OUTLINES OF PALÆONTOLOGY

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PREFACE TO THIRD EDITION

The passage of so many years since this book was first issued, together with the destructive effects of war upon the remaining stocks, has made it necessary to issue a new and thoroughly revised edition. Under wartime conditions the relative inaccessibility of literature has enhanced the difficulty of doing this satisfactorily. In this connection I wish to record my deep gratitude to those many workers who have kept me supplied with copies of their writings. With these at my elbow my task has been made much easier and the work has been greatly expedited.

My thanks are also due to others who have supplied me with corrections and suggestions. Among them especial reference may be made to Dr. W. A. Richardson and to my colleague, Dr. R. M. MacLennan—to the former for having worked carefully through the whole book with this end in view, and to the latter for an equally careful perusal of the proofs.

It is unnecessary to give here a full statement of the alterations that have been made, but a few of the major ones may be indicated. The Section " Protozoa " has been largely recast. Considerable changes have also been made in the section " Cephalopoda," to which a discussion of " Recurrent Morphological Changes " has also been added. The parts relating to Trilobites and Fishes have undergone a similar degree of alteration. With regard to the systematic position of the Graptolites, the traditional view has been retained, but a special reference is given in the text to Dr. Bulman's article in which he draws attention to the very attractive view that *Cephalodiscus* is their closest living ally.

The practice of interweaving the more theoretical aspects of the subject with the particular groups of facts which illustrate them has been maintained, but recent developments of thought along these lines have been incorporated.

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DIVISIONS OF GEOLOGICAL TIME

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  - Holocene
  - Pleistocene
- TERTIARY
  - Neogene
    - Pliocene
    - Miocene
  - Palæogene
    - Oligocene
    - Eocene

MESOZOIC or SECONDARY

- Cretaceous
- Jurassic
  - Upper Jurassic or Oolitic
  - Lower Jurassic or Liassic
- Triassic

NEWER PALÆOZOIC or DEUTOZOIC

- Permian
- Carboniferous
- Devonian and Old Red Sandstone

OLDER PALÆOZOIC or PROTOZOIC

- Silurian
- Ordovician
- Cambrian

PRECAMBRIAN

Further detail has been incorporated in the text wherever it is required : e.g. pp. 44, 53, 121, 160, 170, 207, 241.

OUTLINES OF PALÆONTOLOGY

SECTION I

INTRODUCTION

The Round of Nature.—The living things of the past which have left their remains buried in the rocks form the study of the Palæontologist. As to-day, so throughout all the ages, the animals have depended primarily for their sustenance upon the plants. Where therefore the latter are most abundant and varied, the former are most numerous and diverse.

The land-plants depend for their nourishment upon the mineral substances dissolved from the soil by water, and upon the carbonic acid gas in the air. These materials are stored up, for aquatic plants, in the water which surrounds them, whilst the rocks beneath serve mainly as a base of attachment.

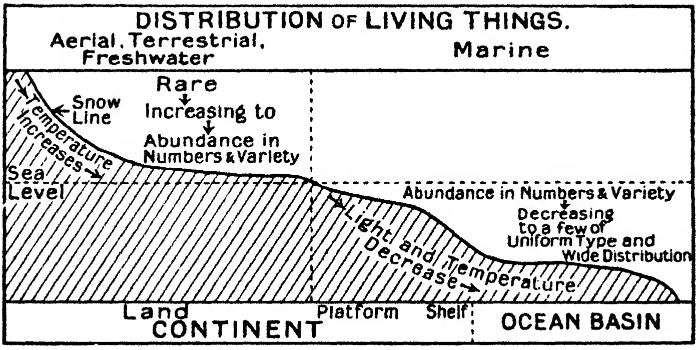


FIG. 1.

The rocky foundations range from the topmost mountains (Fig. 1), which are bathed in sunshine and clothed in perpetual snow, to the abyssal depths of ocean, where light never penetrates, and a general drift of icy-cold water prevails. On the snow-clad peaks life is at its lowest ebb, for here the water is frozen, and mineral substances are therefore not available for use as food for plants. As we descend to more genial zones, vegetation, at first sparse, becomes steadily more varied and abundant. Pine forests give place to woodlands of birches, oaks, and elms ; and these in warmer climes to vineyards, orange groves, and palms. Beneath them, and in open spaces, shrubs, flowers, grasses, ferns, mosses, spread like a living carpet with an ever increasing complexity as the lower lands are entered.

Similar changes in character and increase in numbers and variety of animals take place as the lower altitudes are entered. Here vegetable feeders browse on leaves and juicy shoots by the river side and in the marshes and the woods. Others graze in herds upon the carpet vegetation of the open plains. Some gnaw at hard wood or harder nuts, and scurry for refuge into burrows in the ground, or into holes in the branches of the trees. These animals furnish food for flesh-feeders which pursue them in the open, spring upon them in the woods, steal after them into their burrows or climb to their dwellings in the trees. A few of these animals find a less obvious food supply in such small creatures as insects, worms and snails, which in their turn have derived their nourishment from the plants. Certain animals and plants have, as it were, escaped from the competition on the land and found a place in the rivers and streams. Others again have in the air a vantage from whence they may storm all sources of supply from above ; twigs, fruits, seeds, mice, rats, fish.

Thus every nook and cranny in nature is occupied, and yet very few indeed of these plants and animals leave any permanent record of their existence behind them. A few are buried under wind-blown sand and dust, or perish in bogs and swamps. Others are swept away by rivers and floods, and their remains are buried in alluvium or in deposits on the floor of lakes, estuaries and seas. The vast majority of these land creatures lie where they fall, their flesh is devoured, or is decomposed by minute organisms ; even their bones, left exposed to the air, disintegrate and crumble into dust.

The passage from land into sea is marked by a very sudden change. The character of the vegetation alters completely, trees, flowers, ferns and mosses are replaced by seaweeds and other algæ. These are most varied and abundant where the coast is rocky and stony enough to provide a secure hold ; but where the floor consists of ever-shifting and accumulating mud and sand the larger seaweeds are few, and minute algæ, such as diatoms, are the dominant plants. The waters of the open ocean also teem with freely floating but similarly microscopic algæ.

Though surrounded by water, it is not from sea-water as such that marine plants get their food material ; but from the mineral salts brought down from the land in solution by rivers and streams. The food supply is therefore richest near the shore, and consequently it is here that the vegetation is most abundant.

Light is an equally important factor in determining the distribution of plants, for they depend upon it for their power to use their food materials. Consequently in the sea where the intensity of light diminishes with increasing depth there is a diminution in plant life as deeper water is entered. The depth to which light penetrates depends upon the clearness of the water, being least where the water is turbid and muddy.

In the brightly illuminated regions of the water animal life finds an abundance of food and therefore abounds. The upper part of this region, the beach zone, is subjected twice daily to the tempest of rising and falling tides, and is inhabited by those living things that can endure the constant agitation. From low-tide mark to about 60 feet deep the giant seaweed—Laminaria—luxuriates. Here the water simply sways to and fro with the passing waves, or flows gently along in shore currents and undertow. The " Laminaria Zone " is *par excellence* the abode of life. Here every conceivable variety of bottom exists from bare rock and shingle to mud. Each type of bottom has its own peculiar inhabitants, so that two collections made in spots quite close together may differ considerably. When these animals die, their shells and other hard parts may be buried there and then in sand or mud ; or they may accumulate in some spot where the currents do not admit of the deposition of finer sediments. Sometimes a passing storm sweeps them within reach of the breakers, and then they may be pulverized to sand.

From the margin of the Laminaria zone to a depth of about 400 feet light is dim, and the ordinary seaweeds are gradually replaced by those, called coralline algæ, which encase themselves in a coating of lime. In this coralline zone animal life is still abundant, as is evidenced by the fact that this is the trawling ground for the great fishery industries. So far only those living forms which are attached to or crawl along the floor have been considered. These are called collectively **Benthos,** to distinguish them from those which live in the open water above. Of the latter some are called the **Plankton,** because they merely float or drift about ; others, which swim freely hither and thither, make up the **Nekton.**

The plankton consists of minute animals and plants including embryos and larvæ of benthic types. A few have shells, which unlike those of the benthos are extremely thin and transparent. When these creatures die they sink, and their shells have a share in the formation of the deposits on the floor. If, however, the water be more than 1,000 fathoms deep the shells may dissolve as they sink, and never reach the bottom. Thus though the waters of the open sea teem with plankton, only a mere vestige of its existence is ever likely to be preserved in the rocks.

The nekton includes all the fishes, and even such great creatures as whales, and finds in the plankton its staple food. The skeletons of these, being more massive, are more frequently preserved as the only record of a teeming ocean life.

Below the depth of about 400 feet, where it is probably no lighter than a moonless night, the only plants both on the floor and in the water are minute algæ and bacteria. In the shallower waters even of this dark region animal life abounds, for the food supply is still ample. The muddy floor itself is here a pasturage rich in organic débris, showered from the plankton above, or brought along with the mud by gentle currents. from the more brightly illuminated zones where plants and animals not only live and grow, but also die and disintegrate.

Over these expanses of organic mud, hosts of shell-fish migrate like nomadic flocks and herds. Living or dead these shells provide a foothold for more delicate forms of life such as sea-mosses, which could otherwise find no foothold in such a muddy habitat. These nomadic hosts, and the creatures they carry, are in turn the feeding ground for nektonic animals.

The descent through the lightest regions of the sea is accompanied by a rapid decline in temperature. In the darker depths the decline is very gradual and the temperature is low even in equatorial latitudes. These conditions of darkness, low temperature, and muddy or oozy sea floor, are uniform over the whole of the ocean floor, and consequently the forms of life which are adapted to them have a corresponding uniformity of structure and width of distribution. In the shallow water the benthic fauna is very varied, but the constituents have a more limited geographical range. Plankton and nekton faunas live under moderately uniform conditions, and have a correspondingly extended distribution.

The Forms of Animal Life.—The lowliest forms of animal life are usually so small that they can only just be seen with the naked eye, and for purposes of study they must be examined with the aid of a microscope. The body of each of them is then seen to consist of a blob of colourless and transparent living material (Fig. 2), to which the name **Protoplasm** is given. The major part of the material of this tiny body is of semi-fluid consistency and of granular appearance (*a*), the whole is however usually enveloped in a clearer firmer zone (*b*). There are many other features in the protoplasmic body that are worthy of study, but only the nucleus (*n*) need be mentioned. This is situated in the centre of the animal

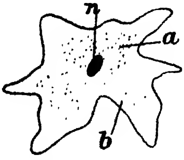


FIG. 2.—An Amœba.
(*a*) Granular, more fluid protoplasm. (*b*) Clear, less fluid protoplasm. (*n*) Nucleus.

and is denser and more finely granular in appearance. The nucleus is of vital importance, for if the body be severed in two, that part which contains the nucleus will live, the other will die. One nucleus with its associated protoplasm is called a **Cell.** All those animals whose bodies consist of only one cell are called Protozoa, as opposed to all other animals whose bodies consist of numerous cells intimately related to one another. These latter are classed together as the Metazoa.

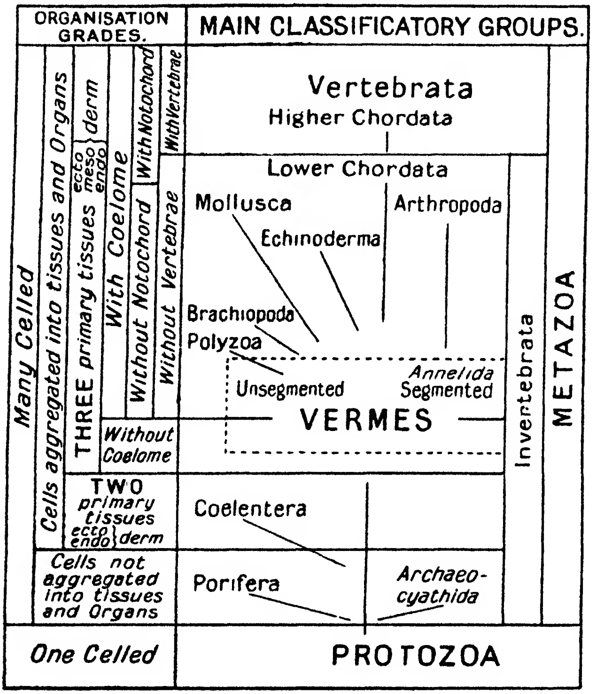
The Protozoa, though usually minute, are exceedingly varied and numerous, and are represented in almost every conceivable habitat, in the sea, in the soil, and even in diseased blood of human beings. A limited number of types form skeletons either by cementing particles of sand together or by secreting horny material, silica, or lime. These alone of all the multitudes of different kinds of protozoa are preserved as fossils. The Metazoa range in size from creatures that are only just visible to the unaided eye to monsters like the elephant and the whale. They are even more varied, if not more numerous than the Protozoa.

Among the Protozoa all the functions of life—breathing, digestion, movement, feeling, reproduction, secretion—are performed by the one cell: but among the Metazoa each of these functions may be delegated, more or less completely, to special cells or groups of cells called organs. This delegation leads to differentiation of bodily structure: thus in man there are lungs for breathing, limbs for walking, eyes for seeing. According as this differentiation is less or more advanced in an animal it is said to be of low or of high organization.

Living animals exhibit many grades of organization, and may be grouped according to the grade into large divisions (Table I), each of which is called a phylum. The phylum is usually divided into smaller and yet smaller sections, viz. Orders, Families, Genera, Species, Varieties and finally individuals. In the lowest phylum of the Metazoa, the Porifera or Sponges, the body has no definite shape due to the existence of definite organs. It consists of innumerable cells mutally dependent upon one another, many of which are still little more than slightly modified Protozoa. Sponges usually produce skeletons of either silica, lime, or a silken material called spongin. These are as little differentiated as the body which made them.

The Phylum Cœlentera is of higher grade. It includes such forms as coral polypes, sea anemones and jelly-fishes. These creatures have a more definite shape partially determined by the existence of well defined organs such as tentacles, mouth, reproductive organs, swimming-bell and the like. They usually exhibit an almost perfect radial symmetry. A thin slice across the body (Fig. 3, *a*), examined under the microscope, shows that it has a central cavity surrounded by a double wall of cells. Those of the outer layer (or ectoderm), serve the functions of sensation and movement; those of the inner layer (or endoderm) are concerned with the processes of digestion. Many Cœlentera produce skeletons which are usually quite external to the body, and which consist of either lime or a horny material.

TABLE I.—Organization and Classification of Animals.



The next higher grade in organization (Fig. 3, *b*), is characterized by the presence of a third layer or mass of cells (the mesoderm), between the other two layers. This is present in all the other types, and may come to exceed the other layers in bulk, for it gives rise to the more massive organs such as bones and muscles.

At the base of this last grade of the animal kingdom is a heterogeneous and very numerous assemblage of soft-bodied bilaterally symmetrical creatures called collectively the worms or Vermes. The biologist divides these among several different phyla of which only one, the Annelida, has left recognizable traces of its existence in the rocks. Whilst in many worms the mesoderm is solid, in the Annelida it is split into inner and outer portions by a cavity (Fig. 3, *c*), the cœlome. This cavity is present in all the higher grades of animals. In them the digestive system, or alimentary canal, hangs suspended in this cavity, and differs from the corresponding structures in the lower grades in having an exit or anus as well as a mouth. As their name implies, the body of the annelids appears to be made up of a number of rings or segments (Fig. 4, *b*), in each of which some of the organs are repeated. Annelids do not produce skeletons, but some have horny jaws. Many make burrows in the sand and mud, which they line with a tube by cementing sand grains together. Some secrete tubes of lime. Such features as these are preservable as fossils.

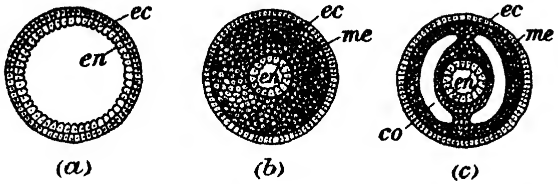


FIG. 3.—The main Grades of Structure of Animals.

(*a*) Two primary tissues. (*b*) Three primary tissues, no cœlome. (*c*) Three primary tissues, cœlome present.

co, cœlome. *ec*, ectoderm. *en*, endoderm. *me*, mesoderm.

In each of the remaining phyla the body attains such an extraordinary complexity of structure in its own peculiar way, that one phylum can hardly be described as more advanced than another.

The Phylum Arthropoda is a very large and varied one, including such familiar creatures as crabs, spiders, and butterflies. Like the annelids these have bilaterally symmetrical, and segmented bodies; but unlike these many of the segments bear pairs of limbs. Each limb has a number of joints, a fact which is reflected in the name Arthropoda. These limbs may be modified to serve other special purposes than walking, such as feeling, grasping, mastication of food. The Arthropoda all produce skeletons, which are secreted entirely by the ectoderm and consist of a horny material called chitin, which may be impregnated with lime. The skeleton encloses the body completely, and because it cannot increase in size

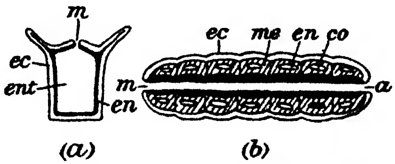


FIG. 4.—Sections of (*a*) Cœlenterate; (*b*) Annelid.

(*a*) anus. (*co*) cœlome. (*ec*) ectoderm. (*en*) endoderm. (*ent*) enteron. (*m*) mouth. (*me*) mesoderm.

after it has set hard it is shed periodically, and a new one formed as the animal grows. It covers every projection, and penetrates every cranny in the surface of the body. Its inner surface provides places for the attachment of every muscle of importance. It therefore reflects to a remarkable degree the detailed organization of the animal, and on that account is of peculiar interest to the student of extinct life.

The two small phyla Polyzoa and Brachiopoda, and the large one, Mollusca, present a marked contrast to the Arthropoda. The body, though bilaterally symmetrical, is not segmented and does not bear limbs. The so-called skeleton or shell has more the nature of a dwelling place, than of a suit of clothes ; and therefore sheds but little light on the organization of the soft parts. Nevertheless the shell itself has many interesting features of its own which, owing to its robust constitution, are frequently preserved intact in fossils, and make it of great value, especially to the stratigraphical geologist. The Polyzoa and Brachiopoda are of simpler organization than the Mollusca. Their nervous, reproductive and blood systems, are quite rudimentary, and they have no head bearing sense organs. They are always passive feeders ; and are provided with an apparatus for directing a stream of water containing food particles, towards the mouth. The Polyzoa are usually colonial animals. Every colony consists of a multitude of individuals of small size, each of which lived in its own horny or calcareous chamber. The Brachiopoda are solitary and of moderate size. An individual is enclosed in a shell consisting of two valves so related to one another that the plane of symmetry of the animal bisects each valve.

The Mollusca rival the Arthropoda in variety and numbers. Many like the cockle and the mussel have a shell consisting of two valves lying one on either side of the plane of symmetry. In others, such as snails and whelks, the shell has only one valve, and this is usually coiled. Others again may have no shell.

In all the above phyla the material for the skeleton has been deposited by the ectoderm. In the Echinoderma and the Chordata the skeleton is largely, if not entirely, of mesodermal origin. The Echinoderma include starfishes and sea urchins ; and in most respects are less highly organized than the Mollusca, and the Arthropoda. Like the Cœlentera they are characterized by a predominantly radial symmetry. The skeleton is, however, complicated, consisting of many parts having an intimate relationship to the soft organs. When preserved in the fossil state it therefore sheds much light upon the original organization of the animal to which it belonged.

The Phylum Chordata includes the most highly organized animals known. In the lowliest chordates the skeleton is merely an elastic rod, the notochord, forming an internal supporting axis for the body. In the higher types this rod is enveloped in a series of gristly or bony bodies called vertebræ, and for this reason the phylum as a whole is often called the Vertebrata. The Vertebrata include such creatures as fishes, frogs, lizards, rabbits. All these are built upon a common plan. They have bilaterally symmetrical bodies consisting essentially of a head, trunk, and two pairs of limbs. The head bears the mouth and the organs of sight, smell and hearing.

The vertebrate skeleton is mainly or entirely internal, and consists of numerous pieces. This is the scaffolding around which the body is built, and in one region or another it often carries the impression of the softer organs. A well-preserved fossil vertebrate skeleton therefore reveals more about its original possessor than does that of any other type of organism.

The Nature of the Palæontological Record.—As compared with the material at the disposal of the student of present-day organisms, that of the palæontologist seems very fragmentary and inadequate. The reasons for this are partly inherent in the constitution of the organisms themselves, partly in the ebb and flow of geological processes. On the whole the body of an animal is compact, and consequently its fossil remains may be as complete as the original skeleton or shell; and one specimen may supply nearly all the information that is ever likely to be available. Inasmuch as the skeleton or shell is only a portion of the body the available information is of necessity always incomplete. Again though the Protozoa, and every phylum of the Metazoa, are represented by fossil remains, large and important sections of them consist of animals which do not possess parts that are likely to be preserved as fossils; and therefore the record for each phylum, like that for each individual, must likewise be incomplete.

Even when the remains of an organism are suitable for preservation in the fossil state it is only by a series of fortunate accidents that a few of them escape destruction, become exposed to view, and are finally collected. First they must be buried under deposits before they are destroyed by the action of air, of waves or of organisms. These deposits must in turn be buried, converted into rock, uplifted to form land, and then undergo denudation until the enclosed remains lie close to the surface. Even then the fossil must lie undiscovered if an excavation does not happen to be made at that particular spot, and an appreciative collector does not happen to turn up there at the right moment.

The consideration of the chances against the preservation, and salving, of a complete record of the past life upon the earth produces a sense of hopelessness in this quest after even a passable knowledge of primeval natural history. Nevertheless there are many compensating factors. For example, the actual quantity of material required for building up such a knowledge is quite small. There may be thousands of tigers in jungles, but at the most a dozen samples suffice to supply the needs of a museum or an average biologist. So likewise if only a few fossils run the gauntlet of geological time successfully, they suffice to tell in broad outlines the story of the multitudes which have perished. Even the most ardent collector usually resists the temptation to carry away all the specimens he sees in one quarry.

Under exceptionally favourable circumstances the soft parts, and bodies of animals without hard parts, may be preserved. Thus the Middle Cambrian shales of Mt. St. Stephen, British Columbia, have yielded exquisitely preserved filmy remains of forms no more substantial than jelly-fishes and worms. These remains exhibit details not only of external but also of the internal anatomy. Exceptional as the circumstances of their preservation may be these few examples suffice to fill up great gaps in our knowledge of Middle Cambrian natural history almost as effectively as would a thousand.

To the student of Biology this fossil record, fragmentary and incomplete as it may appear, furnishes the only source from which he can draw material for solving many of the problems of evolution, or for providing an infallible " control " to put alongside his experiments on living forms. Though there are numerous gaps in the fossil record the knowledge of the missing forms is not necessarily a blank. On the contrary a comparison of similar organisms from before and after such gaps, and a study of the young and the developmental stages of the later organisms, often make it possible to reconstruct that knowledge in its main outlines.

SECTION II

PROTOZOA

Of all the vast multitude of Protozoa known, only a comparative few make shells, and the majority of these belong to two groups or orders, viz. the **Foraminifera** and the **Radiolaria.**

In the latter the shell or skeleton consists wholly of silica. In the former the material used is more varied. It may consist of a horn-like substance called chitin, or of lime (calcium carbonate) secreted by the protoplasm. In either case the skeletal material may be economized by the incorporation of foreign particles, such as sand grains, sponge spicules, and the like.

FORAMINIFERA

The Life-history of Elphidium.—Such a foraminiferan as *Elphidium* starts life (Fig. 5) as a very minute round cell. This is at first naked, but it soon secretes for itself a shell pierced by one main opening, the mouth, and a number of smaller openings, the foramina. Through these the protoplasm extends on to the outer surface of the shell. With the growth of the organism this external protoplasm increases in volume, and secretes for itself a shelly covering attached to the first shell or proloculum. This process is repeated from time to time until a series of chambers has been formed which makes up the full-grown shell (Fig. 6). Each chamber is separated from its fellows by a partition-wall, which is penetrated by one or several openings. Through these, the parts into which the protoplasmic body is divided are connected with one another. In spite of this division of the body it still consists of only one cell, for there is only one nucleus.

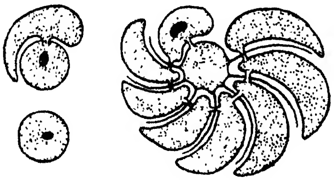


Fig. 5.—Development of *Elphidium*, showing Protoplasm without Shell.

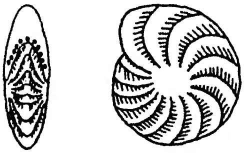


Fig. 6.—Shell of *Elphidium*.

Some time after the organism has attained the fully grown state, it may, in the normal course of events, undergo one of two striking changes. In the one case the whole of the protoplasm is withdrawn from the shell, and is then gradually broken up into a multitude of small spherical pieces like that described at the beginning of this section. In the other case the protoplasm remains within the cell, and the nucleus appears to break up into a multitude of smaller pieces. This process is followed by a corresponding division of the enveloping protoplasm. The minute cells formed in this case, however, are motile, and swim out of the shell. It seems probable that these zoospores, as they are called, unite in pairs; and give rise to rounded cells, each of which likewise forms a shell in the same way as in the previous case.

Between the rounded cells thus formed in two quite different ways, the one by direct division, the other from zoospores, there is a marked difference in size. The former, which is the larger, is called the megalosphere; the latter, the microsphere. Either type may arise from any individual and accordingly there are two types of shell produced by one and the same species. In the one the first-formed chamber or proloculum is large, in the other it is small. A species exhibiting these two forms of proloculum is said to be dimorphic. This phenomenon is described as dimorphism, and is quite common among Foraminifera.

Basal Material and Shell-form.—The most primitive condition among Foraminifera appears to be exemplified by *Allogromia* (Fig. 7). This form is known only from the fresh waters of the present day. Its shell is roughly egg-shaped, and consists of a horny kind of material called *chitin*, which is used also by the lowliest members of other shell-producing organisms. The relatives of this genus differ from it in having a more regularly spherical, ovate or elongate shell with one, two, or several apertures. A few incorporate small particles of sand or minute spicules in the substance of the shell.

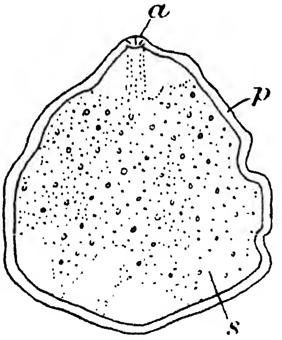


FIG. 7.—*Allogromia* (after Grüber).
a, aperture. *s*, protoplasm. *p*, shell.

The last-mentioned characteristic is carried much further in *Saccamina* (Carb.-Rec.) which occurs in such great numbers, at some horizons in the Carboniferous, as to be a rock builder of some importance. In this the shell is nearly spherical. It is lined with chitin but consists externally of foreign particles closely cemented together (Fig. 8). Its one aperture is placed at the end of a short neck. Closely allied to the primitive Allogromiidæ and to this genus are a number of other types exhibiting a wide range of form. Thus *Astrorhiza* (Jur.-Rec.) has a single chamber with a variable number of tubular extensions each bearing an aperture at the end. In *Hyperammina* (Sil.-Rec.) the initial chamber, or *proloculum*, is oval and extended at one end into a long straight or slightly curved tube. These forms also incorporate foreign particles, including mud, in the shell wall.

