between these definitions has been illustrated under the Graptolites.

As a rule, each of the categories named above consists of several of the next category below, but it may consist of only one—*e.g.*, a genus may include only one species, a family may include only one genus.

If the categories named are not enough for satisfactory classification in any particular case, intermediate grades may be intercalated, denoted by the prefix *sub-*; thus an order may be divided into several sub-orders, each containing several families. Still further grades may sometimes be necessary: they are denoted by the prefix *super-*: thus a sub-order may be divided into super-families, and these into families. The term *variety* is generally used in place of *sub-species*.

The system of nomenclature for species now universally adopted is that of the Swedish naturalist Linné (latinized as Linnæus) and consists in denoting every species by a double name: hence it is often called the binominal system. Thus "*Dalmanites caudatus*" is the **specific name** of a certain species of Trilobite, and is made up of the **generic name** "*Dalmanites*" (the name of the genus to which this species belongs), and the **trivial name** "*caudatus*" which distinguishes this species from others of the same genus.

A generic name is always a single word, either a Latin noun or a word treated as such. In the early days of the Linnæan nomenclature Latin or latinized names of animals were plentifully at hand, but with the increase

in the number of genera new kinds of names had to be sought. Names of mythological characters, such as *Venus* and *Actæon*, were appropriated, but have long been exhausted. Then came more or less descriptive compound words of Latin or Greek derivation, such as *Micraster* (little star), and *Macrodon* (big tooth): Many genera were named in compliment to individuals, as *Murchisonia* and *Lonsdaleia*, or from the locality where they were first discovered, as *Amberleya*, *Bohemilla*. As the number of generic names increased enormously there came a natural tendency to help the memory by compounding similar names for genera in the same class; thus the great majority of crinoid genera have names ending in *-crinus*, those of many corals end in *-phyllum* or *phyllia*, of many starfish in *-aster*, of cephalopods in *-ceras*, of brachiopods in *-thyris*. But there is no copyright in such endings and they must not be trusted as a necessary indication of affinities. Thus *Cryptocrinus* is not a crinoid but a cystid; *Holocystis*, not a cystid but a coral; *Camptoceras* and *Platyceras* are gastropods. Most names ending in *-obolus* denote brachiopods, but *Trochobolus* is a sponge. The attempt to combine the name of a man or a place with one of these terminations has led to such uncouth compounds as *Agassizocrinus* and *Quenstedtoceras*.

It was at one time a rule that the generic name of any fossil should bear the termination *-ites*. Thus a fossil *Nautilus* was called *Nautilites*, not because it was thought to belong to a different genus from the recent *Nautilus*, but merely to emphasize its fossil state. This plan has long been abandoned, but it has led to some confusion in the case of genera entirely extinct. Many modern authors have removed the termination in such cases, thus *Echinosphærites* has been altered to *Echinosphæra*. Unfortunately the same termination has been used as a means of distinction between different genera—*Dalmanites*

was so named, for instance, because its original form *Dalmania* was preoccupied. Hence no rule of universal application can be laid down for such cases, unless it be the strict rule of priority.

If a sub-generic name is needed it is written in parentheses after the generic name; thus *Lichas* (*Corydocephalus*) *anglicus* denotes that the species belongs to the sub-genus *Corydocephalus* of the genus *Lichas*.\*

The best trivial name is a simple Latin adjective, either descriptive of some feature of the species (as in *Dalmanites caudatus*, *Belemnites minimus*) or indicating the locality where it was first found (as *Crania parisiensis*, *Lichas hibernicus*, or the much less pleasing *oyster-mouthensis* and *czenstochovensis*). The adjective must always agree in gender with the generic name, and must be altered if necessary with a change in the latter. Instead of an adjective a noun may be used "in apposition" according to Latin usage, when it keeps its own gender, as *Psiloceras planorbis* (wrongly altered by some authors to *planorbe* as though it were an adjective), *Agnostus rex*, *Rhynchonella vespertilio*. Thirdly, it may be a noun in the genitive case, usually (but not always) a personal name, as *Lingulella davisi*, *Asteroceras smithi*. The rules of the International Zoological Congress only allow a person's name to be made into a trivial name by the addition of the letter *i*, thus not only insisting on some dreadful barbarisms,† but tending to cause great con-

\* Square brackets are sometimes used for a different purpose—the name which they enclose is not a part of the correct specific name, but is a reminder that a change of name has taken place—thus, *Basilicus* [*Asaphus*] *tyrannus* recalls the fact that *Basilicus tyrannus* has long been known as *Asaphus tyrannus*, and is an assistance to those who might fail to recognize a familiar species under a new generic name.

† For instance, *Zaphrentis omaliusi* (instead of *omalii*). But reasons for making this rule will be found in the Introduction to Bronn's *Index Palæontologicus*.

fusion for the following reason: the early palæontologists recognized two ways of dedicating a species to a man, thus d'Orbigny named two ammonites *Ammonites sauzei* and *Ammonites sauzeanus*. Many modern palæontologists insist upon altering all names of the latter pattern into the former, a proceeding creative of much confusion. Whatever rule may have to be kept for the future it best to retain names of old date unaltered in form.

If a sub-species or variety needs to be distinguished, its varietal name should be written immediately after the trivial name, as *Agnostus pisiformis obesus*; but many authors prefer writing *Agnostus pisiformis* var. *obesus*. When a species can be traced, with gradual changes, through a number of zones, each zonal form is called a mutation, and may be denoted by the symbol of its zone (e.g. *Productus concinnus* Sowerby, mut. D<sub>2</sub>) or by an adjective (using *mut.* instead of *var.*)

In view of the mistakes that may arise from over-hasty identifications of a known species at a new locality or horizon, modern palæontologists frequently make use of qualifying or cautionary terms. Their lists frequently contain such records as *Hildoceras* cf. *bifrons* (Bruguière) or *Productus* aff. *productus* (Martin). The first means "a species of *Hildoceras* very much like *bifrons* but probably not exactly identical with it"; and the latter "a species of *Productus* which is certainly not identical with *P. productus*, but appears to be genetically related to it."

As to the mode of writing or printing specific names, the following rules should be most strictly adhered to: (1) A generic name should always bear a capital initial letter; (2) a trivial name should always bear a small initial letter\*; (3) when a generic or specific name comes

\* To this last rule most continental authors allow an exception in the case of trivial names derived from a personal name, but the tendency in England is to make the rule absolute, thus writing *Asaphellus homfrayi* in spite of the fact that the trivial name was given in honour of a Mr. Homfray,

in the course of an ordinary sentence it should be printed in different type from the rest of the sentence (normally, in a sentence of roman type it would be in italics). A few examples will show the importance of adhering to these rules. If in a geological work we come across an allusion to "the *Planorbis* beds," we should know that it referred to beds in which there were abundant gastropods belonging to the freshwater genus *Planorbis*; but when we read of "the *planorbis*-beds," we understand marine beds characterized by the ammonite *Psiloceras planorbis*. The *Productus*-limestone is a well-known Asiatic formation characterized by the brachiopod genus *Productus*; but an allusion to "the *productus*-limestone" would set us puzzling our brains for the genus which had a species with the trivial name *productus*. As to the third rule above, it is only necessary to hunt for the name of a fossil in some work which has not followed that rule to realize its importance.

When several species of a genus are referred to in the same paragraph, it is permissible to use the initial letter only of the generic name, to save repetition.

If no author had ever, by accident or otherwise, broken the rules of nomenclature, the generic and trivial names would suffice to define a species absolutely. It has been found necessary, however, to avoid confusion, to write after the name of a species the name of its author—*i.e.*, of the palæontologist who first applied that name to it; and it is often useful to add the date of his giving the name, thus: *Terebratula intermedia* J. Sowerby, 1812.

There is no rule as to the type in which the author's name should be printed, but it is not desirable that it should be in the same type as either the specific name or the rest of the sentence in which it occurs.

The need for further rules arises from the facts that authors writing at different times have from time to time

(a) given the same name to different genera, or to different species of the same genus, either through a mistake in identification or in ignorance that the name was already in use; (b) given different names to the same genus or species; (c) divided up an existing genus into several genera, or (d) united distinct genera into one.

The most general rule in all nomenclature is the *law of priority*, according to which, other things being equal, the earliest name given to any genus or species must stand: all later names are *synonyms*, and as such are rejected. To this rule there are certain necessary qualifications:

1. The name must have been *published*—i.e., printed and circulated so as to be accessible to the public, and it must have been accompanied by either a description (diagnosis) or a figure (or both) which would make it possible to identify the species to which the name was applied. In the case of a new genus, a diagnosis is not absolutely necessary, if the type-species is given.

2. It must have been applied in accordance with the Linnæan system. This rules out all names published prior to the year 1758 (date of the tenth edition of the *Systema Naturæ* of Linnæus) even if they are binominal in form; for in pre-Linnæan names that form is accidental, the earlier method having been to give a generic name followed by what was really not a trivial name but a description or diagnosis (though occasionally a single adjective sufficed).

3. That the same name has not already been applied — if generic, to some other genus; if trivial, to some other species of the same genus. In case of such previous application the name (in its new application) is a *homonym*. Thus the name *Avalonia* was given by Walcott in 1889 to a genus of trilobites; the same name was applied by Seeley in 1898 to a reptile. Hence *Avalonia* Seeley, 1898,

is a homonym of *Avalonia* Walcott, 1889. Again James Sowerby in 1820 gave the name *Spirifer pinguis* to a Carboniferous fossil; Zieten in 1838 gave the same name to a Jurassic fossil. Hence *S. pinguis* Zieten, 1838, is a homonym of *S. pinguis* J. Sowerby, 1820. When a homonym has to be quoted, it is advisable to make its homonymity clear by putting it thus:

*Avalonia* Seeley, 1898, non Walcott, 1889.

*Spirifer pinguis* Zieten, 1838, non J. Sowerby, 1820.

Generic homonyms are of course suppressed as soon as discovered, and a new name substituted—usually a name only differing slightly from that suppressed. Thus Emmrich in 1844 gave the name *Dalmania* (in honour of the Swedish palæontologist Dalman) to a genus of trilobites which he separated from *Phacops*; but *Dalmania* had been previously applied to an insect, therefore Barrande in 1852 substituted the name *Dalmanites*. Sometimes an author is less fortunate. Thus Goldfuss in 1839 gave another trilobite-genus the name *Brontes*; finding this preoccupied he changed it in 1844 to *Bronteus*, but in the meantime de Koninck had given the same genus the name *Goldius*, and although palæontologists have been accustomed to the name *Bronteus* there can be no doubt that *Goldius* has priority over it and should strictly be used in place of it.

As an example of a specific homonym, we may take the following case: J. Sowerby, in 1818, named a lamelli-branch *Cardita livata*, and in 1819 named another *Lutraria livata*. In 1826 his son, J. de Carle Sowerby, made a new genus, *Pholadomya*, to which he transferred both the above species, each of them thus becoming *Pholadomya livata* (J. Sowerby). The 1818 species having the prior claim of the two to this name, it became a homonym in its application to the 1819 species, and consequently a new name was given to it, and it is now *Pholadomya fidicula* J. de C.