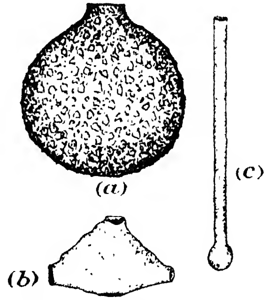


FIG. 8.—Foraminifera with Sandy Shells.

(*a*) *Saccamina.* (*b*) *Astrorhiza.* (*c*) *Hyperammina.*
[Adapted from Cushman.

The variety of shape thus exhibited indicates a high degree of plasticity in organization such as may be expected in a lowly unspecialized section of a large and very numerous group. Little is known of the early history of these primitive representatives of the Foraminifera, but out of this apparently experimental phase in their evolution there emerged a form of shell from which a number of diverging series of modifications arose. This is manifested in three important genera, each of which, however, has its own distinguishing features.

The first is *Spirillina* (Camb.-Rec.) (Fig. 10) in which the shell is devoid of foreign substances and consists wholly of calcareous matter. This is almost glass clear or *hyaline*, and is *perforate*, that is to say pierced, by numerous fine pores. In *Cornuspira* (Carb. ?-Jur.-Rec.), (Fig. 14), on the other hand the purely calcareous shell is white and shiny like porcelain (*porcellanous*) and is not perforate. *Ammodiscus* (Sil.-Rec.) (Fig. 18) has a shell consisting largely of foreign particles and is accordingly described as *arenaceous*.

The coiling potentialities of this long tubular chamber are not, however, limited to the flat or *planospiral*, for in other types allied to *Spirillina*, or *Spirilliniidæ*, various degrees of the " cork-screw " or *helicoid* spiral are seen ranging from a low cone in *Conicospirillina* (Jur.) to a high spire in *Turrispirillina* (Jur.). In others again the coiling may be irregular.

A new feature appears in later developmental stages of some genera in the presence of thin partitions or *septa* which divide the tube and thus give a clue to the origin of the many chambers which make up the shells of most Foraminifera.

Foraminifera with Hyaline Shells.—The genus *Lenticulina* (*Cristellaria.* U. Camb. ?-Tri.-Rec.) is a primitive representative of the *Nodosariidæ* (Fig. 9). Its shell is glassy, perforate and planospiral. The inner coils, however, are almost hidden from view because they are largely enclosed by the margins of the outer whorl or coil which have extended towards the centre. Radially arranged septa divide the shell into chambers of which the last carries a star-shaped opening near the junction of the last septum with the outer rim of the shell. In some species the outer whorl tends to straighten out, a tendency which advances to a marked degree in *Marginulina* (Tri.-Rec.). In this the last few chambers are arranged in a nearly straight line. In *Dentalina* (Jur.-Rec.) this tendency has culminated in a long slender shell which retains traces of the coiled condition only in the obliquely placed septa. The straightening of the shell axis, together with a symmetrical arrangement of the septa and chambers in relation to it, completes the picture for *Nodosaria* (Camb. ?-Tri.-Rec.). This was in turn smitten by a tendency towards a reduction in number of the chambers until finally only one remained, as in *Lagena* (Jur.-Rec.) in which the surface of the shell is often highly ornamented.

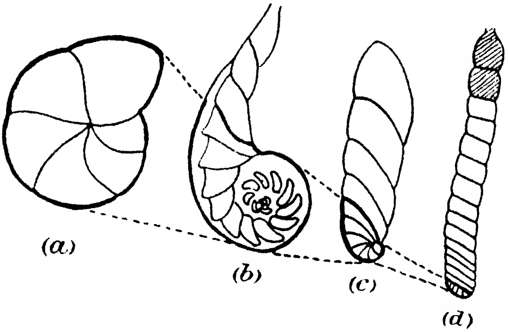


FIG. 9.—Lenticulina and Allied Genera.

(*a*) *Lenticulina articulata* (Reuss). (*b*) *L. siddalliana* (Brady). (*c*) *Marginulina*. (*d*) *Dentalina*. Thickened outline shows coiled or lenticuline stage in development. Thin outline shows uncoiling stage in development. Lined area shows assumption of nodosarian condition with partition wall at right angles to axis of shell.

[Adapted from Cushman. *Amer. Nat.* 1905.

In another series of the same stock the later chambers of the nodosarian shell partially enclosed the earlier, a telescoping process which gave rise to such types as *Glandulina* (Jur.-Rec.) which bears a superficial resemblance to *Lagena* but differs in the presence of several chambers.

Frondicularia (Per.-Rec.) offers an extraordinary but beautiful modification of the nodosarian type. Like that the chambers are arranged in a straight series, but each undergoes marked transverse elongation and is bent in the form of an inverted V (Λ) with the aperture at the apex. In its early development the shell resembles *Lenticulina* and thus provides an illustration of one type of evidence that is used for establishing the affinities of a genus. It also illustrates the principle that during early development an organism may retain some ancestral features.

The genus *Rotalia* (Tri. ?-Cret.-Rec., Fig. 10) is representative of another large and varied family, the *Rotaliidæ*. This probably arose from the Spirilliniidæ through some such form as *Turrispirillina*. Its shell is calcareous, perforate and glassy. It is coiled in a low spire which, viewed from above, sometimes shows at its apex a proloculum followed by a tubular chamber reminiscent of its ancestry. This is followed by a series of slightly inflated chambers. Seen from below the inner edges of the last coil hide the other coils from view and enclose a small space which is called the *umbilicus* which in this genus is filled with extra shelly matter.

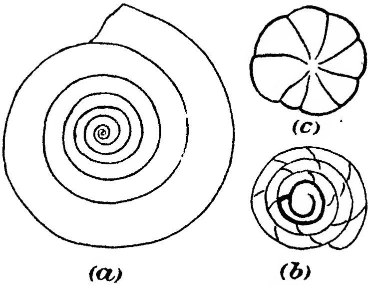


FIG. 10.—Genera of Rotaliidæ (adapted from Cushman).

(*a*) *Spirillina*. (*b*) *Rotalia*—view from above showing spirillina stage by thickened line. (*c*) *Rotalia*, under view showing only the last coil of chambers.

In *Globigerina* (Cret.-Rec.) the young shell resembles *Discorbis* (Jur.-Rec.), a close ally of *Rotalia*, but as development proceeds the chambers become much inflated and globular with thick ornamented walls. At the present day this genus plays an important part in the formation of Globigerina ooze which covers large areas of the ocean floor, amounting in extent to about one-quarter of the surface of the globe. Thus through sheer force of numbers these tiny shells may play a prominent part in the formation of deposits and therefore also of rocks. In *Orbulina* (Tert.-Rec.) the shell is at first like *Globigerina*, but in later life these chambers become completely enclosed in the last one which is highly inflated and spherical. In some cases this enclosure is followed by reabsorption of the early coils.

Nummulites and their Allies.—During late Cretaceous and early Tertiary times Foraminifera of great size came rapidly into being; and formed great masses of rock, especially in the broad seas which joined the area of the present Atlantic to that of the Indian Ocean, and covered South Europe, North Africa and the adjoining parts of Asia. These giant forms belong to one of two main groups viz. the Nummulites group and the Orbitoides group. The former arose from some such structural starting point as that exhibited by *Operculina* (Cret.-Pres.). The origin of the latter is uncertain.

Operculina (Fig. 11) resembles *Elphidium* with which it has some affinity in the bilaterally symmetrical arrangement of its chambers about a median plane, in their simple form and spiral arrangement. It differs in that the septa which separate the chambers are really double; and have, between the two laminæ of which they are constituted, a system of delicate canals lying near the median plane. These are connected externally with a similar system in the substance of a rim of calcareous material around the margin of the shell. Again in the innermost coils of the spiral each chamber is more or less saddle-shaped; and has lateral extensions which overlap the flanks of the inner coils, and hide them from view. The extent of this overlap diminishes as growth proceeds, so that the outer coils are only slightly enclosed by those which follow.

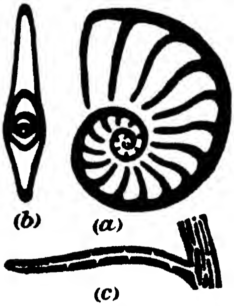


FIG. 11.—Structure of *Operculina*.

(*a*) Median section. (*b*) Transverse section. (*c*) Section of partition wall and periphery showing canal system.

In *Assilina* (Eoc.) this overlap becomes marked in the outer coils also. In *Nummulites* (*Camerina*.-Eoc.-Oligo.) the condition seen in the young *Operculina* is maintained throughout life, so that even in the oldest specimens (Fig. 12*c*) only the outermost coil is visible.

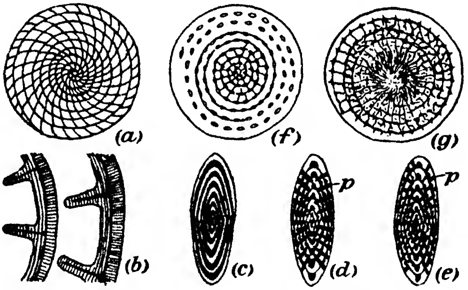


FIG. 12.—Structure of *Nummulites*.

(*a*) Median section. (*b*) Enlarged portion of this section showing primary skeleton and accessory skeleton. (*c*) Diagram of transverse section showing essential relationship of outer to inner chambers. (*d*) Transverse section showing outer pillars continuous with inner. (*e*) Transverse section showing outer pillars not continuous with inner.

(*f* and *g*) Diagrams showing progressive change in ornamentation from periphery to centre. Peripheral ornamentation in (*g*) like central in (*f*).

In the median plane (Fig. 12*a*) the height of the chambers is relatively smaller than in *Operculina*, but the canal system is still maintained. In those portions of the septa which separate the lateral lobes of the chambers from one another there is no canal system, but they are thickened at intervals in the form of stout pillars. In primitive species (Fig. 12*d*) these pillars accord in position with those of the other whorls, so that in a transverse section of the shell they appear as single pillars traversing several layers of chambers. In the more specialized species (Fig. 12*e*) this accordance is lost gradually until no trace of it remains. On the surface of the shell the pillars project slightly in the form of little humps. These humps may be connected with one another by slight ridges which give to the shell a characteristic ornamentation. This latter exhibits a progressive change (Fig. 12*f*, *g*) which renders it valuable for the purposes of identification. Thus in the simplest condition the connecting ridges may lie only in a spiral, then others appear which lie transversely to this spiral and thus produce a rectangular pattern. The transverse ridges next undergo ramification and thus the ornamentation becomes like an irregular network. Thickening now occurs at many points, thus producing a granulation which in the end may completely replace the network. Several steps in this series may be shown by the same shell, the more advanced one being seen near the centre and the less advanced towards the margin.

The genera *Heterostegina* (Eoc.-Rec.) and *Cycloclypeus* (Eoc.-Rec.) belong to another series of forms, also derivable from *Operculina*, which exhibit features of considerable theoretical interest. In the former (Fig. 13) an operculine stage in development is followed by one in which the chambers increase in height and become divided by transverse walls.

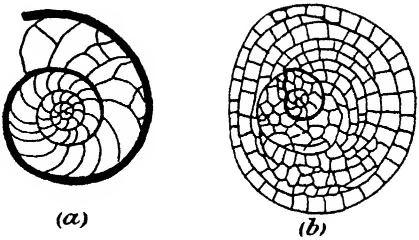


FIG. 13.—Structure of (*a*) *Heterostegina* and (*b*) *Cycloclypeus*.

The thickly-outlined portion of the latter corresponds in degree of structural advance with the whole of the former.

In earlier species of *Cycloclypeus* (Eoc.-Pres.) both operculine and heterostegine stages may be recognized (Fig. 13*b*); but they are quickly replaced by one in which the chambers become more and yet more extended from floor to vault, thus occupying an ever-increasing portion of the periphery of the shell, until at last circular chambers are formed which occupy the whole of the circumference. Meanwhile septa are formed which divide each chamber transversely into numerous chamberlets. These all open by many apertures on the periphery of the shell, through which the protoplasm exuded and formed another circle of chamberlets. This process is repeated and thus the shell grows into a disc-like form, and consists of one layer of chambers with their corresponding chamberlets.

In later species the operculine stage in development disappears and the heterostegine stage undergoes progressive reduction. Meanwhile the characteristic cycloidal chambers, which in early forms appear late in life, shift in subsequent generations back to successively earlier growth stages. This carefully established correlation between the sequence of developmental changes and stratigraphical succession provides a soundly based example of the principle of *Palingenesis* or the recapitulation during individual development of structural conditions exhibited in adult ancestors. The coming on of the cycloidal chambers at successively earlier stages illustrates the principle of *Tachygenesis* or hastening of development. The elimination first of the operculine and ultimately of the heterostegine phases exemplifies the principle of *Lipopalingenesis* or skipping of stages. The recognition of these latter processes which modify the developmental record serves as a warning against a too rigid use of the principle of recapitulation. Nevertheless it is evident that a judicious use of it may serve as a valuable aid to the establishment of relationships between organisms and of the time sequence of the rocks in which their remains are found.

In *Orbitoides* (U. Cret.-Mio.) protoplasm exuded through numerous pores upon the sides as well as upon the margin of the shell and produced layer upon layer of small chamberlets, on either side of a median disc of larger chamberlets. In some Eocene members of the series, *e.g.* *Discocyclina*, these main chamberlets became rectangular in outline when seen in section. In allied genera of the Oligocene and Miocene they became hexagonal or in some cases reverted to a rounded form as in *Orbitoides*.

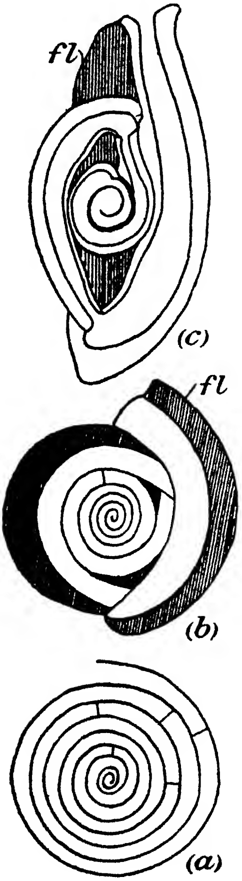


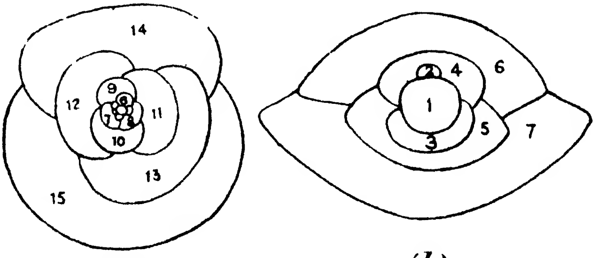
FIG. 14.—Structure of (*a*) *Cornuspira*, (*b*) *Ophthalmidium*, (*c*) *Spirophthalmidium*.

Note the irregular division of *Cornuspira* in the outer coils, the presence of a well-marked Cornuspira stage in the growth of *Ophthalmidium*, the much reduced Cornuspira stage in *Spirophthalmidium*. (*fl*) Flange.
[After Cushman.

Foraminifera with Porcellanous Shells.—The Foraminifera, classed in the order Miliolidea, differ from all others in the shining porcellanous appearance of their shells, and in the absence of those numerous perforations which usually form so prominent a feature in the forms already considered. In the development of several genera, however (*e.g. Peneroplis*), it has been shown that the earliest formed chambers have perforated walls. This fact indicates that the imperforate condition is not, as has been supposed, a primitive character but is secondary. This view receives confirmation from the distribution of the members of this family in time, for whilst perforate forms are known even from Cambrian rocks, none of the imperforata have been found earlier than the Carboniferous.

The simplest genus, *Cornuspira* (Jur.-Cret.), is very similar (Fig. 14*a*) to *Spirillina* a close ally of the Rotaliidæ in that it consists of a single tubular chamber coiled upon itself into a flat spiral. In some species the outermost coils of this spiral are divided by septa at wide and irregular intervals.

In *Ophthalmidium* (Jur.-Rec.) and *Spirophthalmidium* (Jur.-Rec.) the proloculum is followed in development (Fig. 14*b*, *c*) by a short tubular, or *Cornuspira*, stage which passes at once into a chambered stage, but the chambers, unlike those of the other families of foraminifera, frequently retain a tubular character, being elongated parallel to one diameter of the spiral. This feature is seen also in the series *Quinqueloculina* (Carb.-Rec.), *Triloculina* (Tri.-Rec.), *Pyrgo* (Jur.-Rec.) and *Spiroloculina* (Jur.-Rec.) (Fig. 15). In these the first chambers tend to occupy about two-thirds of the circumference of a coil in their length ; but eventually they settle down to one half, and thus the aperture is placed first at one end, and then at the other end of the shell. In the first-named genus the later formed chambers come to lie alongside (Fig. 15), instead of outside of, those already formed, so that the plane of coiling changes with each new chamber. In this series there is a progressive increase in the calibre of the chambers so that the actual number visible from the outside in the full-grown shell steadily diminishes, a fact reflected in the prefixes quinque, tri- and bi-. All these forms



(*a*) (*b*)

FIG. 15.—Diagrammatic Transverse Sections of Pyrgo (*Biloculina*). (*a*) Microspheric, (*b*) Megalospheric.

The former exhibits a fuller developmental record. Up to the formation of chamber 6 it is quinqueloculine in character, during the formation of chambers 9, 10, 11 it is triloculine, subsequently it becomes biloculine. The megalospheric form is biloculine from the outset.

are dimorphic ; and, as in other Foraminifera, it is the microspheric form which exhibits the most complete sequence of stages in development. In the megalospheric forms the earlier stages are omitted.

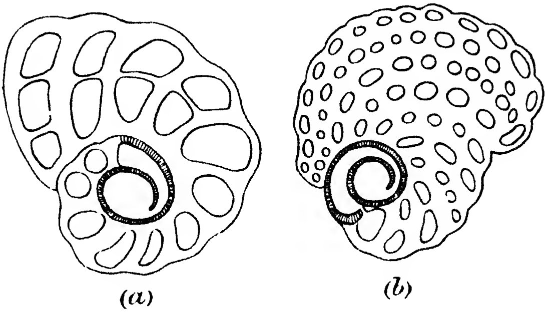


FIG. 16.—Diagrammatic Median Sections of young *Archaias* (*a*) and young *Orbitolites* (*b*).

Early formed portion of the latter is equivalent in structure to the whole of the former. Both are megalospheric.

[Adapted from Cushman.

The genera *Peneroplis* (Eoc.-Rec.), *Archaias* (Mio.-Rec.) and *Orbitolites* (Eoc.) exhibit a structural sequence (Fig. 16*a*, *b*, Fig. 17) parallel to that already seen in the Orbitoides group. In all three genera the proloculum is followed by a brief cornuspira stage in development. In *Peneroplis* a series of globular chambers follows, arranged in a spiral for several complete coils. In *Archaias* the series of globular chambers does not extend even as far as the end of the first coil, since the chambers begin to increase in height just before that. In *Orbitolites* this increase progresses so rapidly from chamber to chamber that, before the fortieth has been formed, each one occupies the whole of the periphery of the shell. From this point onwards the shell is circular. Unlike *Peneroplis* this genus has its chambers divided by septa into chamberlets. In *Archaias* the central portion of the shell is swollen because here the innermost chambers are overlapped by the outer. In *Orbitolites* this swelling is absent, for no such

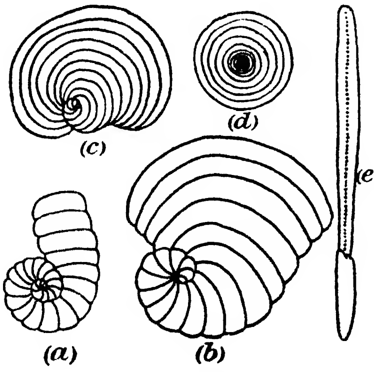


FIG. 17.—Diagrams showing General Plan of Structure of *Monalysidium* (*a*), *Peneroplis* (*b*), *Archaias* (*c*), *Orbitolites* (*d*).

(*e*) Marginal view of *Peneroplis* showing numerous apertural foramina.

overlap occurs. In this genus the spiral series of globular chambers is almost completely cut out of development, for the stage in which the increase in height takes place follows almost immediately upon the *Cornuspira* stage. In *Monalysidium* (Rec. Fig. 17a), as in *Peneroplis* the shell uncoils and straightens out in later growth. In this genus, however, the chambers do not increase in height and thus a nodosarian form is produced.

Thus the two great families, the Nummulitidæ and the Miliolidæ, have parallel series of genera which are strikingly alike in form, even though there is no close relationship between them. The members of one series are therefore said to be isomorphous with those of the other, and the phenomenon is described as Isomorphy. It is quite comparable with the phenomenon of homœomorphy which is so frequently manifested in the higher orders of animals.

Fasciolites and its allies (Cret.-Pres.) are porcellanous isomorphs of *Fusulina* (see below).

Foraminifera with Sandy Shells.—As already seen, the incorporation of sand grains and other foreign particles in the make-up of the shell was a not uncommon feature among the lowliest Foraminifera. This practice is maintained to a greater or lesser degree in those groups which remain for consideration. The basal type for these is *Ammodiscus* (Fig. 18) which has been already described. In *Endothyra* (Carb.-Tri.) the shell is closely coiled and almost planospiral. There are many chambers of which the outer partly or completely enclose the inner. From some such starting condition as this a number of lines of modifications arise and diverge.

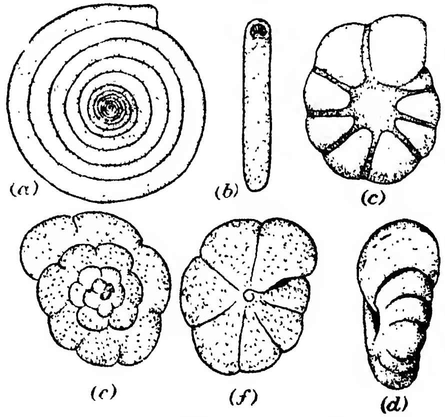


Fig. 18.—Foraminifera with Sandy Shells. (*a*), (*b*) *Ammodiscus*. (*c*), (*d*) *Endothyra*. (*e*), (*f*) *Trochammina*.

One extreme modification is typified by *Fusulina* (Carb.). In this the whorls with their chambers are greatly flattened, widened, and coiled like a ribbon to form a spindle-shaped shell, the outer coils of which completely hide the inner from view.

In *Trochammina* (Carb.-Rec.) modification has not gone far. The shell is coiled in a low spire resembling that of *Rotalia*, but differing from this in the constitution of the shell wall. In the inner whorls the chambers wrap round and embrace the previous ones as in *Endothyra*, but this feature becomes less marked in the outer whorl as though this were beginning to uncoil.

In *Endothyra* the spire is very low and there may be as many as nine chambers in a whorl. In *Trochammina* the spire is slightly higher and there may be only five chambers in a whorl. In *Verneulina* (Jur.-Rec.) (Fig. 19) the spire is very high and the number of chambers has settled down to three for most of the coils thus producing an elongated shell made up of three straight series of chambers lying alongside one another. Such a condition is described as *triserial*. The early stages of growth of *Gaudryina* (Jur.-Rec.) are similarly triserial, but in later life the shell elongates more rapidly and the number of chambers in a coil is reduced to two and thus a biserial condition is established. *Clavulina* (Cret.-Rec.) likewise starts with a triserial arrangement of its chambers. In some species it later exhibits a biserial stage, but in all species coiling eventually ceases entirely and the chambers follow one another in the same straight line. A similar culmination of modification has already been seen in *Nodosaria*.

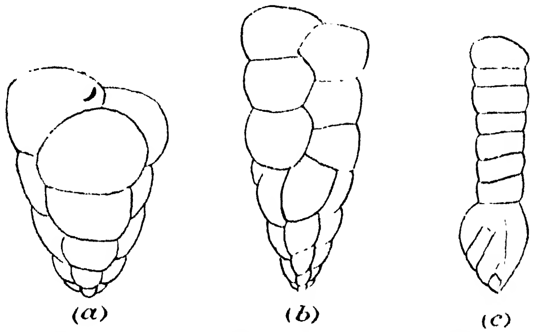


FIG. 19.—Foraminifera with Sandy Shells.
(*a*) *Verneulina.* (*b*) *Gaudryina.* (*c*) *Clavulina.*

In *Spiroplectammina* (U. Carb.-Rec.) (Fig. 20) the youthful shell is coiled in a planospiral. In later life the outer coil breaks away from the inner and continues growth in a straight line which in this case is not also the axis of coiling but is at right angles to this. Nevertheless a biserial arrangement of chambers is produced bearing a close similarity to that already seen in *Gaudryina*. In *Textularia* (Camb.-Rec.) the microspheric individual alone exhibits planospiral coiling in the earliest chambers, otherwise the biserial arrangement supervenes immediately. The chambers become transversely elongated so that the whole shell takes on a triangular outline. In *Bigenerina* (Carb.?-Jur.-Rec.) an early biserial gives place later to a straight uniserial shell. In *Reophax* (Camb.-Rec.) the oval proloculum passes immediately into a uniserial sequence of chambers.

For the purposes of an introductory survey of this amazingly varied and interesting group of lowly organisms the description of representative examples have been arranged as far as possible in progressive series. Care must, however, be taken not to jump to the conclusion that any one sequence constitutes an actual evolutionary series. A primary requisite for the establishment of such a series is that the successive stages shall accord with their order of appearance in time. Thus, for example, while evidence based upon shell form, that is to say morphological evidence, creates a strong presumption that *Textularia* was derived from *Endothyra* through some form like *Spiroplectammina* the stratigraphical evidence places *Textularia* first in order of time. That being so judgement must remain suspended and the series of types must be described as morphological rather than evolutionary.

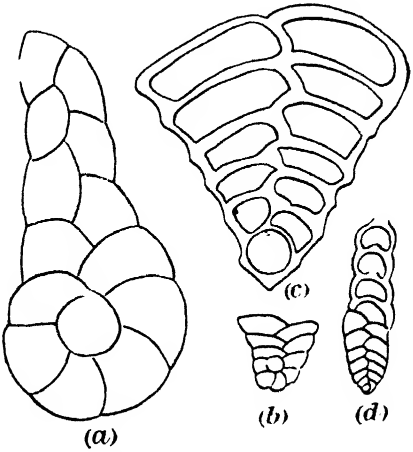


FIG. 20.—Genera of Textulariidæ (adapted from Cushman).
(*a*) *Spiroplectammina*. (*b*, *c*) *Textularia*. (*d*) *Bigenerina*.

RADIOLARIA

The Radiolaria do not play so important a part in the known faunas of the past as do the Foraminifera, nevertheless their shells are found in various horizons from the Precambrian onwards. They have siliceous skeletons which may consist either of loose spicules, or of a rigid but delicate network of great beauty. The form of the latter varies greatly. In the *Spumellaria* it may be spherical or disc-like. In the *Nassellaria* the simpler forms are like a helmet in shape, whilst the more complex ones may have two or several chambers arranged in straight series as in *Nodosaria*.

SECTION III

PORIFERA

The Porifera, or sponges, represent the lowest known grade of multicellular animals. Though they have a body consisting of numerous cells (Fig. 21), those cells are only imperfectly organized into tissues; that is to say into groups of cells which act together for the performance of some definite function. On the other hand the cells themselves retain, to a more marked degree than in the higher metazoa, the characteristics of protozoan cells. This is most strikingly illustrated by the "collar cells" which line many of the cavities in a sponge. The collar cells are oval in shape, and have at one end a delicate goblet-shaped rim. From the centre of this there arises a long vibratile filament of protoplasm, which by its constant movement sets up currents in the water. Between these cells and certain Protozoa there is practically no difference. On the other hand some cells are much modified, thus for example some function only as reproductive cells. Even then, however, they are not grouped together in such a manner as to form a reproductive organ.

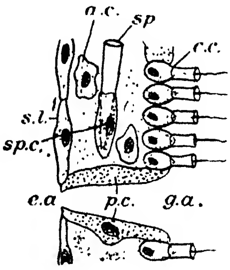


FIG. 21.—Diagrammatic section of Body-wall of Sponge (data for construction from Minchin).

a.c. Wandering amœba-like cell. *c.c* Collar cell. *e.a.* Opening to exterior. *g.a.* Opening to gastral cavity. *s.l.* Layer of cells on external surface. *s.p.* Fragment of spicule. *sp.c.* Cell forming spicule. *p.c.* Cell forming pore.

In its most primitive form the sponge is conceived to have been shaped like a vase (Fig. 22*a*). This was attached by its base, and had its sides perforated by numerous pores, through which water flowed into the large central or gastral cavity, and escaped by the large opening at the top, which is called the osculum. The gastral cavity was lined throughout by a layer consisting of collar cells. Those cells which make up the outside of the cup may be spoken of collectively as the dermal layer. This hypothetical primitive sponge had no skeleton. From it there descended a series of sponges which never acquired the ability to produce a skeleton. Some of these are in existence to-day in a modified form, and are classed as the Myxospongida. Fossil evidence for this theoretic line of descent is, of necessity, not forthcoming.

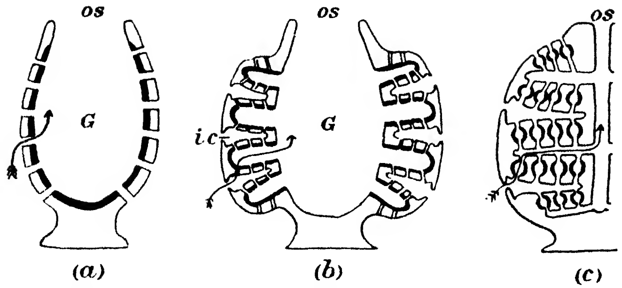


FIG. 22.—Diagrams illustrating three of the main Types of Structure found in the Sponges.

(*a*) Olynthus type. (*b*) Sycon type. (*c*) Leuconoid type. (Adapted after Minchin.) Thick black line shows distribution of Collar Cells. Arrows show direction of flow of water. *G*, gastral cavity. *ic*, incurrent canal. *os*, osculum.

Sponges with Calcareous Skeletons.—Some sponges, whilst still in a state closely similar to that of this hypothetical ancestor, developed the ability to produce a skeleton of calcium carbonate. These sponges are called the Calcarea. Their skeleton consists of small elements called spicules (Fig. 23), each of which is formed by the secretory activity of one cell. The spicules are of three main types. The first, the monaxon, is like a rod with one end pointed and the other differently shaped. The second has three rays lying almost but not quite in one plane. The third is a modification of this formed by the addition of a ray which arises from the junction of the other three. These spicules all lie in the dermal layer, and, inasmuch as they are held together only by the flesh of the sponge they fall apart when this decays. They are therefore of insignificant importance as fossils.

In the more complex calcareous sponges the walls of the gastral cavity become complicated by the outgrowth of a number of hollow outgrowths or diverticula (Fig. 22), the cavities of which are connected with the exterior by numerous pores. The collar cells are now confined to the cavities of these outgrowths, and are absent from the gastral chamber. In this more advanced or "Sycon type" of sponge the skeletal elements, being arranged around the diverticula, have a marked radial arrangement. Fossils exhibiting this arrangement are known from the Carboniferous rocks, and occur at various levels, being most common in the lower Cretaceous, *e.g. Barroisia* (Faringdon, Fig. 24). Sponges of this type still exist.

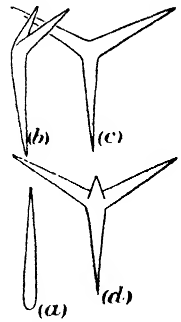


FIG. 23.—Spicules from Calcareous Sponges.

(*a*) One-rayed. (*b*) Three-rayed, side view. (*c*) Three-rayed, full view. (*d*) Four-rayed.

A further complication (Fig. 22*c*) is exhibited by living calcareous sponges. In this, secondary diverticula arise from the cavities of the first, and produce a canal system with small spherical chambers here and there. The collar cells are now confined to these chambers. At the same time the wall surrounding the gastral chamber has by this further development become greatly thickened. This type of structure is described as "Leuconoid," and is reflected in the skeleton, which no longer exhibits that radial plan so conspicuous in the Sycon Type. Such was the condition in an important group of fossil calcareous sponges, viz. Pharetrones. In these the spicules were all bound together in stony strands or fibres which formed an irregular but rigid plexus. They were also characterized by the possession of a special form of spicule which was shaped like a tuning fork. The Pharetrones occur as early as the Devonian, and are represented even in modern seas by a few species. They occur most commonly in the Mesozoic rocks, especially in the calcareous and greensand levels. *Peronidella*, *Rhaphidonema*, *Elasmostoma* are among the more important genera.

FIG. 24.—*Barroisia*. (*a*) External view. (*b*) Longitudinal section.

Sponges with Non-Calcareous Skeletons.—The sponges which produce calcareous skeletons form a very compact group. All other sponges may therefore be referred to collectively as the Non-calcarea. They either possess no skeleton (Myxospongida) or they have one consisting of silica, of spongin, or of both. Spongin is a substance having approximately the same chemical composition as silk. Among the Non-Calcarea no simpler type is known either in the adult condition, or in development, than that described above as the Sycon type. This fact seems to imply that they arose from the main ancestral stock only when this had evolved beyond the stage at which it gave rise to the Calcarea. The Non-Calcarea may be dealt with in two great sections, viz. the Hexactinellida and the Demospongida.

The Hexactinellida are remarkable for the stability of their constitution. Their general plan of structure is constant, and their spicules are formed upon a plan consisting of three axes at right angles to one another. Usually the spicules are six-rayed or hexactinellid. These rays may be modified in form, or even reduced in number; but even in this latter case the traces of the triaxon plan can be still detected in the organic centre of the spicule. Among living Hexactinellids the more primitive have their spicules free from one another. Isolated spicules evidently from similar sponges occur from the Cambrian (*Protospongia*) onwards. In later life the spicules in some genera become united by the deposition of a siliceous cement at the points of contact between them. In other genera this process sets in very early in life, and thus a rigid skeleton capable of being preserved intact is produced. In these cases, owing to the rigidity of the skeleton, growth takes place only around the upper margin where the spicules are still free. Consequently the sponge as a whole becomes cup-shaped (Fig. 25) or cylindrical in form. Such forms are found from the opening of the Mesozoic onwards, but are most abundant in the Cretaceous rocks (*Ventriculites*, *Plocoscyphia*).

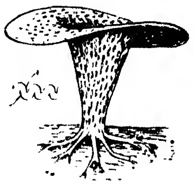


Fig. 25.—Restoration of *Ventriculites* (modified from Minchin). Inset.—Section showing folded structure of wall with incurrent and excurrent canals.

The Demospongida unlike the Hexactinellida exhibit a wide range of spicular form and skeletal substance. Typically the spicule has four axes (tetraxon) with four rays (tetractinellid), which make equal angles with one another. These spicules may be modified, either by the alteration of the angles, or by the reduction of the rays. Thus, for example, the spicule may be reduced to a simple rod having only one axis (monaxon) and one ray (monactinellid). In some this reduction of the siliceous portion of the skeleton is accompanied by the production of spongin fibres binding them together. This tendency reaches its climax in a number of forms in which the skeleton consists wholly of this material. Whilst some fibrous sponges (Pseudoceratosa) must have arisen thus from siliceous sponges, others (Euceratosa) may have arisen directly from the primitive myxospongid stock.

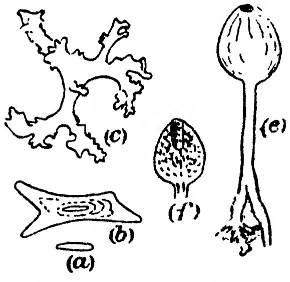


Fig. 26.—Skeletal elements of the *Lithistida*.

(*a*, *b*, *c*) Stages in growth of spicule (after Minchin). (*e*) Siphonia, general view; (*f*) Section of Siphonia (after Zittel).

Among the Demospongida only one order, the Lithistida, attain importance among fossil forms. In these the spicules (Fig. 26) are modified by the secondary addition of silica to their rays, which consequently become covered with tubercles, and branched in an irregular fashion. These spicules become firmly entangled with one another, and because of the complexity of the canal system they support, they produce a massive skeleton. Such sponges occur as early as the Cambrian, and persist until now. Their remains have been found in considerable numbers in the Cretaceous (*Siphonia*).

Pleospongia. **(Archæos).**—The Cambrian rocks of various parts of the world, and especially of South Australia, have yielded remains of a varied series of forms characterized by features indicative of close affinity with the sponges. The simpler members of the series, *e.g. Monocyathus* are single-walled porous tubes comparable with the Olynthus type of sponge (Fig. 22). The more advanced members, such as *Archæocyathus*, exhibit structural elements and a symmetrical arrangement of these indicative of affinity with Cœlentera. The Pleospongia should not be regarded as ancestral to the latter but as sharing along with these and the Porifera the position of lowly Metazoa derived by various routes from the Protozoa.

SECTION IV

CŒLENTERA

HYDROMEDUSÆ

The Structure and Life History of Obelia.—Among multicellular animals the grade of structure next above that exhibited by the Porifera is shown by the Cœlentera. In these the cells of the body are more perfectly co-ordinated in tissues, or groups of cells acting together for the performance of some specific function. These features may be best described by considering the structure and life-history of a typical form such as *Obelia*, one of the so-called Sea-mosses.

Obelia (Fig. 27) starts life as a minute free-swimming larva. This eventually becomes attached by one end to a piece of sea-weed or other similar object, and then secretes for itself a horny or chitinous covering, which is called the perisarc, to distinguish it from the living contents or cœnosarc. The attached end now spreads and forms a base of attachment, whilst the rest elongates, and forms a stalk with a swollen upper portion. Around the latter a ring of tentacles developes, and at its apex a mouth appears. In this way a polype is formed, which on account of its close resemblance to the small freshwater *Hydra* is called the hydroid polype. The stalk is the hydrocaulus ; the base is the hydrorhiza. At this stage the top of the perisarc gives way, thus allowing the polype to protrude and spread its tentacles and catch its food.

The structure of the polype is very simple, consisting as it does of a body-wall enclosing only one cavity which serves all the purposes of a digestive cavity. The body-wall consists of an outer and an inner layer of cells, called respectively the ectoderm and endoderm. Between these is a layer of structureless material, the mesoglœa. This type of bodily structure characterizes all the Cœlentera. At a later stage a bud-like swelling appears on the hydrocaulus, which grows and produces another hydroid individual. This process is repeated until the hydrocaulus attains a considerable height and bears many polypes. Meanwhile the secretion of the perisarc keeps pace with the growth of the colony, and there is formed around each polype a horny cup, the hydrotheca. At the same time the hydrorhiza divides into lobes, which extend over the surface of the seaweed, and send up fresh hydroid bearing branches. Thus the colony spreads and eventually looks like a giant mould.

Sometimes a bud, instead of giving rise to a hydroid, enlarges into an oval body completely enclosed in a capsule of perisarc, the *gonotheca* or *gonangium*. Its fleshy content forms a rod-like *blastostyle* bearing numerous buds, each of which develops into a small jelly-fish or medusa. These break loose from the blastostyle, escape through an opening at the apex of the gonotheca, and swim away. They possess gonads, or organs for producing eggs and sperms which are shed into the water. The eggs are there fertilized by the entry of the sperms into their substance, and then they begin to develop into such free-swimming larvæ as that with which this account started.

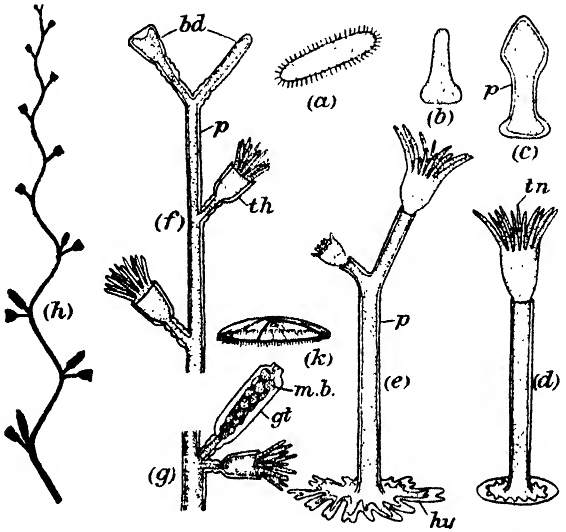


Fig. 27.—Development of a Hydromedusoid (*a–e*) and the structure of Obelia (*f–k*).

(*a*) Larva. (*b*) Larva immediately after fixation. (*c–e*) Development of hydroid. (*f*) Part of an Obelia colony with hydroids. (*g*) The same with gonotheca. (*h*) Diagram of a complete branch of Obelia. (*k*) Medusoid individual.

bd, bud *gt*, gonotheca. *p*, perisarc. *th*, theca. *tn*, tentacles. *hu*, hydrorhiza. *m.b.*, medusa bud.

Thus in the life-history of *Obelia* there is an alternation of a sexual generation, which produces eggs and sperms, with an asexual generation which reproduces by budding. The latter is the *hydroid* generation, the former is the *medusoid* generation. Differences in the relative importance of the part played by either of these generations in the life cycle supply one useful feature in the basis of classification of the Cœlentera. Four main classes are recognized, viz. Hydromedusæ, Anthozoa, Scyphomedusæ, and Ctenophora. The last named includes open water, free swimming, types which have no known representatives in the fossil state. The two first, on the other hand, are of especial interest, for they include numerous fossil forms ; but fossils belonging to the Scyphomedusæ are rare.

The Hydromedusæ include such forms as *Obelia*, which usually possess both hydroid and medusoid individuals in the life cycle. The latter are produced by budding.

The Anthozoa have no medusoid generation. Their polypes are always hydroid, and differ from those of the hydromedusæ in the fact that the internal cavity is partially divided by thin walls, called mesenteries, and is connected with the mouth by a tubular throat or gullet.

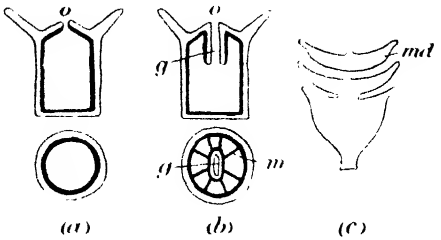


FIG. 28.—Diagrams illustrating some of the differences between three of the classes of Cœlentera.

(*a*) Vertical and transverse sections through one of the *Hydromedusæ*. (*b*) Vertical and transverse sections through one of the *Anthozoa*. (*c*) The formation of Medusoids by transverse fission of hydroid individual in one of the *Scyphomedusæ*.

Thick line, endoderm. *g*, gullet. *m*, mesentery. *md*, medusoid. *o*, mouth.

The Scyphomedusæ have usually only a medusoid generation in the life cycle. In the few cases where hydroid individuals are known they give rise to medusæ, not by budding, but by dividing transversely (Fig. 28) into a number of sections. Each of these, as it breaks loose, becomes a medusa.

The Classification of the Hydromedusæ.—The Hydromedusæ include a wide and varied series of forms. In some the hydroid generation is unknown, but they are classified here because their characters are more in accord with the medusoid individuals of this than of any other class. The remaining Hydromedusæ fall into three living and two extinct orders. All these, like *Obelia*, are colonial forms ; that is to say, they consist of many individuals organically united with one another. The living forms are usually benthic in habit, and grow like moss upon shells, or other large objects, in either shallow or deep water.

The members of the order Siphonophora are exceptional in that they are not benthic in habit. They include such creatures as the Portuguese Man of War, in which the colony as a whole is provided with a float, and leads an open water life drifting about at the surface of the sea. Except for a few specimens, which are interpreted as floats, this order is unknown in the fossil state.

The three other orders, Calyptoblastea, Gymnoblastea, and Hydrocorallinæ, do not seem to have played an important part in the faunas of past times, and are of interest to the palæontologist chiefly because of the light they throw upon the important Palæozoic orders, the Graptolithina and Stromatoporoidea. The Calyptoblastea include those hydromedusæ, such as *Obelia*, which have the hydroid polypes enclosed in hydrothecæ, and the medusoid buds developed inside a gonotheca. No undoubted members of this order have been found in rocks older than the Pleistocene; but, as will be seen later, a very important group of Protozoic fossils, the Graptolithina, bear a closer resemblance to them than to any other group in the animal kingdom.

The Gymnoblastea are those Hydromedusæ in which the perisarc is absent or, if present, does not form a hydrotheca around the hydroid polypes, nor a gonotheca around the medusoid bearing branches. The Gymnoblastea are numerous and varied to-day, but only a few fossil forms are known. Among these *Hydractinia* is of interest. Its hydroid polypes are modified to perform various functions; some for catching food, others for swallowing and digesting it, others again for producing medusæ. They have no hydrocaulus, and consequently each polype rests directly upon the hydrorhiza. This latter by repeated branching forms a close feltwork of cœnosarc threads covering the stone upon which the colony lives like a thin crust. The threads are enclosed in perisarc, which fills up the interspaces between them. When the cœnosarc dies and perishes, the thin feltwork of perisarc tubes remains, but shows no traces of the former presence of hydroid polypes. In section this mass of hydrorhizal tubules appears to be made up of horizontal laminæ with interlaminar spaces, and united by vertical pillars. In a few cases the skeleton is calcareous. Fossils allied to *Hydractinia* occur at various horizons from the Trias onwards.

The Hydrocorallinæ include the genera *Millepora* and *Stylaster*, which are still in existence, and are found in the fossil state in Tertiary rocks. Though the skeleton is wholly calcareous its relationships to the cœnosarc are the same as in *Hydractinia.* Here, however, the polypes can be withdrawn into special cavities, which may be either sunk below the general surface, or project in the form of a cup. *Stromatopora* was a rock-building form which abounded during the Devonian times. Structurally it resembles *Hydractinia*, but like the Hydrocorallinæ it had a calcareous skeleton.

Dendroid Graptolites.—*Dictyonema* (Fig. 29) occurs for the first time in the uppermost beds of the Cambrian, and ranges upwards into the Devonian. It is found in Western Europe and in North America. It includes forms characterized by a multitude of branches arranged conically and united at the apex either to a base of attachment or to a long stalk. Cross connections between the branches produce the appearance of a network.

D. flabelliforme is one of the earliest members of the genus and probably lies close to the ancestral stock of the Graptolithina. Each branch bears hydrothecæ on its inner face, and its structure shows that each hydroid polype produced two buds. One arose from the middle of its long outer surface and, becoming the next polype, formed the next hydrotheca (Fig. 30). The branch as a whole was therefore produced by a succession of buds which, together with the proximal half of each polype formed a growing axis. The other bud was smaller and arose from a point higher up on the side of the polype. The perisarc which enclosed this is called a ***bitheca*** (? gonotheca).

FIG. 29.—*Dictyonema* (diagrammatic).

The Silurian species *D. rarum* (Fig. 30) illustrates the tendency of later forms to develop a more complicated structure. In this the growing axis was more clearly differentiated so that the cavity it occupied within the perisarc may be called the *common canal.* At intervals the axis produced pairs of buds on alternate sides. The inner ones formed the hydrothecæ; the outer the bithecæ, which in this case passed behind the adjoining hydrotheca and opened upon the opposite side. This growing axis bearing successive hydrothecal and bithecal individuals has a resemblance to Obelia (Fig. 27*f*–*h*) sufficiently close to suggest affinity with the Calyptoblastea.

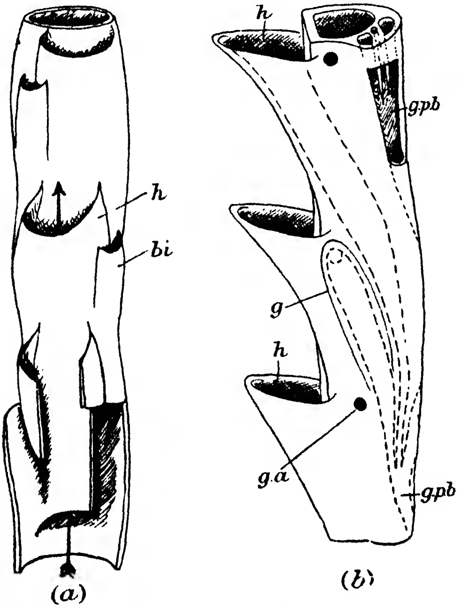


FIG. 30.—Reconstruction of Portion of a Branch of (*a*) *Dictyonema flabelliforme* (based on Bulman). (*b*) *D. rarum* (based on Wiman).

bi, g, Bitheca. *g.a*, Bithecal aperture. *g.p.b*, Point at which growing axis produced buds from which grew hydrotheca and bitheca. *h*, Hydrotheca.

Nevertheless the vast gap of time which intervenes between the extinction of *Dictyonema* and of the multitudes of its Protozoic allies, and the appearance of the first undoubted Calyptoblastea in post-Pliocene times renders it advisable to refer them to a separate order, the Graptolithina. (See Bulman, 1942.)

From an early Dictyonemoid stock there seems to have arisen two quite different series of forms. The one, called the Dendroid graptolites (Dendroidea), included a number of genera and species possessed, like *Dictyonema* itself, of a relatively stable organization; for they also persisted from Tremadocian to Devonian times with comparatively little change. This fact renders them unsuitable for use in correlating the smaller rock divisions of one district with those of another.

The second series of forms, the Graptolites proper (Graptolitoidea), were more unstable in their organization than the Dendroid graptolites. From the Tremadocian period onwards they passed through a series of rapid changes, and became extinct before the close of the Silurian period. A clear conception of these changes furnishes an excellent basis for constructing a time scale wherewith to fix with some degree of accuracy the dates of the deposition of rock layers and the age of volcanic and other phenomena.

Didymograptus and its Allies.—In common with all other true graptolites the first polype of *Didymograptus* was enclosed in a simple conical theca called the sicula. The apex of this is sometimes in the fossil, probably always in the original, drawn out into a long delicate tube, the nema. The apical portion of the sicula (Fig. 32 A) differs from the remainder in being more delicate, and marked with longitudinal striæ. This portion probably contained the embryonic polype. As the latter grew it built up a stronger apertural portion which is marked with transverse lines of growth. Whilst this was going on the polype produced a bud on what may be called the left side. This became the first hydrotheca on the same side. It grew parallel to the sicula, with its aperture facing in the same direction as that of the sicula. There then grew out from this first formed theca two others. One of these passed behind the sicula, and became the first theca on the right side. The other became the second theca on the left. The apertures of these also opened in the same direction as that of the sicula, and from the base of each another theca grew. This process was repeated until two stipes or long series of hydrothecæ, connected by a common canal, were produced. The whole is called a polypary or rhabdosome.

The genus *Didymograptus* (Fig. 31) includes a great number of species, most, if not all, of which may be grouped around six types characterized by the general shape of the polypary. Of these only two need be considered in detail. In both of them the stipes are straight; but in one they are dependent, that is to say that they hang down from the sicula practically parallel to one another like the prongs of a tuning fork ("tuning fork graptolites," *e.g. D.*

murchisoni and *D. bifidus*). In the other type the stipes extend horizontally, thus making an angle of 180° with one another (" extensiform graptolites," *e.g. D. extensus*, *D. hirundo*).

Tetragraptus, as its name implies, differs from *Didymograptus* in having four stipes. Its early stages of development are identical with those of that genus ; but after the first few thecæ have been formed the common canal of each of the two first formed stipes divides. Branching therefore takes place twice, and the polypary has in consequence four stipes. Here again the stipes in some species, *e.g. T. fructicosus*, are " dependent " ; in others, *e.g. T. quadribrachiatus*, they are horizontal.

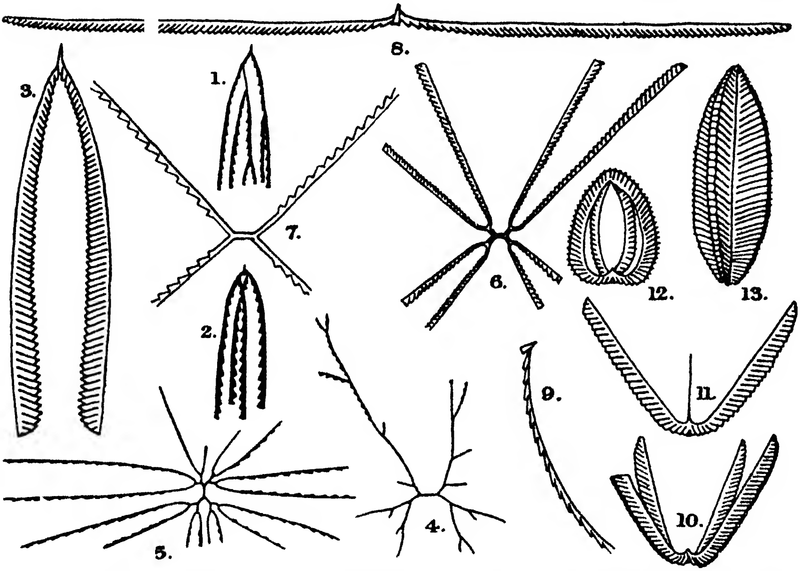


FIG. 31.—Diagrams of various Dichograptidæ. (Based on Figures by Elles, Wood, Lapworth, Marr.)

(1) *Bryograptus*. (2) *Tetragraptus* (dependent type). (3) *Didymograptus* (" Tuning Fork type "). (4) *Clonograptus*. (5) *Loganograptus*. (6) *Dichograptus*. (7) *Tetragraptus quadribrachiatus* (extensiform type). (8) *Didymograptus extensus* (extensiform). (9) *Azygograptus*. (10) *Tetragraptus* (ascending type). (11) *Didymograptus gibberulus*. (12) *Tetragraptus phyllograptoides*. (13) *Phyllograptus*.

In the lowest levels of the Arenig, and even in the Tremadoc beds below, graptolites occur which in development and in the simple sicula-like character of the thecæ resemble the two genera described above ; but they differ in that they exhibit an even yet greater branching capacity. In one of these, *Bryograptus*, the stipes are dependent, that is to say it is like the " tuning fork," Didymograpti and Tetragrapti. The others in addition to being " extensiform " exhibit regular differences in branching capacity ; thus *Dicho-*

graptus branches three times and has eight stipes, *Loganograptus* and *Clonograptus* branch four or five times, and may have from nine to sixteen stipes or seventeen to thirty-two stipes respectively. Of all these genera *Clonograptus* is the earliest and occurs in the Tremadoc beds.