Sowerby, of which name *Lutraria lirata* J. Sowerby is a synonym.\*

The fate of all specific homonyms is not quite so clear, because of the possibility that they may be transferred to other genera. Thus of the two species named *Spirifer pinguis*, Sowerby's is now *Brachythyris pinguis*, and Zieten's is *Spiriferina pinguis*: there can therefore be no danger of confusion between them, and both trivial names may be kept. It is true that the International Congress has a very drastic rule—"Once a homonym, always a synonym," meaning that once a name is suppressed on account of homonymy it can never be revived, even on transference to another genus; but while this applies quite clearly to cases where the homonym has had a new name substituted for it while it was still in its original genus, it is not clear that it applies to cases where the homonymy was overlooked until the change of genus was made, as in the case of *Spiriferina pinguis*.

One more exception to the law of priority must be noted. It has been found impracticable to insist on its covering both Animal and Vegetable Kingdoms simultaneously, so botanists and zoologists have agreed, while each accepting it within his own kingdom, to let the nomenclature of the two be quite independent. Thus *Zeilleria* is the name both of a Carboniferous pteridosperm leaf, and of a Jurassic brachiopod. No practical confusion is likely to arise between the two.

These are the only valid exceptions to the law of priority. There are one or two other exceptions that have been proposed but are now quite rightly rejected. In the first place a name must not be rejected because it

\* It must be clearly understood that the term *synonym* implies two names for one thing, while *homonym* implies the same name for two things.

is inappropriate : to allow this would involve us in endless confusion, since appropriateness is partly a matter of individual judgment, and if one palæontologist thinks the appearance of a certain brachiopod sufficiently suggestive of a coin to justify him calling it *Obolus*, while a later author, failing to see the likeness, is allowed to substitute another name, who is to settle which name is correct ? After all, a name is a name, not a description, and in treating it as such we are following the common-sense customs of ordinary speech. We have in our houses kitchen "coppers" made of galvanized iron, drawing-room fire-"irons" made of brass, and (if still surviving) bedroom candle-"sticks" made of china ; men named Short or Little are often taller than others named Long, yet we neither expect them to change their names nor allow them to do so except with much expense and trouble ; and no registrar of births would think of objecting to such a name as Thomas Thomas on the ground of tautology, or to Violet Green as a contradiction in terms. If we remember that the Latin derivation *lucus a non lucendo* has become a phrase of general application we need not be shocked at finding that a crustacean with an enormous number of legs is called *Apus* (footless), or that *Agoniatites* is not "devoid of an angle" as its name would imply.

Again, just as the change of manufacture from one material to another has led to such anomalies as brass irons, so the transfer of species from one genus to another has produced curious results. Sometimes a species has been thought to have only a superficial resemblance to a genus to which it has afterwards been found to belong, and the trivial name indicating that resemblance has had to be kept : thus we get *Agnostus agnostiformis* (M'Coy), *Axinus axiniformis* (Phillips), *Dendrophyllia dendrophylloides* (Lonsdale), etc. Or again, a species has been named

from its resemblance to some object, such as a sword or an acorn, and the Latin name of that object has later been applied to a new genus into which the species has been transferred: thus we get *Ensis ensiformis* (S. V. Wood) and *Balanus balanoides* (Ranz). Yet again, a character unusual in its genus is taken for the trivial name of a species which is afterwards transferred to another genus in which that character is normal: thus a spiny shell from the Chalk was taken by J. Sowerby to belong to the genus *Plagiostoma*, and as the only spiny species in that genus it was appropriately called *Plagiostoma spinosum*, but later it was transferred to the spiny genus *Spondylus*, but the name *Spondylus spinosus*, though meaningless as a description, serves quite well as a name.

The original Stricklandian code of 1841 proposed that a name might be changed when it implies a false proposition which is likely to propagate important error. For instance, Hyatt named an ammonite *Mantelliceras indianense*, a name apparently implying that it was found in the State of Indiana, whereas it actually came from India. It might seem reasonable in this case to alter the trivial name to *indiense* or *indicum*, were it not that such a change might lead to the idea that two distinct species were in question. Really serious cases of this sort must be so few that they can easily be kept in mind, and once we depart from extreme cases we find individual judgment introducing uncertainties; consequently later zoologists have wisely dropped this proposal and agreed that once a name has been published it may not be altered, even by the author himself, except in correction of an evident slip of the pen or misprint.

The Stricklandian code also proposed that where the trivial name of a species was taken as the generic name for a new genus in which that species was included, the

trivial name must be altered, because they regarded the exact duplication of generic and trivial names as barbarous. For example, Martin, in 1809, named a certain brachiopod *Anomites productus*. J. Sowerby, in 1812, took it as the type of a new genus, which he called *Productus*, and changed Martin's species into *Productus martini* (quite rightly according to the Stricklandian code). Later zoologists have rejected this exception to the law of priority, and the fossil which has long been known as *Productus martini* must be called *P. productus* (Martin).

4. As knowledge increases and becomes more exact, a later author may transfer a species from its original genus to another. Thus *Cheirurus insignis* Beyrich, 1845, is a synonym of *Paradoxides bimucronatus* Murchison, 1839. The law of priority here settles that the earlier trivial name must stand; but as it was recognized that *Paradoxides bimucronatus* Murchison was not a true *Paradoxides*, it was transferred to Beyrich's new genus *Cheirurus*, but the trivial name having priority over Beyrich's name *insignis*, it stands as *Cheirurus bimucronatus* (Murchison), the author's name being placed in parentheses as an indication that an alteration in the generic name has been made. An alternative way of expressing this is *Cheirurus bimucronatus* Murchison sp.

As an example of the importance of these distinctions, which may at first appear an unnecessary refinement, we may take the following case: James Sowerby, in 1818, gave to a lamellibranch the name *Cardita deltoidea*; in 1820 he gave to another the name *Venericardia deltoidea*. In 1826 J. de C. Sowerby made a new genus, *Pholadomya*, into which he moved the former of the above species. In 1871, S. V. Wood transferred the latter of the two from *Venericardia* to *Cardita*. Thus we find that *Cardita deltoidea* (J. Sowerby) is quite a different thing from *Cardita deltoidea* J. Sowerby:

*Cardita deltoidea* J. Sowerby = *Pholadomya deltoidea* (J. Sowerby).

*Venericardia deltoidea* J. Sowerby = *Cardita deltoidea* (J. Sowerby).

A wise precaution to avoid such possibilities of confusion is never to use the same trivial name in genera at all nearly related.

5. A later author may divide a genus into several genera. The original name must then be retained for one of these divisions, and, if possible, for that division which was regarded by the author of the original genus as most typical. With a view to this possibility the founder of a genus should always name one species as most typical: such a species is called the *type-species* of the genus, or, more shortly, the *genotype* (see later). The absence of a specified genotype from the original definition of a genus has often been a source of much confusion when the genus has been subdivided later.

The subdivision of a genus often takes place in two stages: one author divides it into sub-genera, and a later author raises these to the rank of genera. To provide for this possibility it is a rule that when a genus is divided into sub-genera, one of these (the one including the genotype) must bear the same name as the genus itself. To distinguish the sub-generic name from the generic name, the former is written with the addition of the abbreviation *s. str.* (*sensu stricto*, in the restricted sense). Thus Hall and Clarke divided the old genus *Orthis* of Dalman into a number of sub-genera, to all of which except one new names were given, such as *Dalmanella*, *Schizophoria*, etc., but the one which included Dalman's genotype was called *Orthis s. str.* Under this scheme the specific names of some well-known species became—

*Orthis* (*Dalmanella*) *elegantula* Dalman ;  
*Orthis* (*Schizophoria*) *resupinata* (Martin) ;  
*Orthis* (*Orthis*) *callactis* Dalman.

Later authors have raised these sub-genera to the rank of genera, so that the same species now stand as—

*Dalmanella elegantula* (Dalman);  
*Schizophoria resupinata* (Martin);  
*Orthis callactis* Dalman.

The printing of the author's name with or without parentheses in the different cases should be noted carefully.

6. A later author may unite several hitherto separate genera into one. This is a much rarer case than the last, as the whole tendency of advancing classification is to increase rather than to diminish the number of divisions of all grades. In this case the application of the law of priority leads to the rule that out of the names of the several genera which are being united the earliest name shall be retained as the name of the united genus.

The names of categories higher than genera cannot be subject to the same rigid law of priority as generic and specific names.

For families the rule is that the name of the family is formed by combining the name of the type-genus with the patronymic Latin termination *idæ*. Thus the family of which *Olenus* is the most typical genus is called *Olenidæ*. If for reasons of priority it is found necessary to change the name of the type-genus, the family name must change with it. Thus if it is decided that the generic name *Goldius* de Koninck has priority over the usually accepted name *Bronteus* Goldfuss, then the family name *Bronteidæ* must also be altered to *Goldiidæ*.

In the case of sub-families the name is similarly formed by combining the root of the name of the type-genus with the termination *-inæ*. Thus the family *Phacopidæ*, typified by the genus *Phacops*, is divided into three sub-families, named *Dalmanitinæ*, *Phacopinæ*, and *Pterygomelopinæ*, typified by the respective genera *Dalmanites*,

*Phacops*, and *Pterygometopus*. It will be noted that the genus *Phacops* is typical both of the whole family and of one of the sub-families.

As there have been many cases where opinions have differed as to the particular form which was denoted by a certain name, and as neither printed descriptions nor figures can always be interpreted with certainty, it is of the utmost importance that the actual specimens which an author had before him when founding a species should be preserved for reference in case of doubt. These specimens are called **type-specimens** or **types**, and they are now always preserved with the greatest care by all museums which possess any, being usually marked with some special label—*e.g.*, in the British Museum types are indicated by a small circular green label.

Types are of several kinds :

If the author of a new species defines that species with special reference to one particular individual, that individual is called the **holotype** of the species.

If, while specifying a holotype, he also refers to other specimens in his original description, or figures them along with the holotype, these additional specimens are called **paratypes**.

If, however, he uses several specimens in his original description without specifying one of them as the holotype, these specimens are called **syntypes** (or co-types).

If the syntypes of a species are subsequently discovered to belong to two or more distinct species, the original author, or (with his permission, or after his death) any later author, may select one of them as the type of the original species: this is called a **lectotype**. The remaining syntypes, if not identical with other species already named, may become holotypes of new species at the same time.

Types of a much lower degree of value are the following :

Any specimen of a species coming from the same locality and zone as its holotype or syntypes is a **topotype**. Topotypes can be indefinitely increased in number by collecting, whereas there can never be more than one holotype or lectotype, and never more than a few paratypes or syntypes.

A topotype recognized by the original author as belonging to this species acquires additional value thereby, and is called a **metatype**.

A specimen of a species described or figured by the original or any later author at some subsequent date to the original establishment of the species is a **plesiotype**.

What a type-specimen is to a species a type-species or **genotype** is to a genus: that is, it is a more certain means of settling the application and extent of the generic name than any verbal definition.