The existence of two such series suggests strongly that dependent Didymograpti have descended from dependent Tetragrapti, and these in turn from *Bryograptus*; and therefore that these three belong to one genetically related series. On the other hand the extensiform Didymograpti have descended from extensiform Tetragrapti, and these in turn have arisen from *Dichograptus*, and through it from *Loganograptus*, and ultimately from *Clonograptus*. This suggestion, based upon the order of appearance in time and upon the consideration of the shape of the stipes, receives substantiation from the study of other structural details such as the shape of the thecæ, and the angle of inclination of these to the long axis of the stipe.

Evidently an " extensiform " *Didymograptus* is much more closely related to *Clonograptus* than it is to a " tuning fork " *Didymograptus*, and the generic name *Didymograptus* covers species which have descended from quite different ancestral stocks. The same is true also for *Tetragraptus*. These genera, therefore, have descended from two stocks (diphyletic), and, if all species be taken into account, they may even be shown to be derived from several different stocks (polyphyletic). These two genera are therefore not sound, for a genus should be monophyletic, including only those species which are derived from one common ancestral stock. Superficially these two series have undergone similar changes along parallel lines, viz. in the direction of gradual loss of branching capacity. Such parallel modification is a frequent occurrence, and has been responsible for the establishment of many polyphyletic groups in the classification of organisms before the significance of the phenomenon was fully realized.

When once the existence of such a genetic series has been definitely established, by the study of fossils in districts where the succession of rocks is known, it becomes a very reliable time scale by means of which the rocks of other localities may be correlated with those of the type locality. Only once in the evolution of the world has that series been produced. If therefore it be found in the rocks of any other region those rocks must have been laid down whilst that series was being produced.

All the graptolites in the several series described and mentioned above are classed together as the Dichograptidæ. They are all characterized by the same type of earlv development, in which the first formed thecæ make an angle with one another of less than 180°. All the thecæ are simple and sicula-like or tubular, the polyparies as a whole are bilaterally symmetrical, and the branching is of a forking or dichotomous type. The Dichograptidæ include several other genera not mentioned above to which reference should now be made. *Azygograptus* is of interest because it has attained the climax in the loss of branching capacity, for the bud which grows out from the first theca does not divide, and consequently only one stipe is produced. *Phyllograptus* is interesting because it anticipates a feature which becomes the predominant characteristic in many later graptolites. It seems to have descended from a type of *Tetragraptus* in which the stipes curved upwards from the theca, and came ultimately to stand as it were back to back, and with the hydrothecæ facing outwards.

The earliest and most complexly branched Dichograptidæ, *Clonograptus* and *Bryograptus*, spent the term of their existence in Tremadocian waters. They were succeeded immediately in the earliest Arenigian times by descendants, exhibiting every degree of branching capacity described above. These became extinct in the order of decreasing branching capacity, so that at the close of the Arenig *Didymograptus* and *Azygograptus* alone remained. These genera, and with them the family, passed out of existence during Llanvirnian or early Llandeillian times.

The Development and Life History of Graptolites.—The general course of evolution pursued by the dominant graptolites during Arenigian times was along the line of decreasing branching capacity. The disposition of the stipes was also variable, but the characters of the hydrothecæ were always very simple. In later graptolites on the other hand the branching capacity underwent but little change and the number of stipes was usually two or, in the latest, only one. The tendency towards a scandent mode of growth, that is to say towards the upturning of the stipes, was manifested very early in the Arenig, but it later became dominant, and had such a strong hold upon the organism that it affected the attitude even of the first formed theca. As this attitude exhibits a progressive change in the different types, the early development (Fig. 32) may be used as the starting point for the study of those types.

As in *Didymograptus* the first hydrotheca appears as a bud upon the sicula. In this genus it grew parallel to the sicula with its aperture facing in the same direction as that of the sicula. In *Leptograptus* it grew downwards alongside the sicula for a time, and then turned outwards almost at right angles to this. In *Diplograptus* the development was similar, but the theca turned slightly upwards as well as outwards. In *Monograptus* it grew upwards and only slightly outwards from the first.

In *Didymograptus* the first formed theca produced two others. This was the commencement of branching. In the later types the time at which this branching took place underwent progressive delay. Thus in *Leptograptus* it did not occur until after the formation of the second theca ; and in *Diplograptus*, after the third. In *Dimorphograptus* branching took place much later, and in *Monograptus* was cut out entirely.

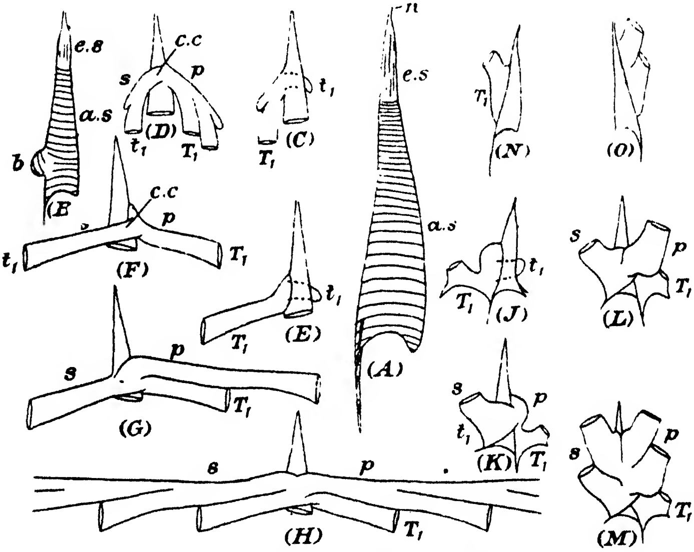


FIG. 32.—Early stages in the development of the main Graptolite Types.

(*A*) Sicula. (*B*) Sicula producing bud. (*C*) *Didymograptus*. (*D*) A later stage for *Didymograptus* seen from the opposite side. (*E–H*) *Leptograptus*. (*J–M*) *Diplograptus*. (*N, O*) *Monograptus*. *a.s*, Apertural portion of sicula. *b*, Bud. *c.c.*, Crossing canal. *e.s*, Embryonic portion of sicula. *n*, Nema tube. *p*, Primary stipe. *s*, Secondary stipe. T_1, First formed theca of primary stipe. t_1, Ditto of secondary stipe.

In *Leptograptus* and *Diplograptus* the second theca crosses behind the sicula and forms the first one of the secondary stipe. In the former each new theca continues the outward direction of growth of the first two, in the latter they follow the lead of the first theca of the secondary stipe and turn upwards. In *Diplograptus* the dorsal margins of the stipes are in contact with one another, and have a delicate canal-like space between in which a stiff rod, the virgula, lies. Such a polypary as this is described as being biserial or diprionidian. Those in which the stipes are separate are uniserial or monoprionidian. In *Monograptus* the new thecæ all remain on the primary side, and consequently the polypary is monoprionidian.

The life history of a graptolite has been most fully worked out for the species, *Diplograptus pristis* (Fig. 33). Probably the general features were the same for many other species and genera. Before the sicula produces a polypary in the way described above for *Diplograptus* it is attached at its apex to a little body—the node—in the centre of a square plate. Whilst the first few thecæ are growing this plate, which consists of two laminæ, increases in size and swells out to form a large horny vessel, the basal cyst. The node evidently contained the living base of attachment of the polype which was in the sicula. As the hydrothecæ grew upwards along the sicula, the latter was carried further and further from the node by the growth of a delicate stalk corresponding to the hydrocaulus of *Obelia*. This seems to have been strengthened by the secretion within its substance of a stiff rod, the virgula, and protected by a thin covering of perisarc, the nema. This vitally important structure was further protected in scandent types by partial or complete enclosure between the ascending stipes.

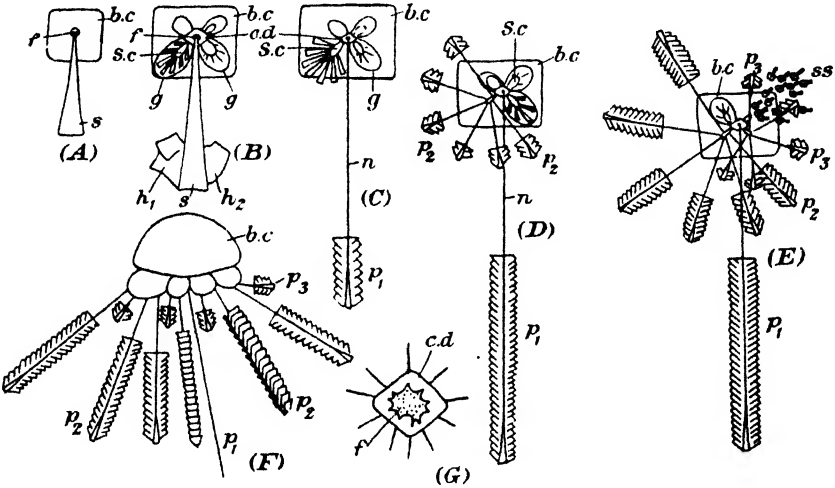


FIG. 33.—Stages in the life history of *Diplograptus pristis*. (Data for diagrams from Ruedemann.)

(*A–F*) Order of stages from freely floating sicula to full-grown colony. (*G*) Enlarged figure of the node.
b.c, Basal cyst. *c.d*, Perisarc around the node. *f*, Node. *g*, Gonotheca. *s*, Sicula. *ss*, Free-floating siculæ. *S.c*, Blastostyle bearing siculæ. *n*, Nema tube. p_1, Polyparies produced by the original sicula. p_2, p_3, Polyparies produced from siculæ in successive gonothecæ.

From the node there grew out oval swellings enclosed in perisarc. Each of these is comparable with a blastostyle, and its corresponding gonotheca. Within them there developed, not medusæ, but polypes enclosed in siculæ. These remained attached to the blastostyle, and grew and formed a cluster of polyparies around the primary polypary. Thus cluster after cluster was formed until a populous colony consisting of polyparies in various stages of growth was formed. These all appear to have hung downwards from the basal cyst, which probably acted as a float. Occasionally the siculæ, attached to one style instead of growing into polyparies *in situ*, developed little square plates at their points of attachment. They then broke loose from the parent colony and each floated away to give rise to new colonies thus serving a similar function to that of the medusoid generation among the Hydromedusæ.

When such a colony ultimately died it would naturally sink, as soon as its float became waterlogged, with the float downwards and the polyparies trailing behind like the feathers of a shuttlecock. Thus the basal cyst would come to rest upon the sea-floor and be buried first. The fact that colonies are preserved in this attitude has given rise to the suggestion that the cyst was not a float, but an anchor.

Post-Arenigian Graptolites.—During late Arenigian times, and when the Dichograptidæ were waning, a number of other graptolite types came into existence, and rapidly attained predominance. Though the relationships of these later types to the earlier are not fully known, there are indications that they arose from them along several lines of descent. Thus some of the Diplograptidæ appear to have arisen, by the suppression of two stipes, from that section of the Dichograptidæ, represented by *Phyllograptus*, which had already reached the scandent stage. On the other hand some of the Leptograptidæ arose from non-scandent Didymograpti in which the thecæ exhibited a tendency to assume a sigmoidal form. In this case the scandent condition was assumed more slowly. Though the Diplograptidæ appeared earlier than the Leptograptidæ the latter may be taken first.

The Leptograptid type of development (Fig. 32 E–H), in which the two first thecæ make an angle of 180° with one another, is characteristic of all members of the family Leptograptidæ. In them the thecæ have also departed from the simple straight-sided conical tube seen in the Dichograptidæ, and have become slightly curved in a sigmoid manner. Moreover the mouth of the theca is no longer at right angles to the axis of the theca, but is tilted towards the dorsal margin of the stipe. *Leptograptus* is the type genus for this family, and exhibits all the features just enumerated. *Pleurograptus* differs from *Leptograptus* in that its two main stipes give off many simple or compound secondary branches at irregular intervals. In *Nemagraptus* (*Cœnograptus*) the two main stipes together make an S-shaped figure, from the convex margin of which the branches arise with beautiful regularity.

The Dicranograptidæ include the two genera *Dicranograptus* and *Dicellograptus*: In them the early development is like that of *Diplograptus* (Fig. 32, J–M.) in that the two first thecæ make an angle with one another much greater than 180°. The thecæ are shorter and broader and exhibit a more marked sigmoid curvature than in the previous family. The apertural end is usually free and bent inwards towards the common canal, *i.e.* introverted. In *Dicellograptus* (Fig. 34) the stipes are free from the outset, as in *Leptograptus*. The apertural portion, however, shows various degrees of introversion leading up to an acme in which it is spirally twisted (introtorted) upon itself; the aperture is thus turned so that it is seen in full view on one side of the polypary, but not on the other. In *Dicranograptus* the first formed portions of the stipes, as in *Diplograptus*, are scandent, but the thecæ exhibit the same series of modifications as in *Dicellograptus*. On this account the species showing the various grades of apertural development may be regarded as having been derived from the corresponding species of *Dicellograptus*.

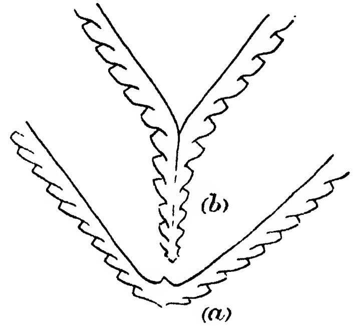


FIG. 34.—Diagram of (*a*) *Dicellograptus*, (*b*) *Dicranograptus*.

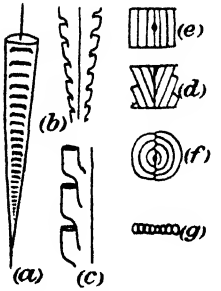


FIG. 35.—Diagrams illustrating Structure of Diplograptidæ.

(*a*) *Climacograptus* " Scalariform " view showing apertures of hydrothecæ. (*b*) Side view. (*c*) Side view enlarged to show characters of hydrothecæ. (*d*) *Orthograptus*, side view. (*e*) Section. (*f*) *Glyptograptus*, section. (*g*) *Petalograptus* section.

In the Diplograptidæ (Fig. 35) the form of the polypary remains practically constant. The differences between species are almost entirely in the thecæ. In the families hitherto considered these are little more than cylindrical tubes slightly flattened where they are in contact with one another. In this family, however, they are broader than deep, and vary greatly in cross-section. In *Diplograptus* this variation in shape of the theca leads to a variation in the shape of the transverse section of the polypary. This may be square (*sub-genus Orthograptus*), circular (*s.g. Glyptograptus*), concavoconvex (*s.g. Mesograptus*). The latest forms exhibit a return to the primitive cylindrical theca (*e.g. Petalograptus*) and consequently the polypary is flat in section.

In *Climacograptus* the axis of each theca is vertical, and the upper part of the outer or ventral wall is straight, and parallel to the axis of the polypary. The lower part has a strong sigmoid curvature. The profile of the polypary consequently shows a straight margin with regularly spaced notches in which the thecal apertures are situated. The condition of the theca in some species resembles that of the more elaborate species of *Dicranograptus* sufficiently closely to suggest descent from the latter.

The Glossograptidæ differ from the Diplograptidæ in the presence of strongly developed spines and filaments, and in the thickening of the perisarc in some places and its attenuation in others. In *Glossograptus* this thickening takes place around the apertural margin, and along the ventral edges of the theca. In *Retiograptus* it extends to the line of contact between the successive thecæ and between the common canals. This process attains its maximum development in the family Retiolitidæ of which *Retiolites* is the most important genus. Here the perisarc is represented almost entirely by a delicate network made up of similar thickenings.

As already seen a number of the so-called genera of graptolites are polyphyletic. This is true to a still more marked degree for *Monograptus*, which appears to have arisen mainly from forms having the diplograptid type of polypary. The transitional changes from that type are well illustrated by *Dimorphograptus*. In this genus the first few thecæ develop as in *Monograptus*. Eventually a stage is entered at which the bud, which grows out from the base of the last formed theca, divides and gives rise to two. From this point onwards the polypary is diplograptid in type. This genus illustrates clearly the principle of *proterogenesis* which is often exemplified among the Monograptidæ, namely that the next stage in evolution may be anticipated during the early life of the polypary. This is true not only for progressive but also for retrogressive series in which there may be a return to more primitive conditions.

The evolution of the monograptid species is expressed mainly by changes in the theca. One complete series of progressive and retrogressive forms has been traced. This commences (*e.g. M. cyphus*) with straight overlapping thecæ having their apertures at right angles to their axes. Starting with a curling over of the mouth margin, the apertural end gradually became free and turned over in the form of a hook (*e.g. M. priodon*). This progressive series of changes, which took place during the Valentian, was followed by a retrogressive series in which the hook was gradually lost and the thecæ reverted to a straight overlapping condition once more (*e.g. M. intumescens*). In a second series of Valentian monograptids the hooked condition of the apertural end of the theca was attained very rapidly, and passed on to a more specialized stage in which this portion of the theca became coiled (*e.g. M. lobiferus*), and gave to the margin of the polypary a lobate appearance. Yet another line of serial modifications was manifested during the Valentian. In this the thecæ first became entirely free from one another down to their bases and assumed a triangular form. This triangle became extended apically and narrowed basally, and thus the thecæ remained connected with one another only by the common canal. This change, which had already taken place in the first 16 thecæ of *M. triangulatus*, extended to the whole polypary in *Rastrites* (Fig. 36*g*). Contemporaneously with these various branches of Monograptidæ, which were evolving at different rates, there was one (including *M. gregarius*, Val., and *M. dubius*, Salopian) which remained comparatively stationary, and retained a straight overlapping type of theca of primitive character throughout Valentian and Salopian times. One other series of species appears to have originated in a Dicellograptid stock. The last member of this series, *M. leintwardinensis*, was also the last representative of the graptolites.

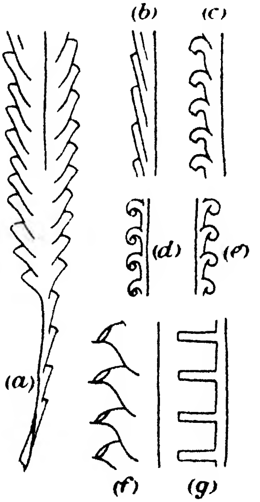


FIG. 36.—Diagrams showing Dimorphograptus and types of Theca among Monograptidæ.

(*a*) *Dimorphograptus* (after Nicholson. (*b*) Cyphus type. (*c*) Priodon type. (*d*) Lobiferus type—obverse view of polypary. (*e*) Ditto, reverse view. (*f*) Triangulatus type. (*g*) Rastrites type.
(*b*–*g* based on Elles.)

In occasional individuals of *Monograptus becki* the sicula, whilst producing a bud to form the first theca of the stipe, acts as though it were itself the first theca of another stipe which grew out in the opposite direction. This condition, which is the exception in *Monograptus*, is the rule in *Cyrtograptus*.

Glancing at the Graptolites as a whole the series of structural modifications to which they were subject are seen to be comparatively few in number. Along any given line of descent the whole series of modifications for every structural element was not necessarily passed through. On the contrary modification might stop short of the acme in one, some, or even all the elements.

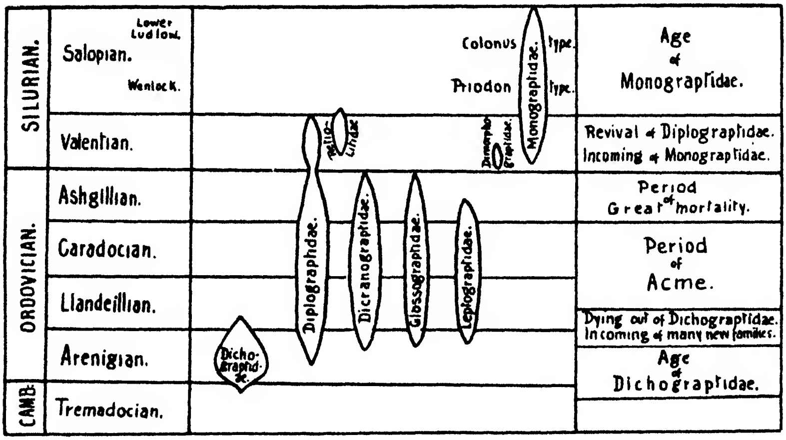
The chief series of modifications are as follows:

(1) A change in the attitude of the stipes, from one in which they

hung downwards from the end of the nema, through one in which they extended horizontally, to one in which they were scandent, that is to say they lay along the nema, and formed an enclosing protection for it. The early stages were dominant during the Arenigian and Llanvirnian. The scandent appeared in a few graptolites during the same period, but became characteristic of later times.

(2) A reduction in the number of stipes from many to one. This took place rapidly during the Tremadocian and the beginning of the Arenigian, so that in late Arenigian times, and indeed until the close of the Ordovician, the dominant number was two. During the Valentian, forms having only one stipe appeared in force, and became the almost exclusive constituent of the graptolitic fauna during the Salopian.

TABLE II.—Summary of the History of British Graptolites.



NOTE.—The adjoining portions of the Arenigian and Llandeillian which contain "tuning fork" graptolites are now usually included in the Llanvirnian.

(3) When the above changes had become far advanced in the majority of graptolites, the evolutionary energy became concentrated upon the modification of the theca. The more important changes which took place in this were:

(*a*) The theca passed from a conical to a tubular and thence to a sigmoid form.

(*b*) The thecæ which in a primitive state overlapped one another began to become free. Most frequently this process affected only the apertural portions, but in some lineages it affected the whole theca.

(*c*) The free portion of the theca became bent over in the form of a hook, or even became coiled upon itself.

These changes in the theca, unlike those described for the polypary, did not affect the fauna as a whole, but graptolites having primitive thecæ, or thecæ exhibiting only lowly grades of specialization, persisted alongside of others in which the most advanced stages were attained.

ANTHOZOA

The Classification of the Anthozoa.—The Anthozoa include the sea anemones and corals, and exceed all other Cœlentera in importance as the producers of skeletons. Like the hydroid types of the Hydromedusæ they were predominantly benthic animals. The members or this order fall naturally into two sub-orders, viz. the Alcyonaria and the Zoantharia, the general characteristics of which may be best appreciated by comparing one of the polypes of *Alcyonium* (dead men's fingers) with an ordinary sea anemone.

These types resemble one another, and differ from hydromedusæ, in the following respects. The mouth is elongated, and thus imparts to the external aspect of the polype a trace of bilateral symmetry. The mouth does not open directly into the body cavity, but is connected therewith by a flattened tubular gullet. The body cavity is partially divided by vertical partitions, called mesenteries, which project inwards from the body wall, and bear bands of muscles and other important organs.

The more obvious differences between *Alcyonium* and the sea anemone may be gathered from the accompanying table :

ALCYONIUM.	SEA ANEMONE.
Eight tentacles.	Five or six tentacles, or some multiple of these numbers.
Each tentacle feathery in appearance owing to the presence of small lateral pinnules.	Tentacles simple finger-like processes without pinnules.
Mesenteries eight in number, and all united to the gullet as well as to the body wall.	Only twelve of the mesenteries are united to the gullet as well as to the body wall, the remainder have their inner edges free.

Alcyonaria.—The Alcyonaria produce many kinds of skeletons. These may be referred to one or other of two types :

(*a*) Skeletons secreted by the ectoderm and deposited externally.

(*b*) Skeletons secreted by ectoderm cells which wander into the mesoglœa and are therefore deposited within the substance of the body wall.

With very few exceptions the living Alcyonaria are all fixed and compound colonial forms. Each colony starts life as a single individual attached to some object upon the sea-floor. From the base of attachment of this there grow out hollow finger-like processes, or stolons, each of which consists of ectoderm and endoderm, with intervening mesoglœa. These stolons extend over the surface of the object, and may unite with one another at intervals, and thus form a network. From this there grow up new polypes. In some the stolon is compound, consisting of a band-like or even sheet-like mass of mesoglœa enclosed in ectoderm, and penetrated by endoderm canals which connect the cavities of the adjoining polypes.

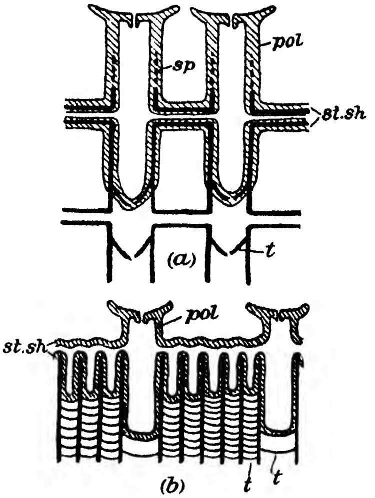


FIG. 37.—Diagrams showing relation of Skeleton to Soft Parts in Tubipora (*a*) and Heliopora (*b*).

Thick lines = skeleton. Shaded areas = soft parts.
pol, Polype. *sp*, Spicule. *st. sh*, Stolon sheet. *t*, Tabula.

In *Heliopora* (Cret.-Rec.) and *Tubipora* (Rec.) (Fig. 37) the polypes are united with one another by sheets of tissue constructed in the manner described above, although the sheet arises not from the base but from the middle of each polype. In *Heliopora* finger-like processes, of smaller calibre than the polypes, hang down from the under side of this stolon sheet. The skeleton is an external one and is secreted by the under surface of the whole colony. Larger calcareous tubes or corallites are formed around the lower portion of the polypes and smaller ones around the finger-like downgrowths; thus the coral appears like a honeycomb of numerous closely-packed tubes of two sizes. As it grows by the addition of fresh material to the top edges of the tubes, the polypes and processes are withdrawn to higher and yet higher levels. The successive stages in this withdrawal are marked by the deposition of thin plates or tabulæ across the cavities of both large and small corallites. In *Tubipora* the skeleton is an internal one. It is deposited in the mesoglœa, of both the polypes and the stolon sheet, in the form of irregularly-shaped calcareous spicules. These by becoming closely connected with one another form a firm framework of porous material which in shape is an exact replica of the mesoglœa, and consists of a number of corallites, the cavities of which are connected with each other by a fine canal running through the substance of the calcareous material deposited in the mesoglœa of the stolon sheet. The growth of these corallites also takes place by addition to the upper edges, so that the living colony is lifted to higher planes. New stolon sheets are then formed. At the same time the colony withdraws from the lower levels ; the canaliculated platforms, laid down in the stolon, are left behind, and tabulæ are formed across the cavities of the corallites.

Modern Zoantharia, their Structure and Development.—This division of Cœlentera includes such types as the familiar sea anemone, which lives attached to stones and other objects in nearly every rock-pool, and the Coral polype, which has its home in warm seas, and secretes for itself a calcareous base of attachment called the " Stony coral." The anatomy of these two types is sufficiently similar to be illustrated by that of the sea anemone. The body is cylindrical, with a flat base for attachment to the rocks below, and a mouth surrounded by many finger-like tentacles above. These last are provided with innumerable minute stinging organs, by means of which the creature paralyses worms and other small organisms which happen to touch it, and upon which it feeds.

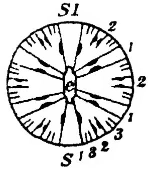


FIG. 38.—Diagrammatic transverse section of a *Zoantharian*.

S, Sulcar side. *SI*, Sulcular side. 1–3, Cycles of mesenteries. 1, Primary. 2, Secondary. 3, Tertiary.

The body-wall, as in *Obelia*, consists of ectoderm and endoderm, with intervening mesoglœa. The mouth opens into the body-cavity through a short gullet (cp Fig. 28*b*) which is flattened like a collapsed tube. Along the margins of this gullet there runs two ciliated grooves, the one being called the sulcus and the other the sulculus. The mesenteries, which partially divide the body cavity (Fig. 38), are classed as primary, secondary or tertiary according to the degree of their development. The primary mesenteries are twelve in number, and are arranged in a radial manner in six pairs, attached along their margins to the gullet, the body-wall and the base. That portion of the margin which is below the gullet is free and bears reproductive organs. On one face of each mesentery a band of muscle extends from top to bottom. The two pairs of mesenteries, called directives, attached to the edges of the gullet have their muscles facing outwards. The remaining pairs, attached to the sides of the gullet, have their bands facing one another. The space enclosed by each pair is called an entocœl, that between two pairs, an exocœl.

The symmetry of the organism is predominantly radial, but the shape of the mouth and gullet and the arrangement of the muscle bands introduce elements of bilaterality. This latter feature is more marked in development (Fig. 39) during which the primary mesenteries appear first, the secondaries next and the tertiaries last. In coral polypes the mesenteries in each cycle do not arise simultaneously, as may be seen from the accompanying diagrams. It will also be seen that bilateral symmetry is marked at all stages and only gives place to radial at the last. In modern coral polypes radial symmetry is evidently a feature of secondary origin, and is based upon a six-rayed or hexameral plan. A few anemone-like forms produce a horny skeleton, but the majority are solitary and deposit no hard parts.

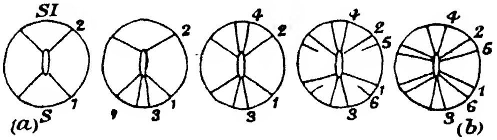


FIG. 39.—Diagrams showing order of appearance of Mesenteries in the primary cycle during development of a coral Polype.

(*a*) Earliest stage. (*b*) Latest. Note the predominance of bilateral symmetry during these changes. *S*, Sulcar side. *SI*, Sulcular side.

The coral polypes, or Madreporaria, nearly all produce hard calcareous "skeletons." In modern forms this secretion does not commence until the polype has reached that stage in development when all twelve primary mesenteries are present. The calcareous material is laid down in the form of minute nodules (Fig. 40), made up of radiating crystals, and secreted by the ectoderm cells covering the base of the polype. These nodules become united with one another and, at first, form a saucer-shaped disc called the prototheca. This is thickened by the addition of further layers of nodules. At the same time the disc is extended, and the prototheca becomes a cup-shaped theca enclosing a cavity the *lumen*. Along that zone on the body surface where the secretory lower or aboral area passes over into the non-secretory oral area, a separate film of skeletal material is formed and laid down upon the outside of the theca. This is the epitheca. Whilst this is taking place a cycle of six, or it may be twelve, radial infoldings appear in the ectoderm of the base of the polype. The secretion of skeletal material takes place in the grooves (Fig. 41) thus formed,

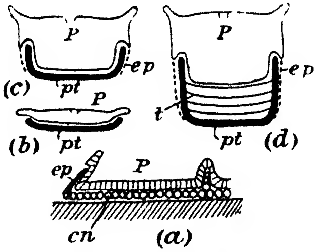


FIG. 40.—Diagrams of early stages in the formation of a Coral by a Polype (*P*).

(*a*) Deposition of first layer of calcareous nodules (*cn*) and epitheca (*ep*).

(*b*–*d*) Formation of prototheca (*pt*), epitheca (*ep*), tabula (*t*).

and produces vertical plates, or septa, within the theca. From the outset these have a hexameral radial arrangement. In due course secondary and tertiary cycles of septa appear between the first formed or primary septa. During their formation radial symmetry is still maintained.

As the edge of the theca is extended upwards the polype may withdraw from the bottom of the cup (Fig. 40). The vacated space is then either filled with calcareous material deposited in the inside of the theca, or thin plates (tabulæ) stretching across the cavity or lumen may be secreted at successive levels. Smaller but similar plates (dissepiments), having a vertical position and situated between the septa, may also be formed. The presence of these gives to this portion of the coral a vesicular appearance.

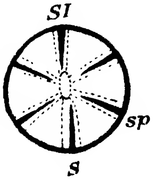


FIG. 41.—Diagram showing relation of septa (*sp*) of Coral to Mesenteries (dotted lines).
S, Sulcar. *SI*, Sulcular.

Early Palæozoic Reef Builders. In the reefs of early palæozoic times corals bearing a striking resemblance to such Alcyonaria as *Tubipora* and *Heliopora* played a prominent part. The balance of evidence, particularly the presence and number of rudimentary septa, strengthens the view that these forms were more closely related to the Zoantharia.

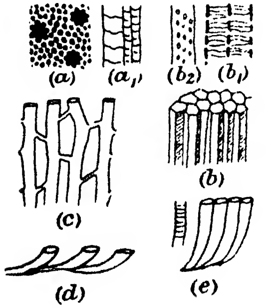


FIG. 42.—Fossil Alcyonaria.
(*a*) *Heliolites*, surface view (*a*) and vertical section (a_1). (*b*) *Favosites*, portion of colony, vertical section (b_1), wall of corallite showing pores (b_2). (*c*) *Syringopora*. (*d*) *Aulopora*. (*e*) *Halysites*.

Aulopora and its allies (Ord.-Carb.) exhibit a very simple mode of colony formation. Each new polype arose as a bud directly from the base of the parent, and formed a trumpet-shaped corallite attached to that of the parent. Thus a skeleton was formed which ramified over the surface of the sea floor.

Halysites (Ord.-Sil.) (Fig. 42*e*) started growth in a similar way but each corallite grew to a considerable height and maintained close contact with both its predecessor and successor.

As the affinities of the above forms are not yet understood it is usual to refer to them collectively as the Tabulata.

The Heliolitida which were contemporaneous with the Tabulata include *Heliolites* (Ord.-Sil.) which bears a striking resemblance to *Heliopora* except in the possession of twelve equally developed septa.

Syringopora, an important reef-building genus of mid-Palæozoic times, resembles *Tubipora* in the presence of upright tubular corallites, having their cavities divided by funnel-shaped tabulæ, and connected by canals from which new corallites arose. In this genus, however, the stolons seem to have been separate, and new ones were produced at irregular intervals and in different planes. *Favosites* and its near allies likewise played an important part in reef formation from Silurian to Carboniferous times. They consist of numerous corallites, which as a rule are so closely packed together that the colony resembles a honeycomb. Each corallite is separated from its neighbour by a thin lamina of different material; but the cavities are connected by openings, which evidently correspond with the connecting canals of *Syringopora* and *Tubipora* greatly shortened.

In *Chaetetes* (Carb.-Jur.) which has a similar honeycomb-like appearance the corallites have a much smaller calibre.

The Structure and Development of a Palæozoic Coral.—The genus *Zaphrentis* (Fig. 43) may be taken as the type for the Palæozoic corals. It appeared during the Silurian, attained its climax in the early part of the Carboniferous, and became extinct before the close of this period.

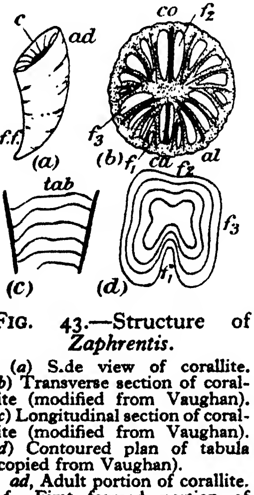


FIG. 43.—Structure of *Zaphrentis*.

(*a*) Side view of corallite. (*b*) Transverse section of corallite (modified from Vaughan). (*c*) Longitudinal section of corallite (modified from Vaughan). (*d*) Contoured plan of tabula (copied from Vaughan).

ad, Adult portion of corallite. *f.f.*, First formed portion of corallite. *c*. Calice. *ca*, Cardinal septum. *co*, Counter septum. *al*, Alar septum. f_1, Cardinal fossula. f_2, Counter fossula. f_3, Alar fossula. *tab*, Tabula.

Zaphrentis is a simple conically-shaped coral, and is usually curved to some extent. The apex of the cone represents the first-formed portion of the coral; whilst the cup-shaped hollow or calice, at the other end, represents the latest product of growth. A series of thin slices taken at intervals from the apex to the calice therefore supplies a record of the stages in development (Fig. 44). The embryonic stage is represented by the prototheca, which is thin and cup-like. Shortly after that has been formed its cavity becomes divided by a median vertical plate the axial septum. This subsequently breaks into two at the centre, and becomes the cardinal and the counter septa. Two new septa next appear on either side of the cardinal end of the median plate. These shift gradually into a radial position, and become the alar septa. Meanwhile another pair appear at the counter end of the plate, and they also shift into a radial position and become the counter-lateral septa. A pause now takes place in development of the coral. It is significant that the number of these first formed septa called protosepta is six and that, in spite of the bilaterality in the order and position of their first appearance, they now exhibit a marked radial symmetry.

If it be assumed that the cardinal side corresponds with the sulcar side a striking parallelism may be detected between the sequence of events in the development of the mesenteries of a modern coral polype and of the septa of *Zaphrentis*. If this has any significance and is not a mere coincidence, then the six septa, which appear simultaneously at the outset of development in the modern coral, may be compared with the protosepta which are in existence when the pause takes place in the development of *Zaphrentis*.

The changes just described are to be regarded as taking place during infancy or the nepionic phase. The next few stages are described as adolescent, or neanic, and include all those changes which lead up to the attainment of the adult or ephebic condition. A final, or old age phase, is recognized in the development of other types, and is called the gerontic stage. With the setting in of adolescence, two pairs of septa appear on the cardinal side of the counter-lateral and alar septa. This again may be compared with the order of formation of the entocœls in the modern coral polype.

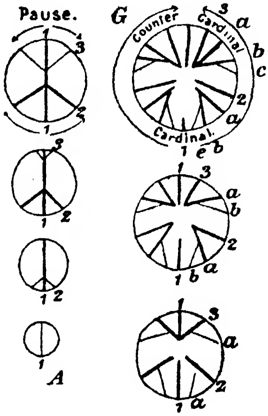


FIG. 44.—Diagrams showing order of development of septa in *Zaphrentis*.

A–G. In order from earliest to youngest. *A* shows the axial septum. *B–D* show the mode of formation of the six protosepta. *E–G* show the order of appearance of the metasepta.

[Adapted from Carruthers.

From this stage onwards parallelism between the two types is no longer manifest; for whereas in the modern coral secondary and even tertiary cycles of septa appear in all six primary interseptal spaces, in *Zaphrentis* the formation of new septa is confined to only four of these spaces, and none appears in the spaces on either side of the counter septum. The spaces on either side of the cardinal septum are called the cardinal quadrants, those between the alar and the counter-lateral septa are the counter quadrants.

In *Zaphrentis* the new septa called metasepta do not appear in cycles, as in modern forms, but they arise in pairs at the thecal margin and on the cardinal side of the last formed septa. This method of growth gives rise to the feathered or pinnate arrangement of septa (Fig. 43), which is so characteristic of many Palæozoic corals, and which imparts to the full-grown coral such a marked bilateral symmetry. The number of septa in the counter quadrant generally exceeds that in the cardinal quadrant. The septa described above, are called the major septa, to distinguish them from shorter or minor septa which appear later, as do the secondaries in modern forms, in the interseptal spaces.

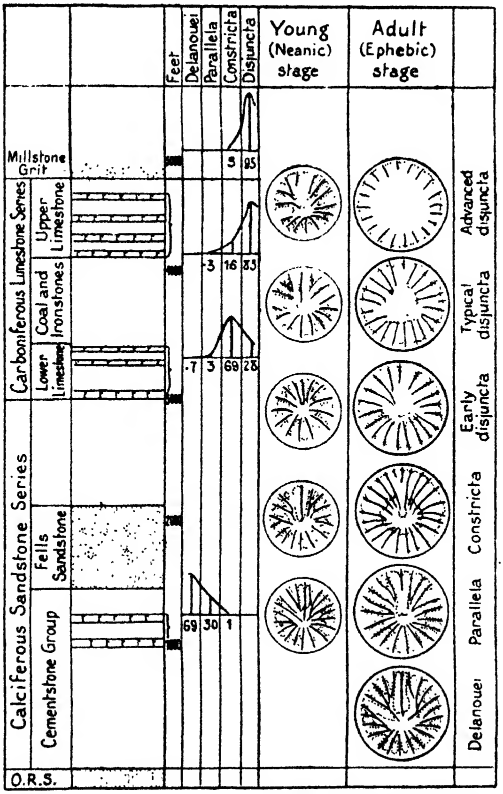
In *Zaphrentis* the cardinal septum is usually arrested in development, and the space on either side is slightly enlarged and forms a gap in the cycle of septa. Similar but less conspicuous gaps may be seen on the counter side of the alar septa and on either side of the counter septum. Each gap is called a fossula. During development additional calcareous tissue or *sclerenchyme* is deposited against the inner face of the epitheca and between the outer ends of the septa ; thus a wall or peripheral stereozone (" theca ") is produced.

With the upward growth of the coral the polype withdrew from the lower parts of the thecal cavity, and secreted tabulæ across the vacated portion of the lumen. These tabulæ bulge upwards, like a dome, in the centre. Down the side of this dome (Fig. 43*d*) four radial grooves run, which coincide in position with the gaps in the septal cycle. These are the fossular depressions of which the cardinal depression is the widest and deepest.

The Evolution of Zaphrentis delanouei (sensu lato).—A great number of specimens were collected by one investigator from different places and different levels from the Carboniferous rocks of the Midland Valley of Scotland. These specimens were alike in the majority of their characters ; they were of the same average size and shape ; the epitheca was ribbed longitudinally ; the cardinal fossula was on the concave side of the coral ; the septa were stout, thickened at their inner ends, and curved so that the convex side faced the cardinal fossula ; the tabulæ were regularly spaced. Careful inspection of the specimens, in thin slices, showed that both at the same, and at different, levels individuals exhibited differences from one another especially in the shape of the cardinal fossula and in the relative lengths of the associated septa. Four specimens were selected to represent typical variations (Table III, p. 53) and were given the following distinctive names ; *Z. delanouei* (*s. str.*) showed the cardinal fossula slightly expanded towards the centre of the coral ; in *Z. parallela* the fossula had parallel sides or tended to narrow centrally ; in *Z. constricta* this narrowing was clearly marked. These three varieties all showed most of their septa meeting in the centre, but in *Z. disjuncta* these had lost touch and had shortened towards the periphery (amplexoid condition). The other specimens exhibited every grade of difference between these types, so that the collection as a whole formed a continuous series ranging from *Z. delanouei* (*s. str.*) at one extreme to *Z. disjuncta* at the other. Nevertheless they were classed into groups each of which clustered round one or other of the types. Specimens that lay half-way between were of course difficult to place.

The fossils were not uniformly distributed throughout the strata, but occurred in limestone beds situated at four levels separated by hundreds or even thousands of feet of barren rock representing long periods of time during which the coral lived elsewhere only to return when suitable conditions were renewed. The existence of such gaps in the record is not such a serious matter as might at first appear, for as an inspection of Table III shows the same varieties occur at two or more horizons and consequently the organic record is not completely broken.

Table III.—Summary of the History of the Gens *Zaphrentis delanouei.*



[Data from Carruthers.

The fact that, for instance, in the Lower Limestones horizon the specimens provide a continuous series from *Z. delanouei* to *Z. disjuncta* creates a strong presumption that these individuals, which often differ only very slightly, freely interbred with one another; that in fact they all belonged to one *biological species.* The four "species" named above are based solely upon morphological differences and therefore constitute *morphological species.* In Geology the recognition of small varietal differences is often of such great value that the creation of reference names or morphological species is almost a necessity. A clear understanding of these two uses of the word species will save much confused thinking.

In the lowest levels, viz. the Cementstone Group, 69 per cent. of the specimens were referable to *Z. delanouei*, 30 per cent. to *Z. parallela* and 1 per cent. to *Z. constricta.* A graph based upon these figures gives the frequency curve of distribution of these three varieties. A comparison with similar curves made for higher horizons shows that with the passage of time the mode, or vertical passing through the crest shifts in position and rises in height progressively from *Z. delanouei* to *Z. disjuncta.* This is accompanied by a reduction in number and the final disappearance first of *Z. delanouei* and then of *Z. parallela.* These facts show that successive communities undergo a progressive change called evolution.

The main direction of evolution is briefly and clearly demonstrated by selecting a series of type specimens from the modes of successive curves. These exhibit representative phases in the sequence. Such phases in evolution were originally called "mutations," a term which has unfortunately in recent years acquired a quite different significance in biological literature. The establishment and description of such series plays a fundamentally important part in the evolutionary study of fossils. Nevertheless care must be taken to avoid the unconscious but false assumption that later varieties have descended from earlier ones of the same name and therefore lie upon a direct line of descent like the lineages of the history books. Individuals do not descend from individuals but from parents, grandparents and any number of ancestors. Moreover, the ancestry of a number of individuals may be interwoven like a network. It follows therefore that it is successive communities that descend from one another and that in dealing with fossils the term lineage has no meaning except in terms of communities. A line of descent is in fact a strip of netting, a plexus of descent as broad as the range of variations at different levels. The term lineage is therefore a misnomer but a useful misnomer for such a series of type specimens as that referred to above. A genetically compact stock like that of the plexus has also been called a "species group" or a "gens." Within a gens there may be any number of "morphological species" the creation of which largely eliminates the necessity for clarifying the use of such terms as " mutation " and " variation " in palæontological literature.

The Development of Z. delanouei.—As far as the earliest or embryonic stages in development of *Z. delanouei* (*s. lato*) are known they are seen to be the same as for other corals (Fig. 44 *A–D*). In this respect they recapitulate the embryonic stages exhibited in those corals.

After a brief transitional phase the neanic stages become established. In *Z. parallela* the structure at this time closely resembles that of *Z. delanouei* (*s. str.*) In like manner the early and late neanic stages of *Z. constricta* reproduce the conditions seen in adult *Z. delanouei* (*s. str.*) and *Z. parallela* respectively. In this appearance of adult conditions at an earlier stage in the growth of later forms there is implied a hastening of development, a commonly recognized phenomenon referred to a *tachygenesis*. The reproduction of the condition seen in earlier adults during the development of later forms is known as the Principle of Recapitulation or *palingenesis*. Incidentally this recapitulation, while helping to bridge gaps in the stratigraphic record, provides further evidence of the very close relationship to one another of the many varieties found in a community, and further supports the view that interbreeding took place freely.

In the development of *Z. disjuncta* the *delanouei* and *parallela* stages are omitted and the transitional phase passes straight into a *constricta* stage. This provides an example of the phenomenon of *lipopalingenesis* or the skipping of stages during development.

The Structural Elements in Carboniferous Corals.—In the British Isles, and in Belgium, the rocks of the Lower Carboniferous age have been divided into a number of zones represented in order from the bottom upwards by the letters K, Z, C, S, D. They are predominantly calcareous in composition, and yield numerous corals at many different levels. These rocks represent a period of time of sufficient length for corals to undergo considerable evolutionary change. So much work has already been done upon these corals, that indications of the courses pursued in the structural evolution of a number of important forms have been detected. A knowledge of these will be helpful for the better understanding of the more fragmentary records in the other systems. If the general structure of the genus *Zaphrentis*, already fully studied, be recalled, it will be soon realized that all the changes which that genus undergoes are rung upon only three structural elements, the epitheca, the septum, and the tabula. Closely allied to *Zaphrentis* is the genus *Caninia* (L. Carb.), which, in such a typical species as *Caninia cornucopiæ* (Z2 zone), exhibits a conical or trochoid lower portion and a cylindrical upper portion (Fig. 45). The form is not always that shown in the figure, for sometimes its shape is curiously distorted, and its conical lower portion may vary greatly in the rate of increase in width in different individuals. Sections through this latter portion are indistinguishable from *Zaphrentis*. As the cylindrical portion is approached an amplexoid type of structure is established, that is to say the septa, as seen in section, withdraw from the centre and at the same time the fossula becomes correspondingly ill defined.

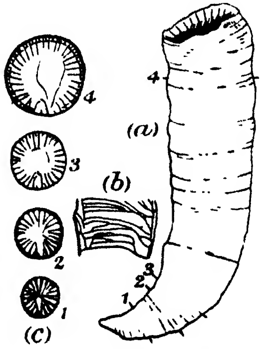


FIG. 45.—Development of *Caninia cornucopiæ*.

(*a*) General view of the coral showing levels at which sections (*c* 1–4) were made. (*b*) Longitudinal section. (*c* 1–4) Transverse sections.

[From Carruthers.

One quite new feature, rarely if ever exhibited by *Zaphrentis*, is the presence of dissepiments. These are small plates similar in constitution to the tabulæ, but they differ from these by being placed vertically between the edges of the tabulæ and the peripheral stereozone. Their presence imparts to the outer zone of the coral a vesicular condition. In allied species the *Zaphrentis* stage in development is much shortened or even absent, and the dissepiments appear early as a feature of great importance. The steps by which this degree of importance is attained, and the varying appearance produced by the changes in extent of the septa, may be illustrated by the mutations of the gens *Caninia cylindrica* (Fig. 46).

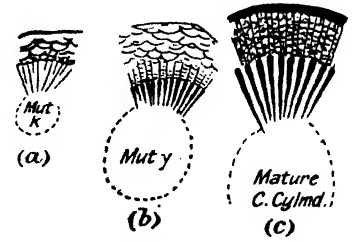


FIG. 46.—Stages in the Evolution of gens *Caninia cylindrica*.

Transverse sections across (*a*) *Mut. k*, (*b*) *Mut* γ, (*c*) *Caninia cylindrica*.

[After Vaughan.

The earliest member of this gens is called *Mutation k*, and occurs in the K2 zone in Belgium. In it the septa are separated from the peripheral stereozonal wall by a relatively narrow zone of dissepiments and vesicles thus resembling *Lonsdaleia*. In Mutation γ from the γ and C_1 levels, the dissepimental area is wider, and has encroached upon the septal area. This is the earliest member of the gens which occurs in England. In Mutation δ from levels C_1–S_1 there is no further widening of the dissepimental area, but the septa now extend quite across it to the outer wall. This form is *Caninia cylindrica* proper. The innermost dissepiments may be thickened by the deposition of sclerenchyme, or they may be so crowded together as to form a clearly marked boundary between the tabular and the vesicular or dissepimental zones. This boundary is often called the inner wall; it is not, however, a new structural element, but only a line of dissepiments much thickened. The so-called "theca" is in some corals a new structure, but more often, like this inner wall, it merely is a thickening of an existing structure such as the septa.

Concurrently with any or all of these changes others may take place, but they need not involve the formation of new structures. Thus in *Mut.* γ the fossula is quite conspicuous, but in *Mut.* δ it has become insignificant. This change, together with an increase in the number of septa, leads to an increasing predominance of radial over bilateral symmetry until ultimately all traces of the latter may disappear.

The genus *Aulophyllum* (Fig. 47) also resembles *Zaphrentis* in its earliest developmental stages, but later becomes identical with the adult *Caninia* in its dissepimental and septal areas. In its central area, however, its development pursues an entirely different course, owing to the introduction of two new structural elements, the tabellæ and lamellæ. At an early stage the tabulæ become strongly arched centrally and then tabellæ appear. These are small plates, similar to dissepiments, but having their convex surfaces facing outwards. Their presence gives rise to a ring of vesicular tissue around the centre of the coral. The lamellæ are septa-like structures which extend inwards from the outer periphery of this ring of vesicles. Some of them appear to be direct continuations of septa, but many have no such relationship.

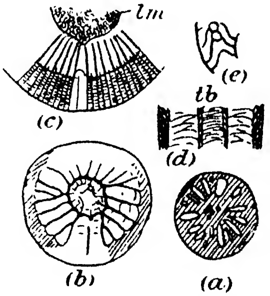


FIG. 47.—*Aulophyllum.* Structure and Development.
Transverse section. (*a*) Close to the apex. (*b*) Further from apex. (*c*) Across mature portion.
Diagrams of longitudinal sections. (*d*) Through nearly mature region. (*e*) Through region near apex of coral. *tb*, tabellæ. *lm*, lamellæ.

The genus *Palæosmilia* (Fig. 48) exhibits the same structural elements as *Caninia.* Indeed between the earlier *Palæosmilia* of the Lower Carboniferous, such as *Palæosmilia* (?) θ (γ Subzone) and *Caninia*, there is little difference beyond the fact that the septa as seen in section are longer and therefore extend nearer to the centre. The fossula is also more fully developed, but this feature only takes it nearer to the zaphrentid end of that stock. In slightly later forms such as *Palæosmilia vaughani* (C2 zone) the fossula has almost disappeared, and nearly perfect radial symmetry has been attained. The septa have increased up to one hundred and twenty in number and extend much closer to the centre. The dissepimental area now occupies one half of the radius of the coral. The tabulæ are no longer simple plates extending across the cavity but are laid down in the form of smaller convex plates which give to the tabular region a coarsely vesicular condition. In *Palæosmilia murchisoni* (S2–D2 zones) these vesicles are more numerous and smaller, and merge without any clearly defined boundary into the dissepimental area. The number of septa is now as many as one hundred and fifty and all reach to the centre of the coral. In *Palæosmilia regia* (D zone), the latest and most advanced of the Lower Carboniferous Cyathophylla, the tabulæ tend to bulge upwards in the centre of the coral and at that point take on the character of tabellæ, whilst the inner ends of the septa fulfil the part of lamellæ.

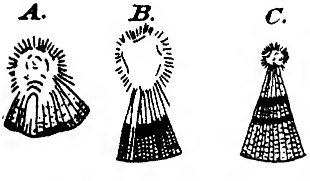


FIG. 48.—Evolution of *Palæosmilia.*

Portions from sections of *A*, *Palæosmilia ? θ.* *B*, *Palæosmilia vaughani* (ψ). *C*, *Palæosmilia murchisoni.*
(*A* and *B* based on Vaughan. *C* on Wilmore.)

The genus *Dibunophyllum* (Fig. 49) is very characteristic of those upper levels of the Lower Carboniferous which are referred to as the Dibunophyllum zone. In the early development of some primitive species a zaphrentis stage can be detected, but in most species it has apparently been cut out. In its dissepimental and septal areas *Dibunophyllum* is like a primitive *Palæosmilia*, but centrally it exhibits in sections a spider-web-like arrangement of tabellæ and lamellæ. Unlike *Aulophyllum* these structures are not concentrated in a ring at a little distance from the centre, but are massed about a median plate-like structure, the columella.