If the author of a genus defines one particular species as typical of the genus, that is the **geno-holotype**.

If he only gives a list of the species which he considers to belong to his genus, these are **geno-syntypes**.

Out of a series of geno-syntypes a **geno-lectotype** may be chosen at any later date, either by the original author of the genus, or (with his permission, or after his death) by any subsequent author.

The collector of fossils who wishes to name his specimens accurately will need to take much trouble in hunting through works in which fossils are described and figured. These works are of several categories.

First, we have monumental works, mostly of rather early date, which set out to describe and figure all the fossils (or all of some great group of fossils) found in some one country or State.

Secondly, there are numerous smaller works, some-



times separately published, sometimes forming parts of scientific journals, in which only some small groups of fossils, or the fossils from some one locality or district, are described.

Thirdly, there are various monographs, such as those published by the Palæontographical Society of London, which aim at a complete description (with revision of all previous publications on the subject), either of some great group as the Brachiopoda, for all geological systems, or for some one system (as the Cretaceous Lamellibranchs or the Carboniferous Trilobites), or, more rarely, the whole fauna of some one system or formation. Such monographs, if properly prepared, are of enormous value to students, as they sum up all that is known up to the date of their publication, and only very special investigators need go behind them to earlier works. These three categories are fairly distinct, but it is not always possible sharply to separate them.

Fourthly, there are catalogues and indexes which, without themselves describing any new genera or species, enable students to find with the least labour those works where they are described.

Some of these monographs, etc., have already been noted in the short bibliographies appended to each chapter. It remains to list a few of the works of more general kind. Fuller bibliographies of particular groups of fossils will be found in some of these.

## General Bibliography.

### I.—INDEXES.

BRONN, H. G.—Index Palæontologicus (1848-49). Records every species of fossil plant and animal named up to date of publication, with references to author, synonymy, geological age, etc.

MORRIS, J.—British Fossils, 2nd edn. (1854). Records all British species up to date of publication, with references.

SHERBORN, C. D.—Index Animalium, Vol. I. (1902). Complete index to all animal genera and species, recent and fossil. The published volume covers publications from 1758 to 1800. Vol. II. will extend to 1850.

ZOOLOGICAL RECORD. — Annual publication by the Zoological Society of London, including lists of all new genera and species of animals published during the year.

PALÆONTOLOGIA UNIVERSALIS.—A series of photographic reproductions of type-specimens and their original figures and descriptions (chiefly of species published before 1865).

FOSSILIUM CATALOGUS, edited by Professor Frech, of Breslau (Berlin, 1913 —).—A series of lists of species compiled by specialists, with geological and geographical range, synonymy, and references, thus replacing Bronn's *Index*, piece by piece. Lists so far published include Cretaceous Corals (by J. Felix), Palæozoic Starfish (C. Schuchert), Tertiary Anisomyarian Lamellibranchs (W. Teppner), Devonian Ammonoidea (F. Frech), Triassic Cephalopods (C. Diener), Triassic Dinosaurs (F. de Huene), Stegosauria (E. Hennig), Lycopodiales and Equisetales (W. Jongmans), and Juglandaceæ (K. Nagel).

## II.—LARGE GENERAL TEXTBOOKS.

BERNARD, F.—Éléments de Paléontologie, pt. i. (Paris, 1893).

FISCHER, P.—Manuel de Conchyliologie (1880-87). Deals with recent and fossil Mollusca and Brachiopoda, and is still the best work on Lamellibranchs and Gastropods.

NEUMAYR, M.—Die Stämme des Thier-reiches (1889). A treatise on phylogeny, left very incomplete by the

author's early death. Deals only with Protozoa, Coelenterata, Echinoderms, and Brachiopods.

NICHOLSON, H. A., AND LYDEKKER, R.—Manual of Palæontology (1889), Vol. I.: Invertebrata, Vol. II.: Vertebrata and Plants. Still useful, though out of date in certain sections.

ZITTEL, K. A.—(1) Handbuch der Paläontologie, 4 Vols. (1876-93); also French translation by Ch. Barrois (1883-94). The most complete textbook, but suffering from the lapse of time since its publication. (2) Grundzüge der Paläontologie (1895, new edition, 1910-11), also English translation by C. Eastman, Vol. I.: Invertebrata (1900, 2nd edn. 1913), Vol. II.: Vertebrata (1902). (3) History of Geology and Palæontology, translated by M. M. Ogilvie-Gordon (*Contemporary Science Series*, 1901). The chapters on Palæontology and Stratigraphical Geology are indispensable to any student wishing to understand the history of research and the work of the great pioneers.

### III.—MONOGRAPHS OF EXTENSIVE NATURE.

BARRANDE, J.—Système Silurien du Centre de la Bohême (1852-99). A series of very detailed and magnificently illustrated monographs on the fossils of the Lower Palæozoic rocks of Bohemia. Barrande's own work covers the Trilobites, Mollusca, and Brachiopods; and after his death other authors have added volumes on Graptolites, Corals, Bryozoa, and Cystids.

DESHAYES, P. G.—Description des Coquilles Fossiles des Environs de Paris, 2 vols. and Atlas (1824-37): Cainozoic Mollusca.

D'ORBIGNY, A. D.—Paléontologie Française (1840-55, with later volumes by other authors). An attempt, never completed, to figure and describe all the fossils of France.

It covers Jurassic and Cretaceous Corals, Echinoderms, Bryozoa, Brachiopoda, Mollusca and Plants, also Eocene Echinoids.

GOLDFUSS, G. A. AND MÜNSTER, G.—*Petrefacta Germaniæ*, 2 vols. (1826-40). An equally ambitious design for Germany, limited in execution to Sponges, Corals, Echinoderms, and Mollusca.

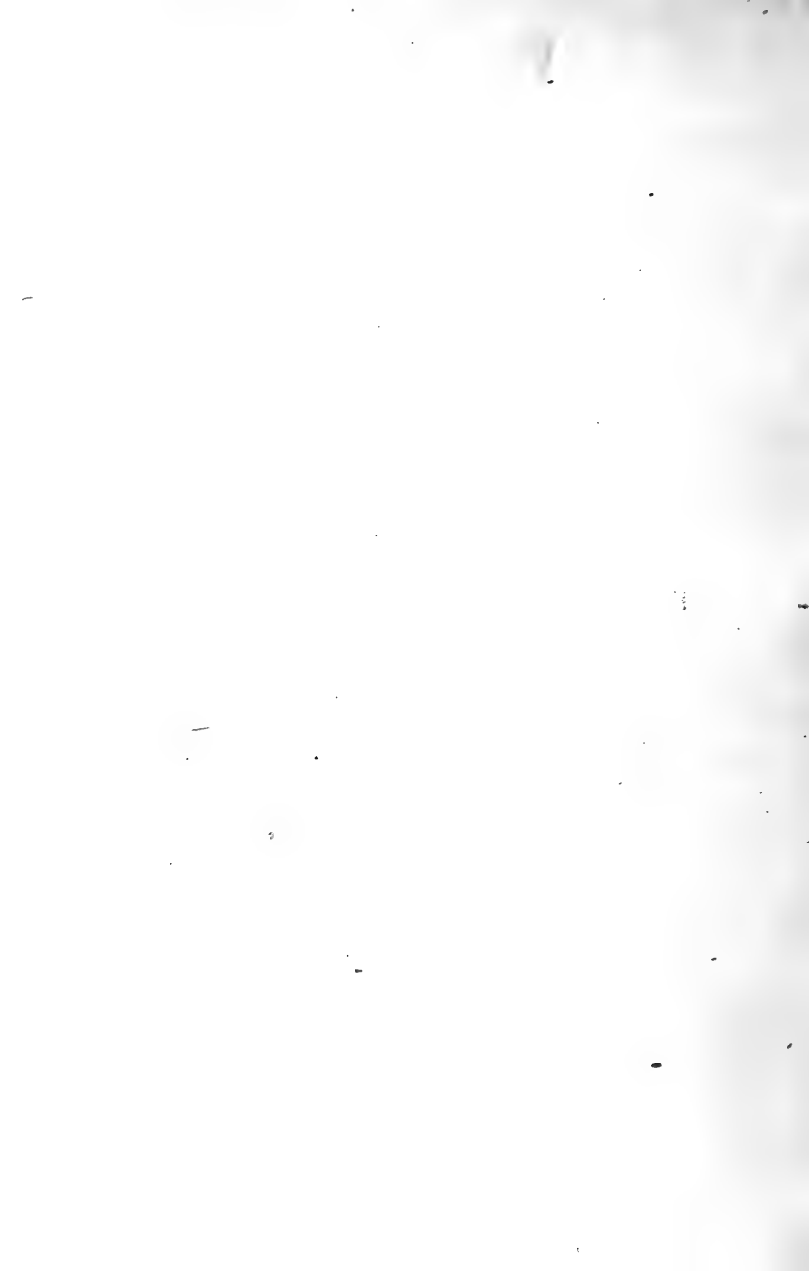
HALL, J.—*Palæontology of New York* (1848-98). A series of elaborate monographs on the Palæozoic Fossils of New York State.

LAMARCK, J. B. DE M.—*Histoire Naturelle des Animaux sans Vertèbres* (1815-22).

SOWERBY, J., CONTINUED BY SOWERBY, J. DE C.—*Mineral Conchology of Great Britain* (1812-46). Published in monthly parts, with interruptions, its object was to figure British fossil shells, *i.e.*, Mollusca as then understood (including Foraminifera, Cirripedia, Annelida, Brachiopoda, and, by mistake, one Coral). In all about 1,250 species were described, and figured on 648 plates, engraved on metal and coloured by hand with great faithfulness to the natural appearance. There is no system in the sequence of species, and as British stratigraphy underwent its development during the publication the geological age is much better treated in the later than in the earlier parts. Many of the types described were unfortunately derived fossils from the Glacial Drift.

The above lists might be extended indefinitely, but their object is to give the student a first general idea of the sort of material available for the purpose of identifying the fossils in his collections, and for extending his knowledge in any department that may specially interest him.

APPENDIX I  
DIVISIONS OF GEOLOGICAL TIME



## DIVISIONS OF GEOLOGICAL TIME.

The student of Palæontology constantly requires to refer to the names which have been given to the divisions, great and small, into which the fossiliferous rocks and the time of their deposition have alike been divided. These are here given in tabular form for convenience of reference. For the grounds on which their limits are fixed the reader is referred to textbooks of Stratigraphy, or he will find a reasoned statement in a paper by MM. Munier-Chalmas and de Lapparent: "Note sur la nomenclature des terrains sédimentaires," *Bull. Soc. Géol. France*, 3<sup>e</sup> sér., t. xxi. (1893), p. 438.

Some possible sources of confusion must be pointed out. First, the necessity for a double series of terms—more or less local stratigraphical terms (such as Wenlock Limestone, Carboniferous Limestone, Gault) and terms of world-wide, or at least international, application (such as Cambrian, Viséan, Cenomanian). Both have their own usefulness, but the attempt to use terms of the first category in place of those of the second has led to much confusion in correlation; while forgetfulness of the fact that the second category should apply, as far as possible, over the whole world has led geologists to coin some unnecessary synonyms. The limits of the first set of terms are determined by marked changes in the character of the sediments laid down in a limited area; those of the second should be determined primarily by widespread changes of fauna or flora, and secondly by great changes in the distribution of land and sea (the biological and geographical changes being intimately related).

The tables on pp. 378-380 must not be taken as fixed and settled. Geologists are not in complete agreement as to the relative importance of many divisions: what is a series to one is only a stage to another, and nomenclature varies accordingly. A few synonyms, etc., are given here, in descending order:

Montian is included in Danian by some.  
Aturian = Maestrichtian + Campanian.  
Senonian = Aturian + Emscherian.

Group Era.	System Period.	Series Epoch.	Stage Age.	Local Stratigraphical Terms (chiefly British) and Synonyms.
CAINOZOIC	NEOGENE ...	Holocene	—	—
		Pleistocene	—	Glacial Drift, River gravels, etc.
		Pliocene	Sicilian	Red Crag — Coralline Crag
			Astian Plaisancian	
		Miocene	Pontian Sarmatian	{ Congeria-beds, etc., of Caspian facies in S.E. Europe
			Tortonian Helvetian Burdigalian Aquitanian	
	PALÆOGENE ... (Nummulitic)	Oligocene	Stampian	{ — —
			Sannoisian	
		Eocene	Bartonian Lutetian	— Calcaire Grossier (Paris) London Clay
Londinian (Ypresian)				
Thanetian Montian			— —	
MESOZOIC	CRETACEOUS ...	Upper Cretaceous (Senonian)	Danian	{ — — Upper White Chalk
			Maestrichtian	
			Campanian Emscherian	
		Middle Cretaceous (often included mainly in Upper Cret.)	Turonian Cenomanian	Middle Chalk Lower Chalk, Chalk Marl, Upper Greensand Gault
			Albian	
		Lower Cretaceous	Aptian Barremian Hauterivian Valanginian	Lower Greensand { Freshwater equiv- alent = Wealden Upper Volgian of Russia



Group Era.	System Period.	Series Epoch.	Stage Age.	Local Stratigraphical Terms (chiefly British) and Synonyms.			
MESOZOIC	JURASSIC ...	Upper Jurassic (Oolitic)	Aquilonian	Freshwater equivalent = Purbeck beds			
			Portlandian	—			
			Bononian	—			
			Kimmeridgian	—			
			Sequanian	} Corallian			
			Argovian				
			Divesian	} Oxford Clay			
			Callovian				
			Bathonian	Great Oolite			
			Vesulian	} Inferior Oolite			
Bajocian							
MESOZOIC	JURASSIC ...	Lower Jurassic (Liassic)	Aalenian	—			
			Yeovilian	} Toarcian; Upper Lias			
			Whitbian				
			Domerian	Middle Lias (Marlstone)			
			Charmouthian (Carixian)	} Lower Lias			
			Sinemurian				
			Hettangian				
			MESOZOIC	TRIASSIC ...	—	Rhætian	—
						Norian	} Non-marine equivalent = Keuper Muschelkalk of Germany
						Carnian	
Ladinian							
Anisian	} Non-marine equivalent = Bunter						
Scythian							
NEWER PALÆOZOIC	PERMIAN ...	Thuringian				—	Magnesian Limestone
		Penjabian				Saxonian *	—
		Artinskian				Autunian *	—
	CARBONIFEROUS	Uralian				Stephanian *	—
		Moscovian	Westphalian *	—			
		Dinantian	Visean	Tournaisian	Carboniferous Limestone		

\* These are not names of stages, but equivalent names for the non-marine equivalent series, the Coal Measures and similar formations, which are of greater importance in these two systems than in any others.

Group Era.	System Period.	Series Epoch.	Stage Age.	Local Stratigraphical Terms (chiefly British) and Synonyms.
NEWER PALÆOZOIC	DEVONIAN ...	Upper	Fammenian	Upper Old Red Sandstone
		Middle	Frasnian	—
			Givetian	—
			Eifelian	—
		Lower	Coblenzian	—
			Gedinnian	Lower Old Red Sandstone
OLDER PALÆOZOIC	SILURIAN ... (Gothlandian)	Downtonian	—	Upper Ludlow beds, etc.
		Salopian	—	Wenlock and Lower Ludlow beds
		Valentian	—	Llandovery beds
	ORDOVICIAN ...	Ashgillian	—	—
		Caradocian	—	Bala beds
		Llandeilian	—	—
		Llanvirnian	—	—
		Skiddavian	—	Arenig beds
	CAMBRIAN ...	Tremadocian	—	—
		Potsdamian	—	Lingula Flags
		Menevian (Acadian)	—	—
		Georgian	—	—

Neocomian = Hauterivian + Valanginian, and is sometimes used to include also Barremian and even Aptian.

Urgonian is the name of a special facies, partly Barremian, partly Aptian.

Tithonian = Portlandian + Aquilonian approximately, as developed in Alpine-Mediterranean region.

Volgian = from Portlandian to Barremian, as developed in Russia.

Bononian is in England generally divided between Portlandian and Kimmeridgian.

Corallian is a facies name of variable age, roughly Argovian and Sequanian.

Oxfordian is used in several senses; it covers Divesian with either higher stages up to Sequanian or part of Callovian below.

Bathonian as originally defined included Vesulian, and Bajocian included at least a part of Aalenian, and these terms are still used in the wider sense.

Toarcian = Yeovilian + Whitbian.

Pliensbachian = Domerian + Charmouthian; and Charmouthian was originally synonymous with Pliensbachian.

Charmouthian has recently been divided by Mr. Buckman into Hwiccian, Wessexian, and Raasayan, and Sinemurian into Deiran, Mercian, and Lymian (see pp. 388-9).

Werfenian = Scythian.

Anthracolithic = Permian + Carboniferous.

Avonian = Dinantian practically.

Silurian is used in three senses: (1) as here = Gothlandian, the usual English use; (2) as = Gothlandian + Ordovician, the usual French and German and former English use: this use may always be assumed when "Lower" and "Upper Silurian" are spoken of; (3) as = Older Palæozoic, not a frequent use.

The division of stratified rocks into *zones*—*i.e.*, divisions less than stages based on palæontological characters alone, and extending, if not over the whole world, far beyond the limits within which lithological distinctions remain constant—was initiated by Opper for the Jurassic system about sixty years ago. It has since been applied to most other systems, but no other system has proved susceptible to such detailed application of the method. As Opper's original zones proved capable of division to a greater or less degree, Mr. S. S. Buckman proposed the term *hemera* as the name of the smallest possible *time-division* which palæontological facts make possible—it is the period of acme of a particular species (or occasionally of a genus). The term *zone* has since been regarded by many as the rock-division corresponding to a hemera; but Dr. Lang and others consider that the zones defined by Opper must continue to stand, and subdivisions made in them corresponding to hemeræ must be called sub-zones. Accordingly, in the table of Jurassic zones, both Opper's original zones and the latest recognized hemeræ are given. In quoting the hemeræ (or zones) it is usual to give only the trivial name of the index fossil, thus: *biarmatum* zone, *obtusum* hemera (or hemera *obtusi*, using the genitive case).

The fossils that have proved of the greatest value as zone-fossils are Ammonoids and Graptolites; but Brachiopods, Trilobites, Foraminifera, and Lamelli-branches (in order of decreasing value) also serve; and isolated species of other groups, *e.g.*, Crinoids, may often be of great use. In freshwater Cainozoic deposits Mammals are of the highest value.

It should be unnecessary to add that these tables of zones are given for reference only, and by no means as an exercise in memorizing!

## 1. FORAMINIFER-ZONES OF THE CAINOZOIC AND CRETACEOUS.

After P. de la Harpe, H. Douvillé, E. Vredenburg, R. Douvillé and P. Lemoine.

System.	Stage.	NUMMULITES.	LEPIDOCYCLINA.		Other large Foraminifera.
			Old World.	America.	
MIOCENE	—	—	—	—	<i>Orbiculina malabarica</i>
	BURDIGALIAN ...	<i>niasi</i>	<i>sumatrensis</i> *	<i>canellei</i>	{ <i>Operculina niasi</i> <i>Miogypsina</i>
	UPPER AQUITANIAN	<i>makullaensis</i>	<i>marginata</i>	—	—
	MIDDLE AQUITANIAN	<i>intermedius, vasculus</i>	<i>dilatata</i> †	<i>chaperi</i>	—
	LOWER AQUITANIAN	—	<i>formosa</i>	—	—
	STAMPIAN ...	<i>sublævigatus</i>	<i>formosa, rau-</i> <i>lini</i>	<i>mantelli</i>	—
	SANNOISIAN ...	<i>complanatus, † sublæv-</i> <i>igatus, intermedius</i>	—	—	{ <i>Orbitolites martini</i> <i>Operculina complanata</i>
	BARTONIAN ...	<i>contortus-striatus, † per-</i> <i>foratus</i>	—	—	—
	UPPER LUETIAN ...	<i>biarritzensis, gizehensis,</i> <i>douvilléi, lævigatus</i>	<i>pratti</i>	—	{ <i>Orbitolites complanatus</i> <i>Heterostegina reticulata</i> <i>Assilina exponens</i> <i>Assilina sufflata</i>
	EOCENE			ORTHOPHRAGMINA.	

Eocene	LOWER LUTETIAN ...	<i>ataicus, irregularis</i>	—	<i>Assilina granulosa</i>	
	YPRESIAN ...	<i>elegans-planulatus</i> §	—	<i>Assilina miscella</i>	
	THANETIAN ...	—	—	—	
	MONTIAN ...	—	—	—	
	DANIAN ...	—	ORBITOIDES,	Series leading to ORBITOLITES.	
	MAESTRICHTIAN (DORDONIAN)	—	<i>gensacica, socialis</i>	—	<i>Fallotia</i>
		—	—	<i>minor, apiculata</i>	<i>Mæandropsina</i>
	CAMPANIAN ...	—	<i>media</i>	—	
	EMSCHERIAN ...	—	<i>media</i>	<i>Broeckina, Præsorites</i>	
	TURONIAN ...	—	—	—	
	UPPER CENOMANIAN	ORBITOLINA.	—	—	
	LOWER CENOMANIAN	<i>concava</i>	—	—	
	ALBIAN ...	<i>plana</i>	—	—	
	APTIAN ...	<i>subconcava</i>	—	—	
BARREMIAN ...	<i>lenticularis</i>	—	—		
	<i>discoidea, conoidea</i>	—	—		

\* The smallest Lepidocyclines.

† The largest Lepidocyclines.

‡ These hyphenated names are cases where distinct trivial names had been given to megal- and micro-spheric forms of the same species.