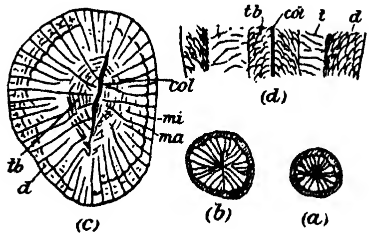


FIG. 49.—Structure and Development of *Dibunophyllum vaughani.*

(*a*) Earliest stage approaching *Zaphrentis.* (*b*) Stage showing columella present before dissepiments and minor septa. (*c*, *d*) Adult—(*c*) transverse section ; (*d*) longitudinal section. *col*, Columella. *d*, dissepiments. *mi*, minor septum. *ma*, major septum. *t*, tabula. *tb*, tabella.

From these descriptions of several of the more important of the Lower Carboniferous coral genera it will be seen that, in spite of their great variety of characters, they are made up of only about seven promine structural elements, epitheca, septa, tabulæ, dissepiments, tabellæ, lamellæ, columella. The actual number present varies from genus to genus, as may be seen in the accompanying table.

TABLE IV.—Showing the distribution of Structural Elements among the more important Lower Carboniferous Corals.

Coral.	Epitheca.	Septa.	Tabulæ.	Dissepiments.	Tabellæ.	Lamellæ.	Columella.
Zaphrentis .	×	×	×	—	—	—	—
Caninia . .	×	×	×	×	—	—	—
Aulophyllum .	×	×	×	×	×	×	—
Palæosmilia .	×	×	×	×	×	×	—
Dibunophyllum	×	×	×	×	×	×	×
Lithostrotion	×	×	×	×	—	—	×

A consideration of the growth of each of the above genera shows that there is no fixed order of appearance of these structures in development. Thus in *Aulophyllum* (Fig. 47) the tabellæ and lamellæ appear before the dissepiments. So likewise in *Dibunophyllum* (Fig. 49) the tabellæ and the lamellæ are so retarded in the time of their appearance that they are preceded by the columella. These facts seem to suggest that a newly added structural feature tends to be hastened in the time of its appearance in development.

If to the corals described above the genus *Lithostrotion* (Fig. 50) be added it will be seen that the presence of a columella does not necessitate the presence also of all the other elements, for in this case there are neither tabellæ nor lamellæ. This may be otherwise expressed by saying that there is likewise no fixed order of appearance of the elements in evolution. That only a few elements suffice to produce these, and many other genera, is due to the fact that each element has its own series of changes through which it may pass during either development or evolution. Thus the septum may extend to the centre, or be withdrawn from the centre or the epitheca, or both. In some corals, not yet considered, they almost vanish. Similarly the dissepiments may be quite absent, or they may occupy any width of the cavity of the theca up to as much as one half of the radius.

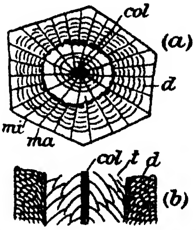


FIG. 50.—Structure of *Lithostrotion*.
(*a*) Transverse section.
(*b*) Longitudinal.
col, Columella. *d*, dissepiments. *mi*, minor septa. *ma*, major septa. *t*, tabula.
[After Edwards and Haime.

The series of changes which the septa undergo is not necessarily bound up with those experienced by the dissepiments. Each element moves through its changes independently of the other; and thus a great number of combinations of states of these two elements alone is possible, combinations which may suffice to distinguish one species from another. When seven, or more, structures enter into the make up of an organism, it is evident that an almost inconceivable number of combinations of structures, in various stages of development, is possible. The number of possible varieties and species is correspondingly great.

A clear understanding of the principle just discussed is of much importance to the student of fossils. It may be referred to as the principle of the independence of structural elements.

Compound Carboniferous Corals.—The corals considered above, with the exception of *Lithostrotion*, usually consist of only one individual. But the members of this genus and of many others consist of numerous individuals, and are therefore described as compound. The fact that such a compound condition exists is due to the ability of the polype to reproduce asexually either by budding or by fission. The former process has already been described for *Obelia*. In the latter the polype divides into two or more parts, each of which grows into a new polype. The corallites, or skeletons produced by new individuals, remain united and thus a colonial or compound coral is formed.

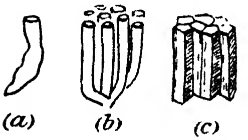


FIG. 51.—Stages in compound Coral Formation.

(*a*) Simple (*Eostrotion*). (*b*) Dendriform (*Lithostrotion martini*). (*c*) Basaltiform (*L. basaltiforme*).

The Upper Avonian Lithostrotiontidæ provide an almost complete series (Figs. 51, 52) illustrating the general modifications experienced by compound corals. The ancestral genus *Eostrotion* (? *Lophophyllum*) was a simple coral, long and cylindrical in form and circular in transverse section, like *Caninia*. In *Lithostrotion martini* the individual corallites are of similar appearance, but inasmuch as a number of them are united by their bases to one another they form a compound coral. Apart from this connection, the corallites are not in contact with one another, so that the colony consists of a mass of widely spaced roughly parallel branches. This early phase in the modification of compound corals is described as *fasciculate*.

In *Lithostrotion basaltiforme*, the polypes appear to have been closely packed against one another so that their bases were squeezed into polygonal shapes. As each polype secreted its own corallite, these latter were also closely packed, and of polygonal outline. The colony as a whole therefore consisted of a number of corallites looking like miniature columnar basalt. This more advanced compact phase in compound coral formation is described as *massive*. Corals exhibiting transitional conditions from one to the other phase are not difficult to find.

At first each corallite in massive form is provided with a well developed epitheca (Fig. 52*c*) and is said to be *cerioid.* In other species the epitheca is thin and inconspicuous, and thus exhibits a transition to the condition in *Orionastræa* (D_2–D_3). This genus is closely allied to *Lithostrotion*, but differs in the fact that the epitheca around the individual corallites has completely disappeared (plocoïd phase), the septa and dissepimental areas of adjoining members of the colony merging into one another. This very advanced phase in the evolution of a compound coral is described as thamnastræoid.

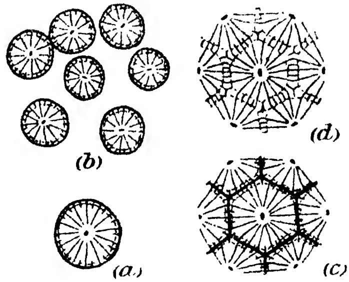


FIG. 52.—Sections of Corals in various stages in Compound Formation.

(*a*) Simple. (*b*) Fasciculate—Corallites separate and round. (*c*) massive and cerioid Corallites in contact, polygonal, but separated by epitheca. (*d*) massive and plocoid—without epitheca thamnastræoid—septa of adjoining corallites united (*Orionastræa*).

These phases in compound coral evolution are not confined to the Lithostrotiontidæ, but may be more or less completely exhibited in other and widely divergent stocks. Thus, for example, they may be detected in the *Thysanophyllum-Lonsdaleia* (Fig. 53) series of Upper Avonian corals. In *Thysanophyllum* the individual corallites are characterized by the persistence, throughout development, of the median plate, which in other corals gives rise to the cardinal and counter septa. The septa are separated from the outer wall by a zone of dissepiments. This coral has already attained the fasciculate phase in its compound development. The same is true also for *Lonsdaleia duplicata*, which has been derived from a *Thysanophyllum* stock. In this species, however, though it is almost identical with *Thysanophyllum* in the early stages of development, the adult corallite possesses the spider-web or clisiophyllid arrangement of tabellæ and lamellæ. In *Lonsdaleia floriformis* the detailed structure is similar to that of *L. duplicata*, but the colony as a whole has passed on to the cerioid phase.

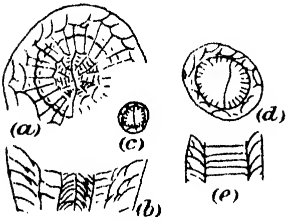


FIG. 53.—Structure and Development in *Thysanophyllum-Lonsdaleia.*

(*a–c*) *Lonsdaleia duplicata* (after Stanley Smith).

a, Transverse section. *b*, Longitudinal section. *c*, Transverse section of neanic stage in development. (*d*, *e*) *Thysanophyllum vermiculare*. *d*, Transverse section (after Garwood). *e*, Longitudinal.

Palæosmilia is often a solitary coral, but its various species exhibit all phases in compound coral formation, including the thamnastræoid which is seen in *P. regium.*

Precarboniferous Corals.—As with the Carboniferous, so with the Precarboniferous systems—it is the limestones which are the chief sources of supply of fossil corals. Generally speaking these earlier limestones are less extensive and not so massive, and the detailed structure and development of their coral contents are not so fully known.

The earliest undoubted corals occur in the Ordovician rocks. Chief among these is *Streptelasma* (Ord.-Sil.). This genus (Fig. 54) is probably the forerunner of the Carboniferous *Zaphrentis*, which it resembles in being a solitary conical coral with septa pinnately arranged. It differs in the larger development of the cardinal quadrants, in the absence of sclerenchyme uniting the septa at the centre, and in having few tabulæ. *Petraia* appears to be a more primitive form than *Streptelasma.* Tabulæ are lacking and the septa are more extended centrally, and become spirally rolled on one another, thus forming a false columella. It has been seen that *Zaphrentis* represents the simple radical from which many of the Carboniferous corals have been derived. *Streptelasma* appears to hold a similar position among the corals of the Silurian and Devonian. Many Silurian corals arose from this simple radical stock, and evolved along widely divergent lines, some of which exhibit a rough parallelism to those lines already studied in the Carboniferous corals. During the Devonian these lines attained the climax or acme of their development. At the close of the Devonian many of them became extinct, so that the Carboniferous opened with a much impoverished coral fauna, in which *Zaphrentis* occupied a most important place.

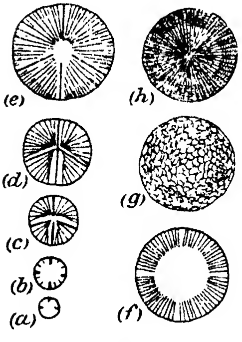


FIG. 54.—Precarboniferous Corals.

(*a–e*) *Streptelasma*, development and structure. (*f*) *Omphyma*. (*g*) *Cystiphyllum*. (*h*) *Cyathophyllum*.

Omphyma (Sil.) represents (Fig. 54*f*) a line similar to *Caninia*, in which dissepiments appeared, and the septa shortened away from the centre leaving an area occupied only by tabulæ. The septa became numerous and radially arranged, but unlike the condition in *Caninia*, all four fossulæ were retained. In *Cystiphyllum* (Sil.-Dev.) a modification is exhibited (Fig. 54*g*) which seems to have no parallel among Carboniferous forms. In it the septa are reduced almost to a vanishing point. On the other hand the dissepiments were greatly developed, and the tabulæ also became highly vesicular so that the whole cavity of the coral became filled with vesicles. Corals exhibiting this modification tended to assume curious external shapes, thus *Goniophyllum* (Sil.) was quadrangular in cross-section, and *Calceola* (Dev.) was slipper-shaped and its calice had a lid or operculum.

In yet other Silurian and Devonian species the septa extended toward the centre and became radially arranged. A wide dissepimental area was produced. These are referred to the genus *Cyathophyllum* (Fig. 54*h*). Almost identical peculiarities appeared in certain carboniferous corals which were also classed with *Cyathophyllum*. As shown in a previous chapter, however, these evolved within carboniferous times through *Caninia* from *Zaphrentis*. Between them and the earlier *Cyathophyllum* no direct genetic relationship exists. They are now therefore placed in the new genus *Palæosmilia* (p. 57). The resemblance between the Devonian *C. helianthoides*, and the Carboniferous *P. regium* is extraordinary, and yet they are not directly related. They are the products of evolution, along parallel lines, of series of organisms derived from earlier and later members respectively of a radical stock, which consisted of a genetically related series, and which itself underwent modification from a streptelasmoid to a zaphrentid condition. Such closely similar, though not intimately related, forms are described as homeomorphs ; and, because they have both attained the same stage of structural, or morphological change, in a number of respects, they are said to be morphologically equivalent. Such phenomena as these are the natural sequel to the evolution of stocks starting with the same few structural elements, each having only a limited range of possible change.

Another example of parallel development is exhibited by those corals which have a clisophyllid, or spider-web, type of centre. It has already been seen that this type of structure becomes a striking feature in *Dibunophyllum* and *Lonsdaleia* and other corals, which characterize the topmost zones of the Lower Carboniferous. The same feature, independently derived, appears also in the Silurian.

Among compound corals *Acervularia* (Sil.) is massive and typically cerioid. *Strombodes* (Sil.) and *Phillipsastræa* (Dev.) exhibit the thamnastræoid phase. These again are cases of evolution, parallel to that undergone by certain Carboniferous corals. A series of changes in a simple or a compound character thus repeated in members of different lines of descent is spoken of as a **trend** and is usually referred to in terms of the end member of one of those lines, *e.g.* amplexoid trend, cyathophylloid trend.

Mesozoic and Later Corals : Simple Types.—Owing to the scantiness of knowledge concerning the Permian and the Triassic corals, but little is known of the precise relationship of the Mesozoic to the Palæozoic corals. Accordingly there seems to be a great break between them which may or may not be bridged over by future discoveries. The extraordinary resemblance of the modern *Moseleya* to a compound *Palæosmilia* has been taken to indicate the origin of later corals from a cyathophylloid stock. But it is probably merely a case of morphological equivalence, and not of genetic relationship. It is unlikely that a highly specialized, often advanced, compound coral like *Cyathophyllum* should become the primitive ancestral stock for a later race. Judging by analogy with the history of Palæozoic corals, it would seem more likely that each group of Mesozoic corals was derived from some simple or solitary type having more or less contemporaneous representatives.

The Mesozoic corals as a whole are characterized by fewer solitary, and a greater number of colonial forms, than are those which lived in the Palæozoic seas. With them, as with the latter, it may be assumed that in any given line of descent the solitary preceded the compound state. As a matter of convenience, therefore, it will be better to deal briefly with a few solitary corals first. By so doing it will be possible to gain a clear idea of the broad characters which distinguished both simple and compound forms, without the necessity of discovering first what features are due to compound growth.

The genus *Montlivaltia* is a solitary coral which appears in the Trias, becomes common in the Lias and Jurassic, and declines through the Cretaceous and the Tertiary. In addition to being one of the earliest corals in the Mesozoic, it possesses more of the characteristics of the Palæozoic types already studied, than does any later solitary form. A comparison with *Zaphrentis* will bring out these resemblances, and will also emphasize those features which distinguish the more modern from the Palæozoic types. Like *Zaphrentis*, *Montlivaltia* has an epitheca (Fig. 55), septa and dissepiments. It has no tabulæ or columella. Its septa show no sign of bilateral symmetry, or pinnate arrangement, but are all radially arranged. In *Zaphrentis* only one set or cycle of secondary septa, the minor septa, appear between the first formed or major septa. In Montlivaltia, as in many Mesozoic corals, with increase in size not only one, but also two, three, and even more cycles may be interposed between the previously formed septa.

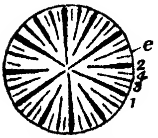


FIG. 55.—Section of *Montlivaltia*.

e, epitheca.
1–4, First to fourth cycles of septa.

Trochosmilia (Jur.-Mio.), like *Montlivaltia*, has numerous septa and dissepiments, but in it the epitheca is missing, and its place is taken functionally by a wall or theca formed by the deposition of sclerenchyme between the outer edges of the septa. *Parasmilia* (Cret.-Pres.) is closely allied to *Trochosmilia*, but in it the dissepiments and theca are absent, as well as the epitheca. The septa are consequently exposed upon the outer surface. A little distance from the outer edge each septum is thickened. By the union of the thickenings of adjoining septa these latter are held together, and a false wall or pseudotheca is produced, which encloses the thecal cavity. A fresh feature is seen in the centre. Here the inner edges of the six first formed septa are united by irregular calcareous bars which produce a column (false columella) of spongy texture up the centre of the coral. In *Turbinolia* (Ter.-Rec.) the columella-like structure is solid.

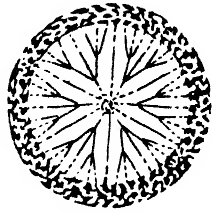


FIG. 56.—Diagrammatic Section of *Balanophyllia* showing porous character of Thecal Wall, and of the inner and outer edges of the Septa.

In *Balanophyllia* (Eoc.-Rec.) the septa (Fig. 56) are many, and the inner edges of the later formed are united to the side faces of those of the earlier cycles. The most striking feature is the perforation of the thecal wall and outer portions of many of the septa by numerous pores. The significance of these perforations can be grasped only by a consideration of the relationships of the soft parts to the corallite. In solitary corals the main part of the body of the polype is situated within the calice or cup, but from the upper part (Fig. 57) of the polype the body wall grows out over the rim, and covers a part of the outside surface of the corallite. This outgrowth is called the edge zone. It is hollow, and its cavity is continuous with that of the organism over the edges of the cup. Any thecal structure that is secreted is deposited in the angle between the edge-zone and the body. In forms, which like *Balanophyllia* have perforated walls, the cavity of the edge zone is also connected with the general body cavity by numerous short canals, and it is the presence of these which necessitates the leaving of the small gaps called pores during the secretion of the wall. Similar canals extend

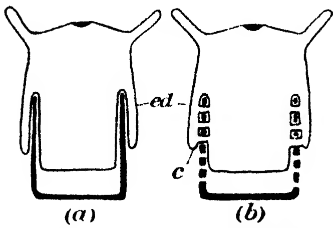


FIG. 57.—Diagrams showing the relationship of the Coral Polype to a non-porous (*a*) and a porous (*b*) thecal wall respectively.

ed, edge zone. *c*, canal joining cavity of edge zone to body cavity.

across the space enclosed by those involutions of the base of the polype in which the septa are deposited.

Mesozoic and Later Corals: Compound Types.—The passage from a solitary to a compound condition is accomplished in consequence of the ability of a polype to reproduce itself asexually. This may be done in one of two ways, by fission or by gemmation i.e. budding.

Fission takes place in either a horizontal or a vertical plane. When horizontal fission takes place the polype divides transversely. The upper part becomes renewed in vigour and forms the new polype, which settles down upon the calice of the corallite, and replaces the lower part. On the corallite itself this change seems to express itself by the presence of constrictions of the outer surface, and by a change in ornamentation and internal structure from the condition seen in that part of the coral just formed by the old polype to that formed at a yet earlier stage. This reversion to an earlier stage in the characters of the corallite is described as rejuvenescence and may be seen in such forms as *Parasmilia*, *Caninia*, *Cystiphyllum*, etc. This process may take place repeatedly in the growth of one corallite. If the explanation given above be the true one, then such a corallite has been formed by a succession of individuals, and is really a linear colony of corallites. This phenomenon appears to have been more common among Palæozoic than among later corals.

On the other hand among post-palæozoic corals longitudinal fission (Fig. 58) is the commoner phenomenon. In this case the polype becomes constricted along a plane parallel to its central axis. In the corallite this process is first indicated (Fig. 58) by an elongation and slight constriction of the calice, this becomes more and more marked with continued growth of the coral until the cup has divided into two. By evolving along similar lines various species of *Montlivaltia* gave rise to corresponding species of *Thecosmilia* (Trias-Tert.). A close packing against one another of the branches of the coral thus formed gave rise to *Isastræa*

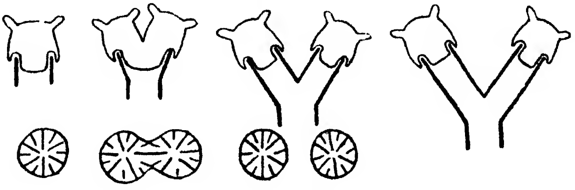


FIG. 58.—Diagrams showing mode of formation of a Compound Coral by fission of the Polypes without deposition of Cœnosteum. Lower line gives views of Calices in successive stages.

(Trias.-Cret.). It should be noted that all these phases in compound coral formation in this series were established before the close of the Trias. In the Jurassic genus *Thamnasteria* the epithecal walls had disappeared, and the septa of adjoining corallites became confluent.

It has been already seen that a similar series of phases in compound coral formation was exhibited by Palæozoic corals. Among Mesozoic forms another (Fig. 59), possibly retrogressive, phase was introduced for the first time. To produce this the process of fission of the polype was not completed, but the new polypes remained connected with one another by their bases. The elongated base thus produced secreted a correspondingly long and narrow calice, and thus gave rise to a condition described as meandriniform (*e.g.* *Comoseris*, Jur.-Tert.). At the *Thamnasteria* level in the series just described perforation of the septa sometimes takes place. In *Comoseris* this feature is very marked. In *Microsolenia* (Trias.-Jur.) both thecal walls and septa are riddled with perforations.

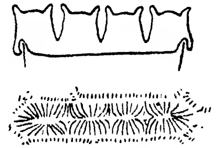


Fig. 59. — Diagram showing mode of origin of Meandriniform Corallite.

In the coral types, in which gemmation predominates, buds may be formed upon almost any part of the body from the margin of the base to the mouth, but they grow most frequently upon the edge-zone. When they appear in the vicinity of the mouth the resultant polypes tend to grow at the expense of the parent, which eventually dies and leaves its daughter or daughters in occupation of the calice. In the latter case there may be several new calices formed in place of the old one. In the former only one is produced, and the result is a condition comparable with that previously described as a linear colony.

In the majority of present-day corals the buds are produced upon the edge-zone (Fig. 60*A*) which appears to be capable not only of giving rise to any new polypes, but of growing indefinitely at its margin. This power must have been acquired some time during the Jurassic period. Each new polype as it arises begins to secrete a new corallite. The space between the corallites is filled up with calcareous material deposited by the under surface of the edge-zone. This calcareous infilling material is called cœnosteum and may be either solid or vesicular. Such cœnosteum appears in fossil forms apparently for the first time during the Jurassic in such genera as *Stylophora* and *Enallhelia*.

In compound as in solitary corals, there were some (Fig. 60*B*) in which the formation of canalicular connections took place between the edge-zone and the body cavity. This feature became especially marked from the Cretaceous onwards. Owing to the presence of these canals, which branched irregularly, the cœnosteum of these forms was spongy, and the walls of the corallites were perforated by numerous pores, *e.g. Dendrophyllia* (Tert.-Rec.). This structural change was carried to its acme by a group of forms represented by the genera *Goniopora* (Cret.-Pres.), *Porites* (Cret.-Rec.) and *Madrepora* (Tert.-Pres.). In them cœnosteum is absent and the skeleton as a whole consists of a delicate latticework of exceedingly fine mesh. This structural feature gave the double advantage of economy of calcareous material, and an intimate connection of the polypes one with another.

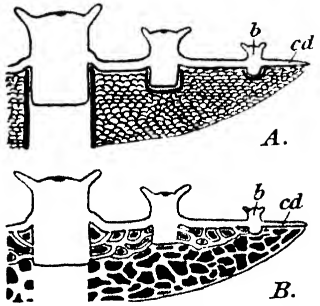


FIG. 60.—Diagrams showing mode of formation of a Compound Coral by growth of buds (*b*) upon the edge-zone, (*cd*) with deposition of Cœnosteum between the Corallites.

A has solid theca and vesicular or solid cœnosteum (compare Fig. 57 (*a*)). *B* has porose theca and porose cœnosteum (compare Fig. 57 (*b*)).

The anatomy of the polypes of these highly porous corals differs in certain fundamental respects from that of any of the other corals considered above. At the same time it resembles that of certain primitive, probably ancient, Zoantharia which do not secrete skeletons. For this reason it seems probable that these essentially modern types of reef-building corals did not arise from any pre-existing stock of reef-builders, but from some stock which did not develop the ability to form calcareous deposits until the Cretaceous period. The rod-like character of the deposit enabled them to produce a coral mass having a much more extended surface, and therefore bearing a greater number of polypes for a given weight of calcareous material than any previous type. With this and other great advantages they rapidly acquired that position of dominance upon the reefs which they possess to-day.

SECTION V

A DIGRESSION ON GENETIC AFFINITY

Before proceeding further with the study of fossils it is necessary to turn aside and consider more precisely what is meant by genetic relationship, and what are the implications it suggests. An organism is directly related to its parents and to its offspring. This relationship is described as genetic. In a series of genetically related organisms the connecting link between successive generations is a single cell, the fertilized germ. This is the only material link (Fig. 61) between parents and offspring, and whatever substance or tendency is passed from one to the other is contained in or carried by that cell, which as a rule is too small to be seen by the unaided eye. This cell divides and redivides repeatedly. The majority of the new cells so formed grow and multiply and ultimately produce the body or soma of the offspring, and become modified to form its special organs. A few cells however remain unmodified, and these give rise to new germ cells or gametes, either male or female. Some of the latter cells, in their turn, take a part in the formation of new fertilized gametes, each of which may grow into a new soma, and produce further gametes.

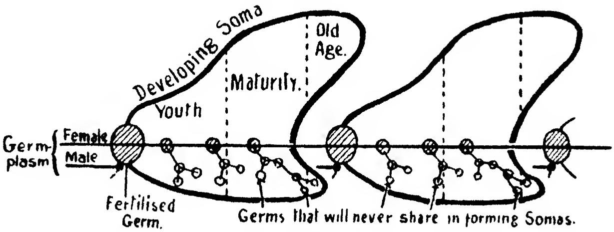


FIG. 61.—Diagram illustrating relationship of Soma to the Germ and Germplasm.

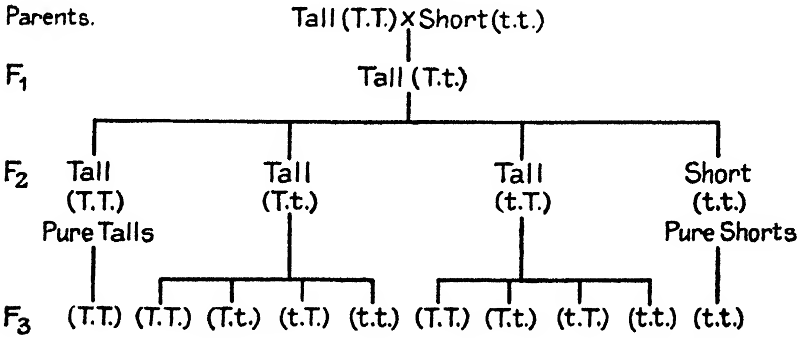
From this it is evident that the individual animal is not the producer, but the carrier, of the germ cells. The germ cells thus form an unbroken series of cells, from which at intervals new somas are produced. These somas and all the cells of which they consist die, but the substance of successive fertilized germs has continued uninterruptedly from the beginning of life upon the earth until now. This unbroken thread of germ substance contains the germplasm. The germplasm is the carrier of all the tendencies which are passed on from one generation to another, that is to say it is the material basis of heredity. The soma on the other hand is the physical expression of these tendencies. Thus the mesentery of a polype is not present in the germ, but there is something in the germ which causes certain groups of cells to become modelled into a mesentery.

The constitution of germplasm is extraordinarily stable, hence the close resemblance of the offspring to the parents. But it is not immutable. In studying the gens *Zaphrentis delanouei* it was seen that a series of gradual changes took place as time passed by, with the result that the soma at the close of the Lower Carboniferous differed in certain clearly recognizable respects from the soma at the beginning of that period. This series of changes can only be regarded as the outward and visible expression of changes taking place in the constitution of the germplasm. The real evolving entity therefore is the germplasm, the changes in which find expression at regular and repeated intervals in the somas. These latter merely develop and die, they do not evolve. It is a convenience, however, to speak of the evolution of *Zaphrentis delanouei*, since this is something tangible; moreover it furnishes the only means of studying the nature of the changes in the constitution of the germplasm in that long-past age.