## 2. CRETACEOUS ZONES.

Stages.	Ammonoid Zones of the South of France, after Kilian, Grossouvre, and Jacob.	Zones of England, North France, etc., after Barrois, Jukes-Browne, etc.
DANIAN ...	<i>Hercoglossa</i> [ <i>Nautilus</i> ] <i>danica</i>	—
MAESTRICHTIAN {	<i>Parapachydiscus neubergicus</i> <i>Bostrychoceras polyplacum</i>	— —
CAMPANIAN ... {	<i>Hoplites vari</i> <i>Mortoniceras delawarensis</i> <i>Placenticeras bidorsatum</i>	<i>Ostrea lunata</i> <i>Belemnitella mucronata</i> <i>Actinocamax quadratus</i>
EMSCHERIAN ... {	<i>Placenticeras syrtale</i> <i>Mortoniceras texanum</i> <i>Mortoniceras emscheris</i> <i>Barroisiceras haberfellneri</i>	<i>Marsupites testudinarius</i> <i>Micraster cor-anguinum</i> — <i>Micraster cor-testudinarius</i>
TURONIAN ... {	<i>Acanthoceras deverianum</i> <i>Acanthoceras ornatisimum</i> <i>Acanthoceras bizeti</i> <i>Mammites nodosoides</i>	<i>Heteroceras reussianum</i> <i>Holaster planus</i> <i>Terebratulina lata</i> <i>Rhynchonella cuvieri</i>
CENOMANIAN ... {	<i>Acanthoceras rotomagense</i> <i>Mantelliceras mantelli</i> <i>Mortoniceras inflatum</i>	<i>Holaster subglobosus</i> <i>Schloenbachia varians</i> <i>Mortoniceras inflatum</i>
ALBIAN ... {	<i>Mortoniceras hugardianum</i> <i>Hoplites dentatus</i> <i>Hoplites tardefurcatus</i>	<i>Hoplites lautus</i> <i>Hoplites interruptus</i> <i>Douvilléceras mammillatum</i>
APTIAN ... {	<i>Douvilléceras nodosocostatum</i> <i>Douvilléceras subnodosocostatum</i> <i>Oppelia nissus</i> <i>Parahoplites deshayesi</i>	— — — <i>Parahoplites deshayesi</i>
BARREMIAN ... {	<i>Heteroceras astierianum</i> <i>Pulchellia pulchella</i> <i>Parahoplites angulicostatus</i> <i>Desmoceras sayni</i>	Russian Zones, after Pavlov. <i>Simbirskites speetonensis</i> <i>Simbirskites subinversus</i>
HAUTERIVIAN {	<i>Crioceras duvali</i> <i>Acanthodiscus radiatus</i>	<i>Polyptychites polyptychus</i> <i>Polyptychites keyserlingi</i>
VALANGINIAN {	<i>Saynoceras verrucosum</i> <i>Kilianella roubaudiana</i> <i>Thurmannia boissieri</i>	<i>Craspedites stenomphalus</i> <i>Craspedites spasskensis</i> <i>Polyptychites gravesiformis</i>

## 3. ZONES OF THE UPPER JURASSIC.

Oppel's Zones (1856-58). Approximate Equivalence.	Quenstedt* (1858).	Stages.	Hemera (Buckman, Salfeld, etc., 1898-1915).
		AQUILONIAN	<i>Craspedites fragilis</i>
<i>Trigonia gibbosa</i>		PORTLANDIAN	<i>Perisphinctes giganteus</i> <i>Perisphinctes pseudogigas</i> <i>Perisphinctes gorei</i> <i>Perisphinctes eastlecottensis</i>
<i>Pterocera oceani</i>		BONONIAN	<i>Perisphinctes pectinatus</i> <i>Virgatites pallasianus</i> <i>Virgatites miatschkoviensis</i> <i>Gravesia irius</i> <i>Gravesia gravesiana</i>
<i>Astarte supracorallina</i>	White Jura ζ	KIMMERIDGIAN	<i>Aulacostephanus pseudo-mutabilis</i> <i>Aulacostephanus yo</i> <i>Rasenia mutabilis</i> <i>Rasenia cymodoce</i> <i>Pictonia baylei</i>
<i>Diceras arietinum</i>	ε δ γ β	SEQUANIAN (Age of <i>Amæboceras</i> )	<i>Ringsteadia pseudocardatus</i> <i>Perisphinctes decipiens</i> (and <i>Amæboceras serratum</i> ) <i>Perisphinctes wartæ</i>
<i>Cidaris flori- gemma</i> <i>Ammonites biarmatus</i>	α	ARGOVIAN (Age of <i>Cardioceras</i> )	<i>Perisphinctes martelli</i> <i>Aspidoceras biarmatum</i> <i>Cardioceras vertebrale</i> (and <i>Cardioceras cordatum</i> ) <i>Cardioceras scarburgense</i>
		DIVESIAN (Age of <i>Quenstedtoceras</i> )	<i>Quenstedtoceras gregarium</i> <i>Quenstedtoceras vertumnus</i> <i>Creniceras renggeri</i> <i>Quenstedtoceras lamberti</i>

\* Quenstedt divided the whole Jurassic System into three—the Black Jura, Brown Jura, and White Jura, for which Oppel's equivalent terms were Lias, Dogger, and Malm. Each of these three was divided into six divisions, marked by the Greek letters α, β, γ, δ, ε, and ζ. The whole of the White Jura and most of the Brown Jura come in the Upper Jurassic; the rest of the Brown and all the Black Jura in the Lower Jurassic.

## ZONES OF THE UPPER JURASSIC—Continued.

Oppel's Zones (1856-58). Approximate Equivalence.	Quenstedt (1858).	Stages.	Hemerae (Buckman, Mascke, etc., 1898-1915).
<i>Ammonites athleta</i> <i>Ammonites anceps</i>  <i>Ammonites macrocephalus</i>	Brown Jura ξ	CALLOVIAN (Age of Cosmoceratids)	<i>Peltoceras athleta</i> <i>Cosmoceras duncani</i> <i>Cosmoceras castor</i> <i>Erymnoceras coronatum</i> <i>Cosmoceras elizabethæ</i> <i>Sigaloceras calloviense</i> <i>Proplanulites kœnigi</i> <i>Macrocephalites macrocephalus</i>
<i>Terebratula lagenalis</i> <i>Terebratula digona</i>	ε	BATHIAN (Age in which Ammonites are rare)	<i>Clydoniceras discus</i> <i>Epithyris marmorea</i> * <i>Ornithella digona</i> * <i>Ornithella digonoides</i> * <i>Epithyris bathonica</i> * <i>Oppelia waterhousei</i> <i>Macrocephalites morrissi</i> <i>Perisphinctes gracilis</i>
<i>Ammonites parkinsoni</i>	ε  δ	VESULIAN (Age of <i>Parkinsonia</i> )	<i>Ostrea acuminata</i> † <i>Oppelia fusca</i> <i>Zigzagiceras zigzag</i> <i>Parkinsonia schloenbachi</i> <i>Strigoceras truellii</i> <i>Garantiana garantiana</i>
<i>Ammonites humphriesianus</i>  <i>Ammonites sauzei</i>	δ  γ	BAJOCIAN (Age of Sonninians)	<i>Strenoceras niortense</i> <i>Teloceras blagdeni</i> <i>Stepheoceras</i> <i>Stephanoceras</i> <i>Stemmatoceras</i> <i>Otoites sauzei</i> <i>Witchellia</i> <i>Shirbuirnia</i> <i>post-discites</i> <i>Hyperlioceras discites</i>

\* Brachiopods.

† Lamellibranch.



## 4. ZONES OF THE LOWER JURASSIC.

Zones (Oppel, 1856-58).	Quenstedt (1858).	Stages.	Hemeræ (Buckman, etc., 1913-19).
<i>Ammonites murchisoni</i>	Brown Jura β	AALENIAN (Age of oxynote Hildoceratids)	<i>Ludwigella concava</i> <i>Brasilia bradfordensis</i> <i>Ludwigia murchisonæ</i> <i>Aucolloceras</i>
<i>Trigonia navis</i>			<i>Tmetoceras scissum</i> <i>Cypholloceras opaliniforme</i> <i>Pleydellia aalensis</i>
<i>Ammonites torulosus</i>	Black Jura ζ	YEOVILIAN (Age of Dumortierians and Grammoceratids)	<i>Dumortieria moorei</i> <i>Catullocceras</i> <i>Dumortieria sp.</i> <i>Hammatocceras</i>
<i>Ammonites jurensis</i>			<i>Phlyseogrammoceras dispansum</i> <i>Pseudogrammoceras struckmanni</i> <i>Pseudogrammoceras pedicum</i> <i>Haugia eseri</i> <i>Grammoceras striatulum</i>
<i>Posidononoma bronni</i>	ε	WHITBIAN (Age of Dactyloids and Harpoceratids)	<i>Haugia variabilis</i> <i>Lillia lilli</i> <i>Collina brauniana</i> <i>Peronoceras fibulatum</i> <i>Frechiella subcarinata</i> <i>Ovaticeras pseudovatum</i> <i>Harpoceras falciferum</i> <i>Harpoceras exaratum</i> <i>Dactylioceras tenuicostatum</i> <i>Tiltoniceras acutum</i> <i>Harpoceratoid</i>
<i>Ammonites spinatus</i>	δ	DOMERIAN (Age of Amaltheids)	<i>Paltopleuroceras spinatum</i>
<i>Ammonites margaritatus</i>			<i>Amaltheus lævis</i> <i>Amaltheus gibbosa</i> <i>Seguenziceras algovianum</i> <i>Cæloceras acanthoides</i> <i>Hildoceras boscense</i> <i>Grammoceras fieldingi</i>

## ZONES OF THE LOWER JURASSIC—Continued.

Zones (Oppel, 1856-58).	Quenstedt (1858).	Stages.	Hemeræ (Buckman, Trueman, Thompson, etc., 1910-19).
<i>Ammonites davoci</i>	Black Jura $\gamma$	HWICCIAN (Age of Liparoceratidæ)	<i>Oistoceras</i> <i>Ægoceras dædalocosta</i> <i>Deroceras davoei</i> <i>Amblyoceras brevilobatum</i> <i>Ægoceras latæcosta</i> <i>Beaniceras</i> <i>Acanthoceras carinatum</i> <i>Liparoceras cheltiense</i>
<i>Ammonites ibex</i>			<i>Acanthopleuroceras valduni</i> <i>Tragophylloceras ibex</i> <i>Acanthopleuroceras ellipticum</i> <i>Uptonia bronni</i> <i>Platyleuroceras</i> <i>Polymorphites trivialis</i> <i>Uptonia jamesoni</i> <i>Cæloceras pettos</i> <i>Polymorphites peregrinus</i> <i>Phricodoceras</i>
<i>Ammonites jamesoni</i>	$\gamma$	WESSEXIAN (Age of Polymorphidæ)	
<i>Ammonites armatus</i>	$\gamma$	RAASAYAN (Age of Deroceratidæ and Echioceratidæ)	<i>Deroceras leckenbyi</i> <i>Echioceras applanatum</i> <i>Echioceras macdonnelli</i> <i>Echioceras varicostatoides</i> <i>Deroceras bispinigerum</i> <i>Bifericeras subplanicosta</i> ist <i>Echioceras</i> ;
<i>Ammonites varicostatus</i>	$\beta$		
<i>Ammonites oxynotus</i>	$\beta$	DEIRAN * (Age of Oxycone Arietids)	<i>Oxynoticeras oxynotum</i> <i>Ætomoceras simpsoni</i> <i>Gagaticeras</i>

\* The existence of several other hemeræ in the Deiran and Mercian is indicated by Mr. Buckman, but they are not definitely established, and are therefore omitted. See *Quart. Journ. Geol. Soc.*, vol. lxxiii, pp. 257-327 (1918).

## ZONES OF THE LOWER JURASSIC—Continued.

Zones (Oppel, 1856-58).	Quenstedt (1858).	Stages.	Hemeræ (Buckman, Tutchet, etc., 1913-19).
<i>Ammonites obtusus</i>	Black Jura β	MERCIAN * (Age of Catagenetic Arietids)	<i>Asteroceras stellare</i> <i>Xiphoceras planicosta</i> <i>Asteroceras obtusum</i> <i>Asteroceras brooki</i> <i>Arietites turneri</i> †
<i>Pentacrinus tuberculatus</i>			
<i>Ammonites geometricus</i>	α	LYMIAN (Age of Anagenetic Arietids)	<i>Microdoceras birchi</i> <i>Arnioceras semicostatum</i> <i>Agassiceras sauzeanum</i> <i>Ætomoceras scipionianum</i>
<i>Ammonites bucklandi</i>			<i>Coroniceras gmuendense</i> <i>Coroniceras bucklandi</i> <i>Coroniceras rotiforme</i> <i>Vermiceras conybeari</i>
<i>Ammonites angulatus</i>	α	HETTANGIAN (Age of Caloceratids)	<i>Schlotheimia angulata</i> <i>Alsatites liasicus</i> <i>Wahneroceras megastoma</i>
<i>Ammonites planorbis</i>			<i>Caloceras johnstoni</i> <i>Psiloceras planorbis</i>
"Bone-bed" (with Rhætic)			<i>Ostrea liassica</i> ‡ <i>Pleuromya talei</i> ‡ <i>Volzella [Modiola] langportensis</i> ‡

\* The existence of several other hemeræ in the Deiran and Mercian is indicated by Mr. Buckman, but they are not definitely established, and are therefore omitted. See *Quart. Journ. Geol. Soc.*, vol. lxxiii., pp. 257-327 (1918).

† There is some uncertainty as to the position of this hemera; it may be below *birchi*.

‡ Lamellibranchs; no Ammonites are known outside the Alpine-Mediterranean province before the *planorbis* hemera.

## 5. TRIASSIC ZONES.

This scheme of zones was drawn up by Suess, Mojsisovics, Waagen, and Diener in 1895. The names of the Stages have been somewhat modified since, and as given here represent Dr. Diener's latest usage.

Stages.	Zones.	Famous Localities.
RHÆTIC ...	<i>Pteria</i> [ <i>Avicula</i> ] <i>contorta</i>	Aust Cliff (Gloucestershire)
NORIC ...	<i>Sirenites argonautæ</i> <i>Pinacoceras metternichi</i> <i>Cyrtopleurites bicrenatus</i> <i>Cladiscites ruber</i> <i>Sagenites giebeli</i>	Hallstadt (Austria)
CARNIC ...	<i>Tropites sub-bullatus</i> <i>Trachyceras aonoides</i> <i>Trachyceras aon</i>	— — St. Cassian (Tyrol)
LADINIC ...	<i>Protrachyceras archelaus</i> <i>Dinarites avisianus</i> <i>Protrachyceras curionii</i>	Muschelkalk of Thuringia, Lorraine, etc.
ANISIC (Dinarian, Virglorian)	<i>Ceratites trinodosus</i> <i>Ceratites binodosus</i> <i>Stephanites superbus</i>	— — —
SCYTHIC ...	<i>Flemingites flemingianus</i> <i>Flemingites radiatus</i> <i>Ceratites normalis</i> <i>Proptychites trilobatus</i> <i>Proptychites lawrencianus</i> <i>Gyronites frequens</i> <i>Octoceras woodwardi</i>	Werfen (Austria) Ceratite Marls and Salt Range (Punjab) Julfa (Armenia)

6. UPPER PALÆOZOIC ZONES.

The zoning of the Upper Palæozoic rocks is in a much less satisfactory state than that of either the Lower Palæozoic or the Mesozoic. Professor Frech, of Breslau, in 1898, proposed a number of broad goniatite-zones (rather stages than zones, really) for the Devonian system, and Professor Haug, of Paris, did the same for the Carboniferous and Permian. These zones, as modified by Professor Haug in his *Traité de Géologie* (1911), are here given :

Systems.	Series.	Stages.	Ammonoid Zones.	Famous Localities.
PERMIAN	THURINGIAN	—	20. <i>Cyclolobus oldhami</i>	Chideru (Salt Range, Punjab)
	SAXONIAN ...	—	19. <i>Xenaspis carbonarius</i>	Virgal (Salt Range)
	ARTINSKIAN ...	—	18. <i>Waagenoceras mojsisovicsi</i> 17. <i>Medlicottia artiensis</i>	Amb (Salt Range) Ural Mountains (Russia)
CARBONIFEROUS	URALIAN ...	—	16. <i>Gastrioceras marianum</i>	Ural Mountains (Russia)
	MOSCOVIAN ...	—	15. <i>Gastrioceras iisteri</i> 14. <i>Glyphioceras striolatum</i>	{ Myachkovo, near Moscow (for Crinoids) The British coal-measures are the non-marine equivalent
	DINANTIAN ...	Visean .. Tournaisian	13. <i>Goniatites striatus</i> 12. <i>Pericyclus princeps</i> and <i>Aganides rotatorius</i>	Bristol, Clitheroe (Lancashire), Tournai (Belgium)
DEVONIAN	UPPER ...	Famennian ...	11. <i>Gonioclymenia plana</i> 10. <i>Clymenia annulata</i> 9. <i>Chiloceras curvispina</i>	Sauerland (Westphalia) Kellerwald
		Frasnian ..	8. <i>Gephyroceras intumescens</i> 7. <i>Gephyroceras hoeninghausi</i>	Büdesheim (Eifel), Naples (U.S.A.)
	MIDDLE ...	Givetian ...	6. <i>Menceras decheni</i> 5. <i>Anarcestes denckmanni</i>	Givet (Ardennes) Paffrath (near Cologne)
		Eifelian ...	4. <i>Agoniatites occultus</i> 3. <i>Anarcestes subnautilinus</i>	Eifel (Rhine) Couvion (Ardennes)
	LOWER ...	Coblentzian Gedinnian ...	2. <i>Agoniatites fidelis</i> 1. <i>Tornoceras inexpectatum</i>	Hunsrück slates with pyritic crinoids, etc.

## 7. LOWER CARBONIFEROUS (DINANTIAN OR AVONIAN) ZONES.

A scheme of zoning for the Carboniferous Limestone of the Bristol district was developed by the late Dr. Vaughan, and published in 1905. It proved applicable over a wide area in South-West England and Wales and, with modifications, to the North of England and Belgium. The zone-fossils being shallow water Corals and Brachiopods, it is doubtful if the zones can hold good over a much wider area. The table on p. 393 gives Vaughan's zones, and those established by Professor Garwood in the North of England.

## 8. FORAMINIFER ZONES OF CARBONIFEROUS AND PERMIAN.

*Fusulina kattaensis* = base of Saxonian.

*Fusulina vernewili* = Artinskian.

*Schwagerina princeps* = Upper Uralian.

*Fusulina longissima* = Lower Uralian.

*Fusulina cylindrica* = Moscovian.

*Fusulinella struvii* = Viséan.

These zones appear to cover the complete range of the sub-family *Fusulininæ*.

VAUGHAN.		GARWOOD.		
Zones.	Sub-Zones.	Zones.	Sub-Zones.	
<p style="text-align: center;">VISEAN</p>	<p style="text-align: center;">Dibunophyllum ...</p>	<p style="text-align: center;">—</p>	<p style="text-align: center;">—</p>	
				<p>D3. <i>Cyathaxonia</i> D2. <i>Lonsdaleia floriformis</i> D1. <i>Dibunophyllum</i> θ</p>
	<p style="text-align: center;">Seminula ficoides ...</p>	<p>S2. <i>Productus corrugato-hemisphericus</i> and <i>Spiriferina laminosa</i> S1. <i>Caninia bristolensis</i></p>	<p><i>Productus corrugato-hemisphericus</i> and <i>Spiriferina laminosa</i></p>	<p><i>Nematophyllum minus</i> and <i>Cyrtina carbonaria</i> Gastropod beds</p>
		<p><i>Syringothyris cuspidata</i> and <i>Caninia cylindrica</i></p>	<p>C2. <i>Cyathophyllum</i> φ C1. <i>Caninia cornucopiae</i></p>	<p><i>Michelinia megastoma</i> ... <i>Athyris glabristria</i> ...</p>
	<p style="text-align: center;">TOURNAISIAN</p>	<p><i>Zaphrentis delanouei</i> and <i>Zaphrentis omaliusi</i></p>	<p>Z2. <i>Zaphrentis koninki</i> Z1. <i>Spirifer clathratus</i></p>	
<p style="text-align: center;">Cleistopora cf. geometrica</p>		<p>K2. <i>Spiriferina</i> cf. <i>octoplicata</i> K1. <i>Spirifer clathratus</i></p>		
		<p>Km. "M o d i o l a phase"</p>		

## 9. UPPER DEVONIAN AMMONOID ZONES.

A much more detailed scheme of zones, comparable with the zones of the older Palæozoic or Mesozoic, has lately been established by Dr. Wedekind of Göttingen for the Upper Devonian of Germany.

Stages.	Zones.
FAMENNIAN ...	VII. } <i>Gonioclymenia</i> VI. }
	V. { <i>Clymenia</i> cf. <i>undulata</i> <i>Clymenia lævigata</i>
	IVβ. <i>Postprolobites yakelowi</i> and <i>Clymenia tenui costata</i>
	IVα. <i>Clymenia crassicosta</i> and <i>Prolobites delphinus</i>
	IIIβ. <i>Clymenia involuta</i> IIIα. <i>Tornoceras sandbergeri</i>
FRASNIAN ...	IIβ. <i>Cheiloceras</i> and <i>Dimeroceras</i> IIα. <i>Cheiloceras</i>
	Iδ. <i>Crickites holzapfeli</i> and <i>Manticoceras crassum</i>
	Iγ. <i>Manticoceras carinatum</i> and <i>Manticoceras cordatum</i>
	Iβ. <i>Manticoceras nodulosum</i>
	Iα. <i>Prolecanites lunulicosta</i>

Zones Iα-δ correspond to 7 and 8 of the preceding list; IIα and β to 9; IIIα to V. to 10; VI. and VII. to 11.



10. SILURIAN GRAPTOLITE ZONES.

After Lapworth, Elles and Wood.