The biologist approaches the study of these problems from a very different angle. Unlike the palæontologist he has not access to the somas of successive ages, but he has the advantages of access to the germplasm itself, and to the complete somas of the present age. Much light has been thrown upon the present constitution of gametes, and therefore of the germplasm, by the mode of experimentation associated with the name of Mendel. A brief description of one experiment must suffice.

Two varieties of edible pea were chosen, the one a tall variety, the other a dwarf variety. The first step taken was to cross-fertilize the flowers of these two types (Table V, page 71), that is to say the pollen of one was used to fertilize the ovule of the other. The seeds thus produced were sown and grew into what may be called the first filial generation (F_1); all the members of which were tall! The quality of shortness had apparently disappeared. The flowers borne by this first generation of peas were all self-fertilized, that is to say each was fertilized by means of its own pollen. The plants which grew from the resultant seeds may be called the second filial generation (F_2). Of these 75 per cent. were tall and 25 per cent. were dwarf. Evidently then the quality of shortness had not been suppressed in F_1, it was only overshadowed by the quality of tallness. Tallness is therefore described as being dominant, and shortness, recessive. The flowers borne by this second generation were also self-fertilized, and a third generation (F_3) was produced. This process was repeated for several generations. Those plants derived from the 25 per cent. dwarfs were all short. As long as their flowers were self-fertilized only dwarfs were produced, so that the quality of tallness had been quite eliminated. This proves that they were pure dwarfs, and therefore that their gametes were pure, that is were free from the tendency to produce tallness. Similarly 25 per cent. of the F_2 generation turned out to be pure talls. But the remaining 50 per cent. were mixed talls and dwarfs, for they continued to yield in successive generations pure talls, mixed talls and dwarfs, and pure dwarfs in the proportion of 25 : 50 : 25 in each generation.

Table V.



From these facts it follows that the qualities of tallness and dwarfness are not, in this case, characters which merge into one another to produce the character of medium height, when the gamete with the one is fertilized by a gamete with the other character. On the contrary they are entities, which remain independent of one another, and may be followed unerringly and separated out at the will of the experimenter. This independence has been established for a number of other characters in peas, such as the arrangement of the flowers upon the stalk, the colour and shape of the pods, the colour of the seed, etc. It is still more strikingly manifested when two pairs of characters are made the subject of experiment. If tall peas having purple flowers be crossed with dwarf peas having white flowers the first generation consists of tall purple-flowered peas only. From these, however, there may be produced not only pure strains like the original parents, but also pure strains of tall plants having *white* flowers, and dwarf plants having *purple* flowers. Thus the characters are so independent that they may be taken out of one stock and transferred to another to produce a new variety of plant. The general impression produced by such experimentation is that an organism is made up of a combination of characters, and the germplasm a combination of tendencies, which under favourable conditions may be shuffled about from one stock to another. This throws a flood of light on the origin of varieties and on the phenomena of variation or variability.

Thus the work of the palæontologist and of the experimental biologist agree in indicating that an organism is built up of a number of unit characters, which though they may be to some extent correlated with one another have nevertheless a considerable degree of independence. The unit in these two cases is not, however, precisely the same. In experimental work it is usual to think of the unit character in terms of the fully developed condition seen in an adult. That may be described as an *hereditary unit.* In palæontological work the structural unit undergoes a series of changes during the course of evolution. Thus in *Z. delanouei* the cardinal septum underwent progressive shortening, other septa gradual elongation. The palæontologist's independent unit is a series of changes which may be passed through by a given structural element during a long succession of generations and may be usefully referred to as an *evolutionary unit.*

The key to the understanding of the relationships of these units to one another is provided by individual development. During its growth a short pea passes through a series of changes identical with those passed through by a tall pea in its youthful stages. From this it follows that the difference between the two does not lie in the absolute height of the full-grown plant but in the rate and extent of change during lifetime. In dealing with *Z. delanouei* it was seen that the sequence of changes undergone by any one structural element during growth and during evolution was identical.

The important and valuable results of experimental work upon two extreme conditions of one structural element must not be allowed to divert attention from the graded series of variations which may actually exist in nature between these two extremes. Under natural conditions breeding is not restricted to specially selected pairs of individuals but takes place freely between the members of a community. Thus the wide and graded range of variation with respect to one morphological element is maintained from generation to generation.

Hitherto only one structural element, and the changes it undergoes, have been considered. But an organism is made up of many such elements. In the course both of evolution and development a series of changes may be experienced by one structure quite independently of the series experienced by any other structure. Thus the behaviour of a septum in a coral is independent of that of a dissepiment.

Such facts and considerations make it evident that, whilst the evolution of a structural element is always, and that of a species often, gradual, it is quite possible that a striking new species or variety may arise suddenly by the transference of an element in an advanced stage of evolution from one type to another in which it is less advanced.

It must always be borne in mind that a natural species consists of a multitude of individuals living on the landscape. These may be referred to collectively as a community. An experimenter naturally thinks in terms of a succession of individuals forming what may be called a *line of descent.* For the palæontologist there is strictly no such line, for he must think in terms of successive communities each produced from its predecessor as the result of free interbreeding. The lines, which in hereditary diagrams link parent to offspring, become multiplied a thousandfold and more in diagrams of successive descendant communities, and are seen to be constituent parts of a highly complex network or *plexus of descent.* One important contribution that experimental work has made to palæontological studies is that it has gone a long way towards the elucidation of the detailed structure of the plexus of descent.

SECTION VI

VERMES

The Annelida.—For no organisms is the palæontological record so incomplete as for that heterogeneous assemblage included under the term Vermes or worms. This is because they are all soft-bodied animals, and it is only under exceptional circumstances that they have been preserved as fossils. Such conditions existed for a short while during the early Palæozoic times in the region of Mount St. Stephen, British Columbia ; for the Middle Cambrian rocks there have yielded a suite of exquisitely preserved remains of many delicate organisms including some worms.

Worms exhibit a wide diversity of form, structure, and mode of life. It is on this account that zoologists divided them into a number of separate phyla of which the Annelida include the most highly organized. The majority of Annelida live in the sea. A few live in fresh-water, or, like the common earthworm, in the soil. They may be classed according to their mode of life into active and sedentary worms. Active annelids swim freely in pursuit of prey or crawl along the sea-floor, or they may hide beneath stones or burrow in the sand and mud. The tracks and the burrows they make are sometimes common features in rocks that yield no other traces of organic remains. Some are predaceous forms, and are provided with horny jaws. These latter are the only portions which occur as fossils with any frequency. Some sedentary worms also live in burrows, which they line with tubes made up of fragments of sand and shells fastened together. Others secrete tubes of lime, which may be aggregated in masses or be attached singly to stones or shells or other objects on the sea-floor. *Serpula* and *Spirorbis* are fossil examples of such.

To the palæontologist the interest of worms, especially of the annelids, is mainly a theoretical one ; for they represent the ancestral stock from which other groups of higher animals have been derived. Some knowledge of their development and structure is therefore essential to a full understanding of many of the problems suggested by the fossil remains of those higher groups. For this purpose a simple annelid (*Polygordius*) from the Mediterranean and the North Sea, may be briefly described.

Polygordius (Fig. 62) has a long slender body. At its front end is a fleshy lobe, the prostomium, which bears the sense organs. These latter consist of a pair of short tentacles and a pair of black spots or eyes. Behind and beneath the lobe is the mouth. The remainder of the body is made up of numerous divisions, or segments, all very much alike externally and internally, so that a thin section cut across one segment gives an idea of the structure of all. In the centre is a space, the cavity of the alimentary or digestive canal, the wall of which is lined by a layer of endoderm cells, and is encased in a thick layer of muscle. Outside this is a cavity, the cœlome or body cavity in which are lodged blood vessels, excretory and reproductive organs. Around the cavity is the body wall consisting of a thick layer of muscle covered externally by a single layer of ectoderm cells. Polygordius thus resembles Obelia in possessing ectoderm and endoderm, but differs in having the space between these layers filled with a complex mass of tissue called mesoderm, from which the various vital organs are derived. The presence of mesoderm carries the animal organization to a much more advanced stage than that seen in the Cœlentera, and is a characteristic feature of the annelids and of all the higher animal types.

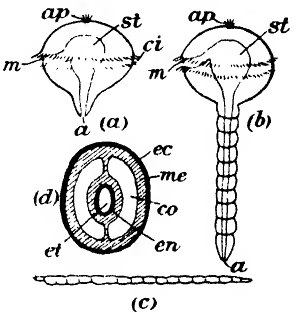


FIG. 62.—Development of an Annelid (*Polygordius*).

(*a*) Trochophore larva. (*b*) Annelid developing from the larva (*a* and *b*, after MacBride). (*c*) Adult annelid. (*d*) Transverse section showing structure of the Annelid (compare Fig. 4, *b*).
ec, ectoderm. *en*, endoderm. *me*, mesoderm. *co*, cœlome. *et*, enteron. *m*, mouth. *a*, anus. *st*, stomach. *ci*, cilia. *ap*, apical disc.

At a very early stage in the development of *Polygordius*, the embryo, whilst still quite unlike the parent, escapes from the egg, and begins to lead a free life seeking its own food. That is to say it becomes a larva. This larva bears a superficial resemblance to a minute medusoid jellyfish, but differs from that in many fundamental respects. It is shaped more or less like a top and propels itself through the water by means of numerous short motile processes or cilia arranged in two rows at the circumference of the thickest part. The mouth is situated between these two rows which thus mark off the upper from the lower portion of the body. The mouth leads into an alimentary canal, which passes through the body and eventually opens to the exterior at the apex of the post-oral region by an aperture called the vent or anus. The surface of the body consists of ectoderm, and the wall of the digestive canal of endoderm. Between is a space in which various organs lie. In the region of the anus, however, this space contains mesoderm. A larva exhibiting these peculiarities of form and structure is described as a Trochophore larva.

The change or metamorphosis from the larval into the adult condition is brought about by the elongation of the narrow portion of the lower part of the body. As this elongates it becomes segmented, new segments being added just above, that is anterior to, the anus. Whilst this region increases to the worm-like proportions of the adult the prostomial region with tentacles and eye-spots develops, and unites with the worm-like body. Any remnants of the trochophore that are left are shed. Many marine worms pass through a similar metamorphosis from a trochophore larva. This fact suggests that this larva represents more or less accurately an ancestral stage in the evolution of the Annelida.

SECTION VII

BRACHIOPODA

The Development and Structure of a Typical Brachiopod.—The Brachiopods, or Lamp-shells, are all salt-water animals. As their popular name implies, the shell as a whole, when held in a certain position, is not unlike an ancient lamp in form. It consists of two valves (dorsal and ventral) which correspond in their relationship to one another with the upper and lower portions of the lamp. At one end there is a hole which suggests the place for the wick, through which there emerges during life a fleshy stalk by means of which the creature is attached to some object on the sea-floor. The changes undergone by this opening during the evolution of the Brachiopods have provided a useful basis for their classification. In the Atremata, as this name implies, no such special opening exists. On the other hand in the Telotremata it attains its most perfect development. The anatomy of the animal is comparatively simple, and its main features may be easily grasped by making a brief study and comparison of the development of two living forms, viz. *Terebratulina* and *Lingula* which represent the Telotremata and Atremata respectively. As with so many marine organisms the eggs of a brachiopod are small and when they hatch there issues forth from each a minute larva (Fig. 63) quite unlike the parent. At first this little creature swims about freely in the water by means of numerous vibratile cilia. At a late stage in larval development the body of *Terebratulina* is marked by two constrictions which divide it into three parts; the anterior, or head; the posterior, or foot; and the one between, which bears a pair of folds of the body wall, called the dorsal and ventral mantle lobes respectively. After a brief period of free life the creature attaches itself to some object upon the sea-floor by means of the " foot " which elongates slightly, and forms the stalk or pedicle; the mantle-folds also flap upwards, and enclose the " head." In Lingula a fundamental difference manifests itself at this critical stage of development. The mantle-folds here retain their original attitude, and the stalk develops as an outgrowth from the ventral fold. These differences are associated with other features some of which are recognizable in the adult shell. Here, then, is a basis upon which the Brachiopoda may be divided into two major sections, viz. the *Pygocaulia*, in which the pedicle is formed from the tail segment of the larva; and the *Gastrocaulia*, in which it develops from the ventral mantle lobe. These two probably separated from one another at a very early stage in the evolution of the Brachiopoda. In *Terebratulina* these folds are at first practically equal in size; but the ventral lobe outstrips the dorsal in growth, and becomes the larger of the two. Each fold now secretes a shell upon its outer surface, and thus the central and anterior parts of the body becomes enclosed in a protective covering consisting of two valves.

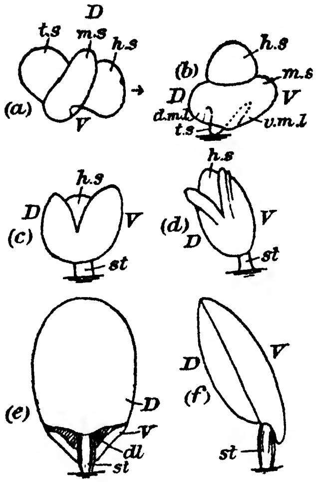


Fig. 63.—The Development of a Brachiopod (*Terebratulina septentrionalis*).

(*a*) Free-swimming larva (after Conklin). (*b*) Larva just becoming fixed by means of its tail segment. (*c*) Stage at which mantle lobes have flapped forwards over the head segment. (*d*) Later stage, showing same condition. (*e*) Dorsal view, after formation of embryonic shell. (*f*) Side view, after formation of embryonic shell. (*b–f*, after Morse).

D, Dorsal. *V*, Ventral. *h.s*, head segment. *m.s*, mantle segment. *t.s*, tail segment. *d.m.l*, dorsal mantle lobe, *v.m.l*, ventral mantle lobe. *st*, stalk. *dl*, delthyrium.

Meanwhile a mouth has appeared upon the "head." Dorsally to the mouth tentacles grow out which, as they multiply in numbers, extend in a semicircular, and then circular, fashion until they meet upon the ventral side of the mouth. On either side of this circle a lobe-like outgrowth of the head appears, and as it grows carries the laterally placed tentacles with it. Thus a horseshoe-shaped, tentacle-bearing organ is produced, which is called the lophophore. At a later stage a median lobe grows out dorsally. This likewise bears tentacles upon its margin, and may become coiled upon itself as its length increases. The lophophore is provided with cilia which by their movements set up currents in the water. These flow towards the mouth and carry with them the minute organisms upon which the brachiopod feeds.

Whilst all these changes have been taking place the mantle has been growing and secreting more shelly material. The shell is at first little more than a thin horny pellicle, and at this early stage it is described as the *proteguIum*. In Gastrocaulia the shell usually becomes strengthened in subsequent development by the deposition of calcium phosphate. In Pygocaulia calcium carbonate is added in fibrous and prismatic form to the inner surface, and to the margins. The successive additions are indicated on the outer surface by fine lines (growth lines) which are concentric with one another. From the arrangement of these it is easy to see that the shell grows most rapidly along its anterior margin, and that very little additional material is deposited posteriorly. The point about which the growth lines are concentric lies on or near to the posterior margin and is called the umbo. That of the ventral valve is much larger and more conspicuous than the other.

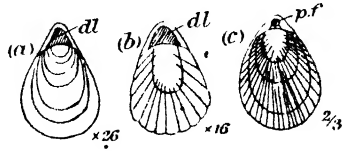


FIG. 64.—Stages in growth of Shell of *Terebratulina septentrionalis*.

(*a*) Protegulum. (*b*) Neanic shell. (*c*) Ephebic. (*a*, *b*, after Beecher, *c*, after Davidson).
dl, delthyrium bounded on either side by the palintrope. *p.f*, pedicle foramen.

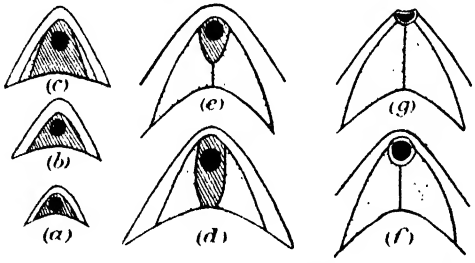


FIG. 65.—Diagrams illustrating the General Changes in the region of the Pedicle Opening of one of the Telotremata during development and evolution.

Black = cross-section of the pedicle. Lined area = dethyrial opening. Dotted areas = deltidial plates. *a*–*g* gives the order of the stages.

Between the umbo and the posterior margin of the valve the growth of the shell undergoes a reversal of direction from posterior to anterior with the result that this portion of the margin folds inwards towards the cavity of the shell. This infolded portion (Fig. 64) is variously named *palintrope*, *interarea*, *cardinal area* and is much more extensive in the ventral than the dorsal valve. With further growth a triangular notch, the *delthyrium*, appears in the ventral palintrope and gives passage to the pedicle. A shell margin exhibiting this feature is said to be *mixoperipheral*. At first the stalk is stout in proportion to the whole animal and occupies the whole delthyrium. During further growth the stalk does not keep pace with the rest of the body, and thus comes to occupy relatively less and less of the delthyrial space. At the same time the posterior margin of the ventral mantle lobe extends round the stalk on to its dorsal side, and there secretes a pair of small plates (deltidial plates) in that part of the delthyrium left unoccupied by the stalk (Fig. 65). At first these are mere splints lying along the lateral margins of the delthyrium. Each plate, however, as it grows, becomes triangular in shape with its base in a line with the margin of the valve. As the two bases extend they meet in the middle line of the delthyrium and thus complete a shelly boundary around the actual opening through which the pedicle passes. This opening is now oval in outline, but with the further growth of the deltidial plates, and extension of the line of junction between them, it becomes relatively smaller and more circular. This continued growth of the plates seems as though it must lead eventually to a crushing of the pedicle against the umbonal margin of the valve. Such fate is, however, avoided, because the material of this margin undergoes reabsorption, and the pedicle opening actually travels a short distance into the substance of the ventral valve, and in the adult even occupies the site of the ventral umbo.

At the two points where the valves are in contact on either side of the delthyrium a pair of processes, called teeth, grow out (Fig. 74) from the margin of the ventral valve, and project into hollows or sockets in the corresponding positions on the dorsal valve. Thus a hinge is produced and the line which passes through the two points is therefore called the hinge line. Between the sockets a stout process grows and projects into the cavity of the shell. This is the cardinal process. To the inner margin of the sockets there is attached, in the adult shell, a complex calcareous framework (Fig. 77) which supports the base of the lophophore and is called the brachidium. The animal is furnished with two sets of muscles. One works the pedicle, and enables the creature to alter its position within the radius of this organ. The other opens and closes the valves. These are all attached to the inner surface of the shell and make marks which, with care, can be seen in fossils and be used for systematic purposes.

Changes in and about the Pedicle Opening.—If the growth of a brachiopod shell proceeded at the same rate upon all margins, each valve would be conical in shape and have its umbo centrally placed and at the apex of the cone. Usually, however, it is less rapid on the posterior margin than upon any other, and consequently the umbo tends always to lie nearer to this margin. Such is the condition (Fig. 66) in *Paterina* and *Rustella* (L. Cam.), which approximate closely to the ancestral forms of the Gastrocaulia and Pygocaulia respectively. In them the two valves are of almost equal size, the ventral being only slightly larger than the dorsal. The umbo of this valve is also more conspicuous. Both valves in *Rustella* are convex, and together they make a biconvex or lens-shaped shell of oval outline. In this and other respects it resembles the protegulum of many brachiopods.

In *Obolus* (L. Cam.-Ord.) and other very primitive Gastrocaulia the pedicle passes out from the shell between the posterior margins of the valves. They possess no delthyrium, that is to say there is no notch, in this margin of the valves, caused by the cessation in deposition of shelly matter around the pedicle, and consequently there is no break in the growth lines, but these can be followed completely across the posterior surface of the valve. Such uninterrupted growth produces a continuous or holoperipheral shell margin. This condition in which no delthyrial opening exists is described as atrematous, and characterizes many Cambrian and early Ordovician forms.

In other forms these lines, as they pass round the pedicle, are deviated away from the plane which separates the valves. That portion of the posterior surface over which they are thus deviated is more conspicuously marked on the ventral than the dorsal valve.

More frequently, however, the deposition of shelly material does not take place along this portion of the posterior margin and, consequently as in *Paterina* (Fig. 66) a notch is produced in each valve which has the characters of a true delthyrium.

In this case the margin of the shell is not continuous and is accordingly said to be hemiperipheral.

From such a condition arose one in which (Figs. 67, 70) the delthyrium became confined to the ventral valve from the outset. In it, as the pedicle decreased relatively, the ventral mantle extended round to its posterior or dorsal side and united there to form a continuous mantle margin. Shelly material was now deposited here in continuity with the rest of the shell, and as the growth lines were no longer broken a holoperipheral condition was resumed. The pedicle opening now presented the appearance of being merely an opening through the substance of the shell itself, and with the growth of the shell was carried further and further away from the margin. This condition is described as neotrematous.

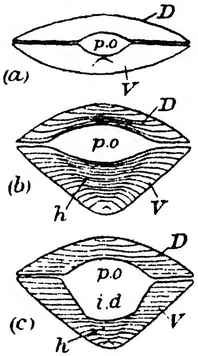


FIG. 66. — Posterior Margin of primitive shells.

(*a*) *Rustella.* (*b*, *c*) *Paterina.*

D, dorsal valve. *V*, ventral valve. *p.o*, pedicle opening. *h*, continuous growth lines. *i.d*, incipient delthyrium in a hemiperipheral margin.

Rustella, which may be regarded as the most primitive known member of the Pygocaulia, possesses a rudimentary palintrope notched by a delthyrium in both valves. This condition is described as palæotrematous. In subsequent stages of evolution the palintrope became more clearly defined and the delthyrium as a whole was diamond-shaped (Fig. 71), owing to the presence of a triangular notch on both valves. There was always a tendency, however, for that in the ventral valve to become the more prominent, and that in the dorsal to disappear. As in development, so in evolution, the stalk decreased in calibre relatively to that of the body. Consequently the delthyrial space became partially vacated, and thus the pedicle opening ceased to coincide in extent with the delthyrial opening. The vacated area frequently became filled with shelly or calcareous material, but several divergent methods of forming this were employed. These are sufficiently distinctive to be of value for differentiating other stocks of Pygocaulia from one another.

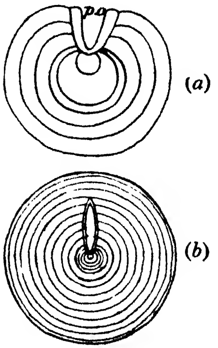


FIG. 67.—Neotrematous Shell. Ventral Valve.

(a) Young shell of *Orbiculoidea minuta* (from Beecher).
(b) Adult shell of *O. circa* (modified from Billings).

In one of these stocks some members exhibited a neotrematous condition during the earliest growth stages (Fig. 68*a*.) In this case, however, the pedicle degenerated and ultimately disappeared, meanwhile its opening remained minute or became completely sealed. During later growth a palintrope with delthyrial notch was formed. The latter became more or less fully closed by the deposition of a convex calcareous plate across it (d.p.). This was secreted by that portion of the ventral mantle lobe which adjoined the pedicle.

A similar plate, called the chilidium, closed up the dorsal notch. Such was the protrematous condition.

In the other stock deltidial plates (Fig. 65) of the kind described on a previous page were formed. The various stages there described in development are paralleled in the adult shell among fossil forms, especially during the Silurian to Carboniferous periods. In Mesozoic and later members of this stock the plates were usually fully formed, and the pedicle opening usually encroached to a greater or less extent upon the umbo. These phases all characterize the telotrematous condition.

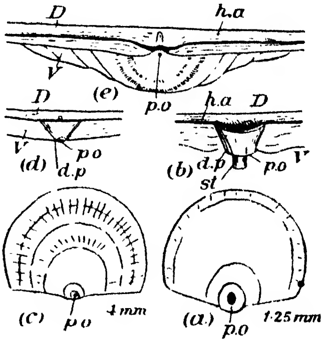


FIG. 68.—Development of a Protrematous Shell *Leptæna rhomboidalis*) (modified from Beecher and Clarke.)

(*a*) Ventral valve of shell, 1·25 mm. diameter. (*b*) Posterior margin. (*c*) Ventral valve of shell 4·0 mm. diameter. (*d*) Posterior margin. (*e*) Posterior margin of adult shell.
D, dorsal valve. *V*, ventral valve. *h.a*, hinge area, palintrope. *p.o*, pedicle opening. *st*, pedicle. *dp*, deltidial plate.

Independently of the changes just described there was a tendency for the palintrope to vary greatly in its extent. Along the hinge margin it may be shorter than the general width of the shell or it may be longer. Its height, from margin to umbo, may be small and markedly concave, or it may be great and flat or even slightly convex.

Five orders of brachiopods characterized by these differing conditions are recognized and are classed as the Atremata, Neotremata, Palæotremata, Protremata, and Telotremata respectively.

Major Changes in the Form of the Shell.—The nearest approximation to what is believed to be the primeval form of the brachiopod shell is that exhibited by *Rustella* (Figs. 66*a*, 69*a*, *b*). In this genus the shell is transversely oval and biconvex, and the ventral valve is slightly larger than the dorsal. Judging by the relative size of the pedicle opening the pedicle must have been stout enough to hold the shell in a perpendicular position similar to that shown in the very young *Terebratulina* (Fig. 63).

The changes of form experienced by the Atremata may be illustrated by the series of genera *Obolus* (Fig. 69*c*, *d*), *Lingulella* and *Lingula* (Fig. 69*e*). In the first genus the shell is usually transversely oval. In the second it becomes more or less elongated along the antero-posterior axis, while in the last it is always much elongated in that direction. In all three forms the palintrope is vertical, that is to say it lies in the plane which separates the two valves. On the ventral valve, this area is marked by a groove from the margin to the umbo, in which the pedicle must have lain during life, a fact which may be taken to indicate that the usual attitude of the shell was vertical. This is certainly the attitude in the living *Lingula*. This form lives with its stalk anchored deep in the fine sand. When the stalk contracts the shell is withdrawn into the sand, when it extends the shell is pushed up until its anterior margin is almost flush with the surface. It may be that in the elongation of the shell, and the sharpening of the valves at their posterior end, a progressive adaptation to such a sand-dwelling habit is manifested in *Lingulella*. The equality of the valves, and the almost complete suppression of the "palintrope" in *Lingula* appear to be further adaptations to this habitat.

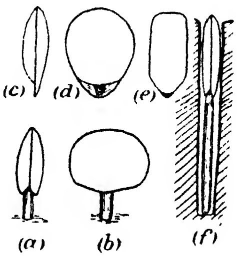


FIG. 69.—Diagrams showing form of Shell among *Atremata*.

(*a*, *b*) Hypothetical reproduction of *Rustella* attached by a pedicle. (*c*, *d*) Side and dorsal view of *Obolus* (after Walcot). (*e*) Dorsal view of *Lingula*. (*f*) Side view of *Lingula* with its stalk attached to the bottom of a hole in the sand.