Series.	Stages.	Graptolite Zones and Sub-Zones.	Famous Localities.
DOWNTONIAN	—	No Graptolites known	Ludlow (Shropshire), bone-beds, etc.
SALOPIAN ...	Lower Ludlow	36. <i>Monograptus leintwardinensis</i> 35. <i>Monograptus tumescens</i> 34. <i>Monograptus scanicus</i> 33. <i>Monograptus nilssoni</i> * 32. <i>Monograptus vulgaris</i>	Aymestry (Shropshire), non-graptolitic <i>Conchidium</i> limestone Ludlow district (Graptolites and Nautiloidea, etc.)
	Riccarton or Wenlock	31. <i>Cyrtograptus lundgveni</i> 30. <i>Cyrtograptus rigidus</i> 29. <i>Cyrtograptus linnarsoni</i> 28. <i>Cyrtograptus symmetricus</i> 27. <i>Monograptus riccartonensis</i> * 26. <i>Cyrtograptus murchisoni</i> *	The uppermost zone is the approximate horizon of the highly fossiliferous (but non-graptolitic) Wenlock limestone of Wenlock Edge (Shropshire), Dudley, Walsall, etc. For Graptolites, Builth (Radnor), Riccarton (S. Scotland)
VALENTIAN	Gala or Tarannon	25. <i>Monograptus crenulatus</i> 24. <i>Monograptus griestonensis</i> 23. <i>Monograptus crispus</i> 22. <i>Monograptus turriculatus</i> Band of <i>Rastrites maximus</i>	Galashiels (S. Scotland), Tarannon River (Central Wales)
	Birkhill	21. <i>Monograptus sedgwicki</i> * Band of <i>Cephalograptus cometa</i> * 20. <i>Monograptus convolutus</i> * 19. <i>Monograptus gregarius</i> : <i>M. argenteus</i> † <i>M. triangulatus</i> † <i>M. fimbriatus</i> † 18. <i>Monograptus cyphus</i> * 17. <i>Mesograptus modestus</i> and <i>Orthograptus vesiculosus</i>	For Graptolites, Dobb's Linn (Dumfriesshire), Donaghadee (Ireland) For Brachiopods, etc., May Hill (Gloucestershire), Malvern (S. Shropshire), Girvan (Ayrshire)

\* Zones also recognized in Scandinavia and (nearly all) in the Ordovician zones apply here also.

† Sub-zones.

## 11. ORDOVICIAN GRAPTOLITE ZONES.

After Lapworth, Elles and Wood.

Series or Stages.	Graptolite Zones.	Famous Localities.
ASHGILLIAN (Upper Hartfell)	16. <i>Cephalograptus acuminatus</i> * 15. <i>Dicellograptus anceps</i> 14. <i>Dicellograptus complanatus</i> *	Dobb's Linn, near Moffat (Dumfriesshire)
CARADOCIAN (Lower Hartfell)	13. <i>Pleurograptus linearis</i> * 12. <i>Dicranograptus clingani</i> * 11. <i>Climacograptus wilsoni</i>	Dobb's Linn and Hartfell (Dumfriesshire)
LLANDEILIAN (Glenkiln)	10. <i>Climacograptus peltifer</i> and <i>Mesograptus multidentis</i> 9. <i>Nemagraptus gracilis</i> * † 8. <i>Glyptograptus tereiusculus</i>	Glenkiln Burn (S. Scotland)
LLANVIRNIAN	7. <i>Didymograptus murchisoni</i> 6. <i>Didymograptus bifidus</i> †	Aberiddy Bay (Pembroke)
SKIDDAVIAN (Arenig)	5. <i>Didymograptus hirundo</i> 4. <i>Didymograptus extensus</i> 3. <i>Dichograptus</i>	Skiddaw (Cumberland)
TREMADOCIAN	2. <i>Bryograptus</i> * 1. <i>Dictyonema sociale</i> *	— Pedwardine (Herefordshire)

NOTE.—Zones marked \* occur in the same sequence in Scandinavia as in Britain, and those marked † in North America. The identity of other zones may be masked by difference of name; or greater or lesser thickness of sediment or abundance of fossils may lead to a larger or smaller number of zones being recognized; or zones may be wanting through non-sequence.

## 12. CAMBRIAN TRILOBITE ZONES.

After Walcott, Moberg, Fearnside, Illing, and others.

Series.	Zones.	Famous Localities.
TREMADOCIAN (Transition to Ordovician)	<i>Angelina sedgwicki</i> <i>Bryograptus</i> and <i>Shumardia</i> <i>Asaphellus homfrayi</i> <i>Dictyonema sociale</i>  <i>Niobe homfrayi</i>	Tremadoc (N. Wales) Shinerton Brook (Shropshire) Pedwardine (Herefordshire) Penmorfa (N. Wales)
POTSDAMIAN ...	<i>Peltura scarabæoides</i> <i>Sphaerophthalmus alatus</i>  <i>Eurycare latum</i> <i>Orthis lenticularis</i>  <i>Olenus truncatus</i>	Scania White-leaved Oak (Malvern) — Portmadoc district (N. Wales) Hartshill and Oldbury (Warwickshire)
MENEVIAN ... (Acadian)	<i>Paradoxides forchammeri</i> <i>P. davidis</i>  <i>P. tessini</i> { <i>Conocoryphe æqualis</i> <i>Agnostus parvifrons</i> <i>Ctenocephalus exsulans</i>  <i>P. ölandicus</i>	— St. David's (Pembroke) Bornholm (Baltic Sea) Scania Scania —
GEORGIAN ...	<i>Protolenus</i>  <i>Olenellus</i> <i>Callavia</i> <i>Elliptocephala</i> <i>Nevadita</i> .	Comley (Shropshire), Newfoundland — Comley (Shropshire) — —



## APPENDIX II

### STRATIGRAPHICAL PALÆONTOLOGY.

#### I.—GENERAL FEATURES OF OLDER PALÆOZOIC FAUNAS TAKEN AS A WHOLE.

PRESENCE in abundance of **Graptolites, Brachiopods, and Trilobites**; in fair abundance of **CORALS, CRINOIDS,** and **CYSTIDS, NAUTILOIDEA** (mainly straight or slightly coiled). Rarity of **Lamellibranchs** and **Gastropods**. Complete or almost complete **absence** of **Echinids, Ammonoidea, Vertebrata, and Plants.**

#### SPECIAL FAUNAL FEATURES OF THE SEPARATE SYSTEMS.

1. **CAMBRIAN.**—**Absence** of Graptolites (except in uppermost beds), Corals, Crinoids, and Cephalopods.

**BRACHIOPODS** are mainly **horny Inarticulata**; the **Orthids** are the only other common forms. **TRILOBITES** are micropygous (except *Agnostus*); they serve as zone-fossils. The index-species of the Upper Cambrian are mainly of the family *Olenidæ*, those of the Middle Cambrian, *Paradoxidæ*, while Walcott's rather tentative divisions of the Lower Cambrian are based on genera of *Mesonacidæ*. For details see p. 397.

2. **ORDOVICIAN.**—Abundance of **branched Graptolites**, the most complexly branched being the earliest. The Graptolites serve as zone-fossils (see p. 396), but are almost confined to the black-shale facies. The *Lower Ordovician* (Skiddavian-Llanvirnian) is characterized by Dichograptids, the *Upper* by Leptograptids (Llandeilian), Dicranograptids and Diplograptids.

BRACHIOPODS: **Orthids** and **Strophomenids** abundant; horny Inarticulata reduced in numbers; **Rhynchonellids** and **Spire-bearers** appear, but are rare.

TRILOBITES of nearly all families abundant; most distinctive are the **Trinucleids** and **Asaphids**. Trilobites may serve as zone-fossils in beds of "shelly" facies.

3. **SILURIAN**.—Few branched Graptolites; **Monograptus** is the predominant genus, and its species (chiefly) serve as zone-fossils (p. 395).

**Corals** and **Crinoids** very abundant in the limestones.

BRACHIOPODS: **Pentamerids** first appear and are abundant; Ordovician forms continue; **Rhynchonellids** and **spire-bearers** (*Atrypa*, *Meristina*, *Spirifer*) common.

TRILOBITES as in Ordovician except for **absence** of Trinucleids and Asaphids. Encrinurids and Illænids do not survive beyond this system.

VERTEBRATA (primitive **Fishes**, represented by skin-teeth and fin-spines) first appear near the top of the system.

## II.—GENERAL FEATURES OF NEWER PALÆOZOIC FAUNAS TAKEN AS A WHOLE.

**Fishes** and **land-plants** appear and become abundant.

**Corals**, **Crinoids**, and **Brachiopods** continue abundant. Among the latter, **Loop-bearers** (*Terebratulids*) first appear, and **spine-bearers** are very abundant.

**Echinoids** and **Blastoids**, previously very rare, become fairly common, especially Blastoids, which, however, die out in this era.

**LAMELLIBRANCHS** and **GASTROPODS** increase in numbers.

**AMMONOIDEA** (**Goniatites**) first appear and become abundant.

**NAUTILOIDEA** continue common, and fully-coiled forms become more frequent.

**TRILOBITES** and **CYSTIDS** become **rarer**.

**Graptolites** are completely **extinct**.

## SPECIAL FEATURES OF THE SEPARATE SYSTEMS.

4. **DEVONIAN.**—BRACHIOPODS: of horny Inarticulata, only *Lingula* and Discinids (*Orbiculoidea*) survive (lasting to the Recent period). *Terebratuloids* first appear, but are not common. Most other Silurian families survive. **Spire-bearers** abound.

**Goniatites** are common, with very simple suture-lines; they serve as zone-fossils.

TRILOBITES: much reduced in numbers, but the same families as in the Silurian **except** *Illanids* and *Encrinurids*.

FISHES very abundant, especially **Ostracoderms** and **Ganoids**.

LAND-PLANTS (PTERIDOSPERMS, etc.) not very common.

5. **CARBONIFEROUS.**—**Blastoids** commoner than in any other system.

BRACHIOPODS: **Productus**, **Spirifer**, and *Rhynchonellids* most abundant. *Terebratulids* fairly abundant.

CEPHALOPODA: **Goniatites** with suture-lines a little more complex than in Devonian; tightly-coiled NAUTILOIDS.

TRILOBITES rare, of only one family (*Proetidae*).

VERTEBRATA: **fish-teeth** and **spines** common in some beds. OSTRACODERMS are **extinct**. AMPHIBIA in Coal Measures, rare.

PLANTS abundant in the coal-bearing beds. In the northern hemisphere (except India) the fern-like leaves of **Pteridosperms**, and stems of **Lepidodendron**, **Sigillaria** and **Calamites** are common. In India and the southern hemisphere, there is a totally distinct flora (Permo-Carboniferous), with the fern-like **Glossopteris**.

The zoning of the Lower Carboniferous is based on shallow-water Corals and Brachiopods, and the zones may be of restricted geographical extent (pp. 392-3). The Upper Carboniferous (Coal Measures) are classified, but scarcely zoned, by the flora: their marine equivalents by **Goniatites**, as are the marine Permian.

6. **PERMIAN.**—The true marine fauna is only known in a few restricted (tropical and sub-tropical)

regions. It is very similar to the Carboniferous fauna, except that the **Ammonoidea** have far more complex suture-lines, frequently with many-pointed lobes and rounded saddles.

In other areas an impoverished (inland sea) fauna is found, consisting mainly of BRACHIOPODS and LAMELLIBRANCHS, and a terrestrial flora which is an impoverished form of the Carboniferous flora.

### III.—GENERAL FEATURES OF MESOZOIC FAUNAS.

CORALS are less abundant and of entirely new types.

Cystids and Blastoids are *extinct*, CRINOIDS become less and *less common*; **Echinids** are abundant, and include *Irregular* as well as *Regular* forms.

**Brachiopods** are common, especially Terebratulids and Rhynchonellids.

**Lamellibranchs** are abundant, and **Gastropods** are common.

**Ammonoidea** are very abundant, except towards the end of the era; their suture-lines are extremely complex as a rule. They serve as zone-fossils (pp. 384-390).

Trilobites are quite extinct.

VERTEBRATA: **Fishes** (sharks and Ganoids) and **Reptiles**, both terrestrial and marine, are abundant. MAMMALIA are exceedingly rare and small.

LAND-PLANTS: principally **Cycads**, also CONIFERS and FERNS.

#### SPECIAL FEATURES OF THE SEPARATE SYSTEMS.

7. **TRIASSIC**.—As with the Permian, though to a much less extent, the true marine fauna is restricted in area, being preserved principally in the Alps and other great mountain chains.

ECHINOIDS are rare and of very special types.

**Brachiopoda**: *spire-bearing* forms are still numerous, as well as *Terebratulids* and *Rhynchonellids*, but nearly all other Palæozoic families are extinct.



**CEPHALOPODA: Ammonoidea** with ceratitic suture-lines are very abundant, but there are others with more complex (ammonitic) suture-lines.

Primitive **BELEMNOIDEA** also occur.

**VERTEBRATA: Reptiles**, especially terrestrial forms, are abundant. Some marine reptiles.

**ZONE-FOSSILS: Ammonoids** (and **Lamellibranchs**).

8. **JURASSIC.**—**Echinoids** are abundant, especially in certain beds. *Clypeus* is confined to this system, *Hemicidaris* nearly so. *Acrosalenia*, *Holactypus*, *Pygaster*, *Nucleolites*, and *Collyrites* are Cretaceous also.

The last *spire-bearing* Brachiopods occur in the *Lower* Jurassic.

**Lamellibranchs** are abundant, especially **Trigonia** and **Oysters**.

**Ammonoidea** with highly complex suture-lines (**Ammonites**) and typical **Belemnites** are abundant.

Large marine and terrestrial **Reptiles** are common.

**LAND-PLANTS** (**CYCADS**, etc.) are common in estuarine deposits.

The **Lower** Jurassic is characterized by the presence of the brachiopod **Spiriferina**, the **absence** of Irregular Echinoids, and the dominance of **keeled** forms among the Ammonites (though in particular zones this dominance may be reversed). The **Upper** Jurassic is characterized by the absence of *Spiriferina*, the presence of **Irregular Echinoids**, the dominance of **unkeeled** Ammonites (reversed in particular zones), and the frequency of **lappets** on the apertural margin of Ammonites (whether keeled or unkeeled).

**ZONE-FOSSILS.**—Ammonites or, in their absence, Brachiopods (pp. 385-9).

9. **CRETACEOUS.**—**Echinoids** of several new families appear, among which the *Echinocorythidæ* and *Spatangidæ* at once become abundant.

In the Alpine-Mediterranean province, numerous very peculiarly-shaped inequivalve Lamellibranchs (**Rudistes**: *Monopleura*, *Caprotina*, etc.) occur in the Lower Cretaceous, and are followed in the Upper by the **Hippurites**, whose habit of growth is more like that of rugose Corals than Lamellibranchs.

The last British *Trigonia* is found in the Cenomanian (Middle Cretaceous.)

**Ammonoidea** and **Belemnoidea** become gradually less abundant and finally die out. More or less **uncoiled Ammonoids** are common.

In certain regions (especially North Africa, Syria, South America, and the southern U.S.A.) there are Upper Cretaceous Ammonoids with suture-lines closely resembling those of the Triassic Ceratites (**pseudo-ceratites**).

In the *Upper* Cretaceous there is a sudden appearance of **Fishes** and land-plants (**Dicotyledons**) of much more modern types than those of the Jurassic and Lower Cretaceous.

**ZONE-FOSSILS.**—Ammonites and Belemnites, supplemented by Brachiopods and Echinoids in Northern Europe, by Rudistes and Foraminifera in the Mediterranean province.

#### IV.—GENERAL FEATURES OF THE CAINOZOIC FAUNAS.

**Foraminifera** are abundant and include forms of much greater size than in most earlier systems. These, where they occur (mainly in tropical and sub-tropical regions), are the best zone-fossils.

Corals are not abundant except in warm latitudes.

Crinoids and Brachiopods are rare.

**Echinoids** are common, especially in warm latitudes, where two new families abound: the flat *Scutellids* and the flat or pyramidal *Clypeastrids*. *Spatangids* increase in abundance.

**Lamellibranchs** and **Gastropods** are extremely abundant, and include many new families. Their species have too long a range to serve as zone-fossils, but the age of a bed can often be fixed exactly by the association of several species, some of which range upwards and others downwards.

**CEPHALOPODA** are rare, Ammonoids and typical Belemnoids being extinct.

VERTEBRATA: **Fishes** are of modern types; many Mesozoic types of Reptiles are extinct, only those surviving which last to the Recent period (crocodiles, turtles, lizards, snakes). **Mammals** are abundant, mainly in freshwater deposits, and serve to some extent as zone-fossils.

PLANTS are of modern types, but many now confined to warm climates (such as palms) are found fossil as far north as the Arctic regions.

#### SPECIAL FEATURES OF THE SEPARATE SYSTEMS.

10. **EOCENE**.—The foraminifer **Nummulites** is very abundant, especially in the Middle Eocene. **Ortho-phragmina** is confined to this system, except in America.

The Echinoids *Conoclypeus* and *Nucleolites* survive from the Cretaceous, but not beyond the Eocene.

The same is the case with the **Pycnodonts** (GANOID fishes).

The Molluscan fauna of this period (in Britain and elsewhere) resembles that now living in the Indian Ocean.

The **Mammalia** of the Lower Eocene are all small and primitive, with forty-four low-crowned teeth and five-toed limbs. In the Middle and Upper Eocene they rapidly become larger and more specialized.

11. **OLIGOCENE**.—The foraminifera **Nummulites** and allied genera continue in some abundance. **Lepidocyclina** replaces *Ortho-phragmina*.

The Irregular Echinoids *Scutella* and **Clypeaster** first appear.

**Mammals**.—In Europe and America new families appear, including the first (hornless) rhinoceros. In Africa a distinct fauna was developing, including the early ancestors of the elephant.

12. **MIOCENE**.—*Nummulites* is practically extinct. *Lepidocyclina* persists at first, but is finally replaced by *Miogypsina*.

The *Spatangids* *Micraster* and *Holaster*, which have

survived from the Cretaceous, now appear for the last time, alongside *Schizaster* and others which continue to the Recent period.

*Mammalia* include the first antlered deer, first horned rhinoceros, first ape. Ancestors of elephants suddenly appear in Europe.

13. **PLIOCENE**.—During this period there is in the northern hemisphere a gradual southward migration of the marine fauna, Arctic species appearing in Britain and, later, in the Mediterranean area. The horizon of any normal marine bed in the Pliocene system can be determined by the percentage of its species which are (*a*) extinct, (*b*) surviving in more northern or (*c*) in more southern latitudes.

*Mammalia* attain their greatest size. The first one-toed horse appears. *Mastodon* is characteristic.

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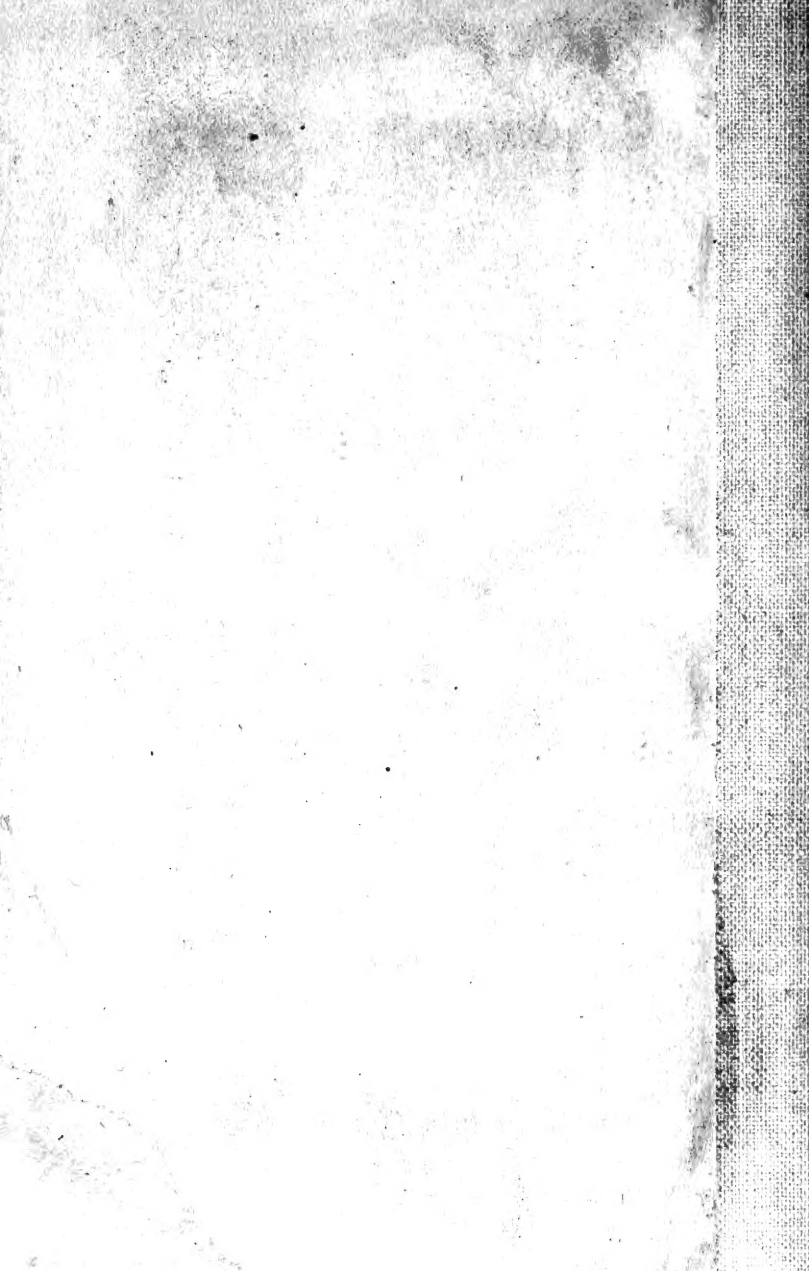
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