Any departure from the vertical attitude for the shell must be a falling over on to either the ventral or the dorsal valve. The former was usually the case among the Neotremata (Fig. 70). In association with this new position the plane of separation between the valves rotated away from axis of the pedicle and came to lie more or less at right angles to this. In *Obolella* (L. Camb.) the form of the shell showed no marked departure from the primitive form seen in the earlier atrematous genera. In *Acrotreta* (Camb.-Ord.) the ventral valve tended to become like a tall inverted cone with the pedicle emerging near the apex, but the dorsal valve retained the more primitive form and rested on the base of the cone like a lid or an operculum. In *Orbiculoidea* (Ord.-Cret.) the organic centre or umbo of the ventral valve shifted along with the pedicle opening towards the geometric centre (Fig. 67). The outline of the shell became nearly circular and thus provides among the brachiopods an example of the tendency of fixed animals to become radially symmetrical. In *Crania* (Ord.-Pres.) the pedicle was suppressed in later life and the ventral valve became cemented to the ground (Fig. 70*c*).

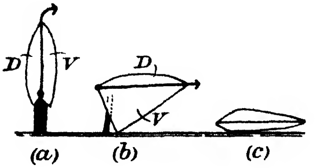


FIG. 70.—Shape and attitude of Shell among *Neotremata*.

(*a*) Hypothetical ancestral condition, cp. *Rustella*. (*b*) *Acrotreta* with pedicle restored. (*c*) *Crania* cemented to substratum. *D*, Dorsal valve. *V*, Ventral valve. Arrow suggests direction in which the shell has fallen phylogenetically.

Among Protremata and Telotremata the shell appears either to have remained erect or to have fallen over (Fig. 71) towards the dorsal side so that the ventral valve came to lie uppermost. In both of these great groups the general outline of the shell was largely affected by the character of the hinge line. This either remained short and curved (Fig. 71*f*) as in the primitive members of the two orders already mentioned, or it became elongated and straight (Fig. 71*g*).

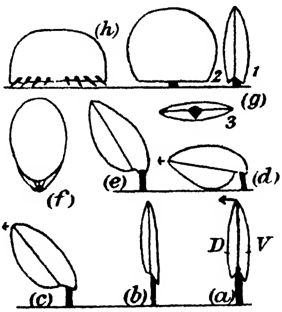


FIG. 71.—Shape and attitude of Shell among *Protremata*.

(*a*) Hypothetical ancestral condition. (*b–f*) Attitude and form in those having moderately long pedicle. (*g*) Attitude and form in those with very short pedicle. (*h*) Form attached by spines.

In forms in which the hinge-line remains short and curved (Fig. 71*a–f*) it is probable that the stalk was of sufficient length to allow of some movement of the shell as a whole. In them the general tendency was for the shell to elongate slightly in an antero-posterior direction, and for both valves to be markedly convex.

It has been suggested that the long straight hinge-line was associated with the presence of a stalk so short that the posterior margin of the shell lay close to the ground. Among those Protremata such as the Strophomenacea, in which this feature attained its maximum development there was a marked tendency for the two valves to become bent in the same direction and thus for the shell as a whole to assume a concavo-convex form. This peculiarity does not show itself among the straight-hinged members of the Telotremata (*e.g.* many Spiriferacea). In the Strophomenacea the pedicle, which was partly enclosed in a calcareous tube, became relatively more and more insignificant and in a larger number of forms it even disappeared (Fig. 68). Whilst some of these must have lain loose upon the ground others such as *Chonetes* (Ord.-Perm. Fig. 71*h*) and *Productus* (Camb.-Perm.) developed long spines, which among other functions may also have provided a means of attachment or of anchorage upon the mud.

Within the limits of these broad changes of shape there was much detailed variation. Indeed even for the individual there appears to be no such thing as fixity of shape, as this undergoes quite regular changes during its lifetime. The case of *Atrypa reticularis* (Sil.-Dev.) will serve to illustrate this. In this brachiopod (Fig. 72) in very early life both valves are only slightly convex. The palintrope of the ventral valve slopes away from the dorsal valve as it passes from hinge-line to umbo. With increasing age, however, the valves become more and more convex, whilst the palintrope rotates around the hinge-line carrying the ventral umbo closer and yet closer to the dorsal valve, until at last it touches this, and no space is left for the exit of the peduncle. Other changes in the shape of this brachiopod are reflected in the line of separation between the two valves at the anterior margin (Fig. 72). In the earliest stages of development this line exhibits a gentle bend in the middle towards the ventral side. As growth proceeds this fold flattens out, and the marginal line becomes straight. Finally it bends once more but this time towards the dorsal side.

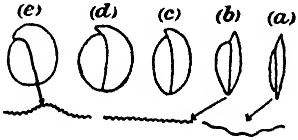


FIG. 72.—*Atrypa reticularis*, development. Side view showing Shapes at different stages in Development, having the following length of Shell.

(*a*) 2·25 mm. (*b*) 4 mm. (*c*) 7 mm. (*d*) 20·0 mm. (*e*) 24 mm.

Lower line of figures shows condition of anterior free margin of valves. (*a*) sulcate. (*e*) plicate.

[Based on Beecher and Clarke.

Again a wide range of form may be exhibited by the individuals in a large collection of specimens belonging to the same species. Thus in *Reticularia lineata* (Carb.-Lmst., Castleton, Derbyshire), there are broad forms and narrow forms, stout and thin forms; some with the umbo twisted to the right, others with it twisted to the left. The reasons for regarding all these as coming under the one specific name may be understood by a brief consideration of certain measurements which were made upon about one thousand individuals. One set of these measurements must suffice for the purpose, namely, those which gave the ratio of the length to the breadth. This ratio was plotted (Fig. 73) against the number of individuals measured as shown in the accompanying graph. The specimens having a ratio greater than 1·2 were evidently narrow forms, those with a ratio of less than 0·7 were broad. These represent the extremes. They were few in number, and therefore could not be regarded as typical of the species. The number having a ratio between 0·9 and 0·8 was greater than for any other ratio. This ratio is therefore to be considered as the typical one. The way in which the graphs rise up to, and fall away from, an apex in the neighbourhood of this ratio, shows that the deviations from this central type form a continuous series, and that therefore all the specimens taken together form a compact assemblage. Had there been two crests in the curve that would have shown that the collection contained specimens belonging to two species, or tending to form two species. These facts illustrate the idea that a species has not fixed and easily defined characters but is the subject of numerous grades of variation within certain limits.

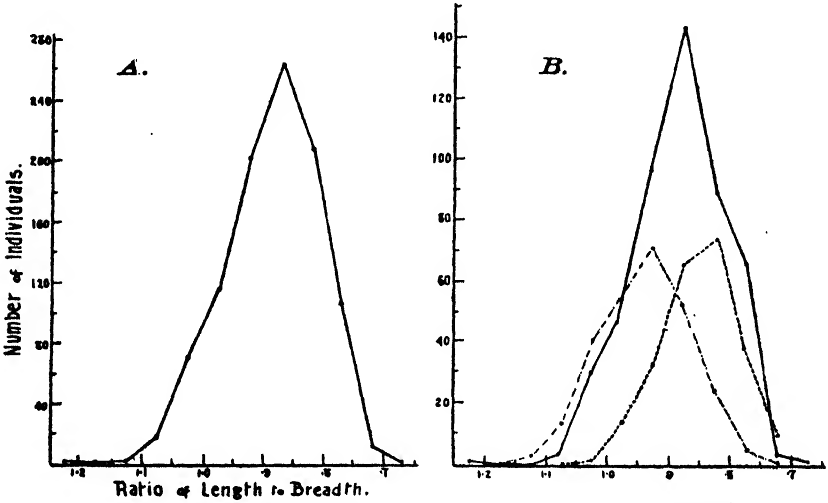


FIG. 73.—Graphs showing the Frequency Distribution of the ratio $\frac{\text{Length}}{\text{Breadth}}$ among 1,000 Individuals of *Reticularia lineata*.

(*A*) Without relationship to age. (*B*) Individuals grouped according to size; and therefore in all probability according to age.

Dot-dash line = individuals with length 0·15–0·45 in.
Continuous line = " " " 0·45–0·75 in.
Dotted line = " " " 0·75–1·05 in.

[From Day.

Among the thousand specimens thus examined there were specimens of various sizes and obviously of differing ages. They were therefore divided into three groups having the following lengths: 0·15 mm.–0·45 mm., 0·45 mm.–0·75 mm., 0·75 mm.–1·05 mm., and a similar graph to that just studied was constructed (Fig. 73B) for each group.. An inspection of these graphs reveals the interesting fact that the ratio exhibited by the greatest number in each group changes during life from a narrower to a broader type. Whether a similar change took place during the evolution of *Reticularia lineata* cannot be stated, for all the specimens were apparently from one horizon. The history of *Zaphrentis delanouei* (see p. 52) suggests that such a change did probably take place.

Internal Structural Features.—In the most primitive brachiopods the margin of the valves is of uniform character all round, and exhibits no indication of special thickening or thinning in any part. Such was the condition probably in all Precambrian and certainly in the majority of Cambrian forms, which included representatives of all the orders except the Telotremata. During the Lower Cambrian, however, a few forms exhibited a tendency to acquire a genuine articulation between the two valves. The appearance of the first rudiments of this marked a new era in the evolution of the brachiopod, and opened for the phylum a new lease of life and vigour.

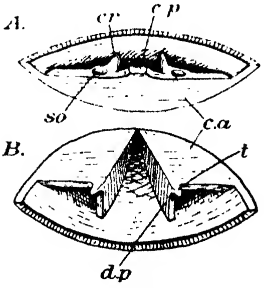


FIG. 74.—Diagrams illustrating the Structural Features of the Hinge Margin. *A*, dorsal valve. *B*, ventral valve. *c.a*, palintrope. *c.p*, cardinal process. *cr*, crura. *d.p*, dental plate. *so*, socket. *t*, tooth.

The structural changes involved a thickening of the hinge margin, the growth of a pair of blunt processes (teeth) on the ventral valve, and the formation of a pair of shallow sockets on the dorsal valve on either side of the pedicle opening. The first beginnings of such changes seem to have been exhibited as early as the Lower Cambrian by some advanced members of the Palæotremata (*Kutorgina*) (L.-U. Cam.). In certain primitive Protremata such as *Billingsella* (L. Cam.) and *Eoorthis* (M. Cam.-Ord.) both teeth and sockets were already well formed, and further accessory structures had been added. In the ventral valves of these two genera (cp. Fig. 74) a pair of vertical plates extended across the cavity of the shell below the umbo from the margin of the delthyrium to the inner surface of the valve. The presence of these plates strengthened the delthyrial margin, and by so doing provided a strong support for the cardinal teeth, which in reality project as a continuation of that margin. These two plates usually have the name of dental plates, though in actual practice they do not always form a direct support to the teeth. The triangular space between these dental plates was occupied by the muscles which worked the pedicle and closed the valves. In the dorsal valve two accessory structures appeared. The one was the cardinal process which by projecting slightly into the cavity of the shell, and providing a point of attachment for the muscles which open the valves, functioned as a short lever. The other accessory structure was a pair of crura. These were slight expansions of the hinge margin which projected into the cavity of the shell from between the sockets.

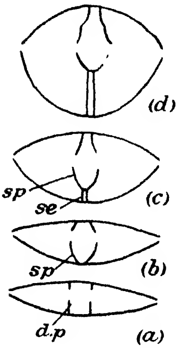


Fig. 75.—Diagrams showing mode of evolution of Spondylium and Septum along with the increasing convexity of the Valves.

dp, dental plates. *sp*, spondylium. *se*, septum. (*d*) after Shipley.

Such then was the condition of the hinge and internal features in the Protremata. In many forms, *e.g. Orthis* (Ord.-Sil.) *Strophomena* (Ord.) and *Productus* (Carb.-Perm.), in which the hinge margin tended to elongate in a straight line, and the space between the valves remained restricted, this condition underwent but little modification. In others, *e.g. Syntrophia* (M. Cam.-L. Ord.), *Conchidium* (Sil.-Dev.) and *Pentamerus* (Sil.), in which the hinge margin was short and curved, the valves bulged considerably away from one another and left a spacious internal cavity, further modification of these structures took place (Fig. 75). The ventral edges of the dental plates became united with one another (Fig. 75*b*) and the spoon-shaped structure, the spondylium, thus formed carried the muscle attachments. At the same time a single vertical plate, or a pair, arose from the inner surface of the shell and supported the spondylium on their free margins (Fig. 75*c*, *d*). A similar but less advanced change took place in the dorsal valve. Plate-like outgrowths appeared between the crura which like the spondylium bore the muscle attachments. These either remained separate, or became supported by a pair of plates or by only one.

During the Ordovician and Silurian periods there came into prominence another internal structural feature, the ***brachidium***. This was a calcareous framework, which according to the degree of its development provided a more or less complete support for the lophophore. This feature was to a large extent the structural descendant of the crura, and occurred only in the Telotremata.

In the earliest and most primitive Telotremata, viz. *Protorhyncha*, the crura were absent. In one large section of the order, Rhynchonellacea, to which *Rhynchonella* (Jur.-Cret.) and many allied forms belong, the crura are present, but do not exhibit any change in character beyond progressive lengthening and retrogressive shortening. Among the other Telotremata a wide range of further changes takes place, a clear appreciation of which may be gained by a consideration of the development of these parts in *Zygospira* (Ord.-Sil.).

In the very young *Zygospira* (Fig. 76) extensions from the crura are produced which expand distally and by uniting with one another form a loop (*a*). These extensions are called lamellæ to distinguish them from the crura. With further development the extremity of this loop became reabsorbed so that the loop now had the appearance of two lamellæ united by a cross connection or jugum (*b*). At first the lamellæ projected only slightly beyond the jugum as two little processes, but in subsequent development they elongated greatly (*c*) and coiled up into a pair of spirals (*d*). Further coiling took place in *Retzia* (*e*, *f*). *Zygospira* existed in Ordovician times, so that already within the limits of that period, this complicated type of brachidium had evolved, and evolved rapidly from simple crural processes. Through the remainder of the Palæozoic era numerous brachiopods, including such familiar genera as *Spirifer* (Dev.-Per.), *Atrypa* (Ord.-Dev.), possessed a similarly complicated brachidium. These are grouped together as the Spiriferacea. But though this group became an abundant and very varied element in the later Palæozoic fauna no new feature was added to its brachidium. Such changes as this experienced were rung upon structures already present in Ordovician genera ; thus the jugum was shifted in position and the spires were readjusted in attitude.

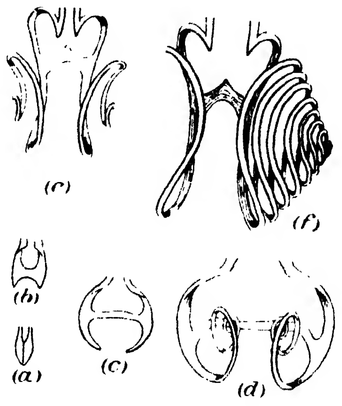


Fig. 76.—Development of the Brachidium in *Zygospira recurvirostra* (*a*–*d*) and *Retzia evax* (*e*, *f*).

(*a*) Centronella stage. (*d*) Adult. (*e*) Brachidium in young individual 2·5 mm. (*a*–*d*) after Schuchert. (*e*–*f*) after Beecher and Clarke.

During the Ordovician period there must have existed somewhere brachiopods which, in their adult state, had simple loop-like brachidia of the type seen in the early development of *Zygospira* (Fig. 76*a*). But the earliest form in which such a brachidium is found is *Centronella* from the Devonian. For this reason this is described as the centronellid type of brachidium. From a Centronella-like ancestor there evolved that great division of the brachiopods, the Terebratulacea, to which *Terebratula* (Tertiary), *Terebratella* (Jur.-Rec.), *Terebratulina* (Jur.-Rec.) belong. This became the dominant brachiopod type during Mesozoic and later times, and includes all forms without spires, but having a brachidium (Fig. 77) formed by a modification of the centronellid loop.

In the terebratuloid types the simple condition of the loop underwent but little change, though it varied in size up to that in *Stringocephalus* (Dev.) in which the loop was limited in size only by the periphery of the shell. A curious addition was also made to the loop the nature of which can be best understood by a brief survey of the development (Fig. 77) of the brachidium in *Terebratalia* (Rec.). In this genus, when as yet the brachidium consists of little more than a pair of elongated crura (*a*) there projects inwards from the centre of the dorsal valve a ridge-like septum. The free edge of this is grooved and bears a small ring-shaped loop at its hinder end. During later stages this loop increases in size but thins away and eventually breaks down on its dorsal side. Meanwhile the lamellæ, growing forwards from the crura, first become united to the septum, and then become continuous with the liberated ends of the loop. Both lamellæ and ring now break loose from the septum. Thus a curiously shaped brachidium is produced which has the appearance of being a simple centronellid loop bent back upon itself, but which really consists of two parts of quite different origin. A closely similar brachidium is found in *Magellania* (Jur.-Rec.). But in this genus the steps by which it has been produced during development are in important respects different from those just described for *Terebratalia*.

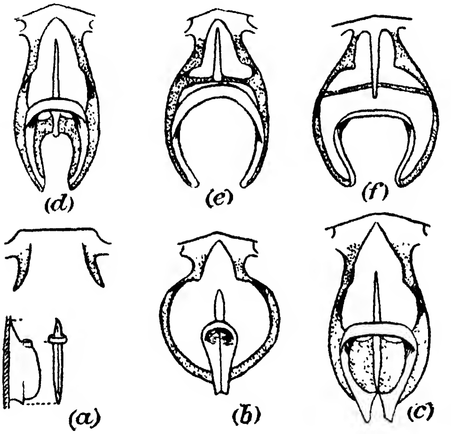


FIG. 77.—Development of Brachidium in *Terebratalia obsoleta* (Beecher).

(*a*) Embryonic stage. (*f*) Adult. Dotted area = Crura and parts which have grown out from these. Cp. centronellid stage in *Zygospira*. White area = part derived from anteriorly placed median septum.

For both genera the stages seen in development have their counterparts in the adults of various fossil forms, so that the developmental stages evidently accord with those passed through in evolution.

These two genera then belong to two quite distinct lines of descent; and therefore the close similarity which exists between their brachidia is but another illustration of the phenomenon of homeomorphy. In this case, however, the result is not due to parallel evolution, that is to say to the passage of both forms through a like series of changes, since the similarity becomes evident only in the later stages of evolution, and is therefore the outcome of convergent evolution.

General Classification and History.—The Brachiopoda were already a clearly defined group before the commencement of the Cambrian period, the Atremata and Palæotremata representing the most primitive sections. From the former the Neotremata, and from the latter the Protremata, and possibly also the Telotremata evolved before the close of the Precambrian. In the earliest stages of their evolution they probably did not possess a shell. When, however, this did appear, it would no doubt be little more than a horny covering for the mantle. Very soon this was strengthened by the addition of both phosphate and carbonate of lime. In the majority of forms the carbonate practically excludes the phosphate.

THE ATREMATA.—At the opening of the Cambrian these, the most primitive, of the Gastrocaulia were already present. The shell was either simply horny or was impregnated with phosphate and carbonate of lime. It was characterized by the absence of many features which distinguish the later brachiopods, such as a special pedicle opening, a palintrope, hinge apparatus and brachidium.

The Atremata continued to flourish during the Ordovician, but began to decline during the Silurian. From that time until the present they have been represented by only one family (Lingulidæ).

THE NEOTREMATA.—The members of this order like the Atremata still retained many primitive characters. Thus the shell was frequently horny, and both hinge apparatus and brachidium were absent. On the other hand the shell tended to lose its original oval form and to become conical. A special opening for the pedicle arose and often shifted towards the apex of the cone which was more or less centrally placed. In some genera (*Crania*, Ord.-Pres.) the pedicle disappeared and the shell became cemented to the substratum.

During the Cambrian the Neotremata rivalled the Atremata in variety and numbers. It was not, however, until the Ordovician and Silurian that they attained the acme of their evolution. They maintained a position of importance in the brachiopod fauna until almost the close of the Palæozoic, but from late Carboniferous times until now they have been represented by only two families (Discinidæ and Craniidæ).

The Palæotremata.—These include the most primitive of the Pygocaulia, and differed from the Atremata in having a calcareous shell with palintrope and delthyrium. They were represented in the Lower Cambrian by two very short-ranged families—the Rustellidæ and Kutorginidæ.

The Protremata.—This order was represented in the Cambrian period by only one family, the Billingsellidæ, in which the shell had passed beyond the horny condition and had become quite calcareous, and in which traces both of hinge teeth and crural processes were present.

During the Ordovician the Protremata developed rapidly to their heyday which was long and lasted until as late as the Carboniferous period. The Orthacea had a straight hinge line and a pedicle, which passed out through the delthyrium and functioned throughout life. In the Strophomenacea the hinge line became long and straight, a stout cardinal process developed, and the valves pressed closely against one another, giving to the shell as a whole a concavo-convex form. The pedicle passed out through a special opening in early life, but later both atrophied and a delthyrium developed. In another equally great section of the order, the Pentameracea, the hinge line was usually short and curved, the shell much inflated and the dental plates with their adjoining parts correspondingly modified.

The Protremata declined during the Permian and were represented throughout Mesozoic and Tertiary times by only one family, the Thecidiidæ, which is still extant.

The Telotremata.—In this order the shell was wholly calcareous and all the structural features exhibited by the Brachiopoda as a whole were present, as for example hinge apparatus, crura, brachidium, cardinal area, deltidial plates. Within the order the most striking changes were those which affected the crura and brachidium. These have furnished a basis for a natural and threefold division of the order.

The lowliest division is the Rhynchonellacea. One of the most primitive members of this and indeed of the order was *Protorhyncha* (Ord.) which closely approached the orthids. In it both deltidial plates and crura were absent. In all the other genera the crura were present, but varied greatly in length. The Rhynchonellacea were in existence as early as the Ordovician and have lasted with a comparatively uneventful career until the present day.

The next division, the Spiriferacea, arose from a Rhynchonellid stock probably as early as the Ordovician period. In them the hinge line became long and the shell correspondingly broad. Internally the crura gave rise to a complex brachidium characterized by the development of spires. They became the dominant Telotremes during the later half of the Palæozoic, but became rapidly extinct during the early portion of the Mesozoic.

The Terebratulacea seem to have arisen independently from a protrematous ancestral stock. In them the hinge line became short, the shell elongate and the brachidium pursued an entirely different course in its evolution from that of the Spiriferacea.

The earliest known and most primitive member of this division (*Centronella*) occurs in the Devonian. The group then developed gradually during the remainder of the Palæozoic, and at the close of this period had risen to a position of pre-eminence not only among the Telotremata, but also among Brachiopoda. This position it has maintained until the present time. Nevertheless its members are not so varied and numerous now as they were in the Mesozoic period.

SECTION VIII

POLYZOA

The Structure and Development of a Polyzoan.—The Polyzoa are colonial animals of predominantly marine habit. On the whole they appear to prefer deep clear water which is being constantly renewed by wave-movements and currents.

Each individual in the colony is called a polypide. It is of small size and rarely exceeds one-eighth of an inch in length. It consists of a sac-like body-wall (Fig. 78) enclosing a body cavity in which a U-shaped alimentary canal is freely suspended. The outer surface of the wall secretes a chitinous and calcareous covering (zoœcium) which is capable of enduring long after the soft parts of the body have died and perished. All the zoœcia taken together make up the skeleton, or asty, of the colony. Portions of such skeletons occur commonly as fossils from the Ordovician onwards. Both the mouth and the anus are situated at the upper end of the body sac, which likewise carries a ring of ciliated tentacles. In a few Polyzoa (the Endoprocta) this ring encloses both the mouth and the anus. These will not be considered further inasmuch as they are unknown in the fossil state. In the majority of Polyzoa (the Ectoprocta) the anus lies outside the ring of tentacles, which therefore encloses only the mouth. The upper part of the sac, which carries these two openings and the tentacles, can be withdrawn from the surface into the cavity of the body like a glove finger that has been introverted.

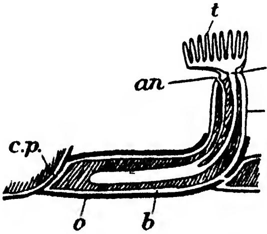


FIG. 78—Diagram showing main Structural Features of an individual Polyzoan.

an, anus. *b*, body wall. *c.p*, communication pore. *m*, mouth. *o*, zoœcium. *r.b*, retractile portion of body sac. *t*, tentacles.

Each colony (zoarium) originates in one egg, from which a larva (Fig. 79A) develops. This larva swims about freely by means of cilia and is structurally similar to a trochophore. In its most primitive form the polyzoan larva is helmet-shaped. At its apex there is a thickening of ectoderm cells (apical plate) and on the under surface there are the mouth and the anus. In some cases the larva is enclosed in a bivalve shell. Eventually the larva becomes attached to some object on the sea-floor such as a shell, a seaweed or a grain of sand. Upon the surface of this it spreads itself out in the form of a plano-convex disc (Fig. 79B) and undergoes an extraordinary change internally; for all its organs, with the exception of the apical plate, disintegrate into an indefinite mass of tissue. Meanwhile the two shell valves flatten out and overlap one another, thus forming a protective covering to the disc. A similar calcareo-chitinous covering, called the protœcium, occurs as the first formed portion of the asty of all polyzoa. After a while the apical plate recommences to develop, and produces a polypide. The skeletal covering of this is the first zoœcium and is called the ancestrœcium. Thus the series of developmental changes from the embryo to the adult, which in other animal types already studied have been found so illuminating, are entirely omitted, or hopelessly obscured, in the Polyzoa.

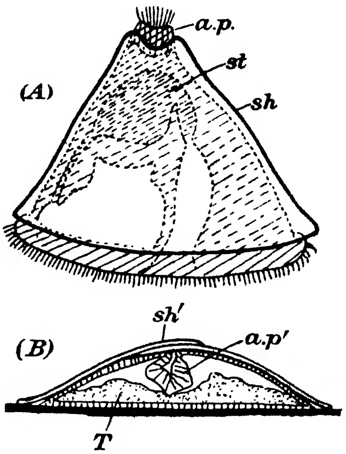


FIG. 79.—Early Development of a Polyzoan.

(*A*) Free swimming Larva (modified from Korschelt and Heider.) (*B*) Metamorphosing larva (modified from MacBride).
a.p, apical plate. *a.p'*, apical plate developing into a polypide. *sh*, bivalve shell. *sh'*, valves of shell overlapping. *st*, stomach. *T*, undifferentiated tissue formed by disintegration of organs.

From the first polypide many others are produced in succession by budding. As these all remain connected with one another a colony or zoarium results. This connection is maintained by means of strands of living substance which pass through openings (communication pores) in the zoœcial walls.

Methods of Colony Formation.—The genus *Stomatopora* is the simplest of all the more familiar Polyzoa. It likewise has a very long range in time, for it occurs in the Ordovician rocks and is still living in modern seas.

The protœcium of *Stomatopora* (Fig. 80) is large and almost spherical. It is clearly marked off from the ancestrœcium, for the latter in addition to being of smaller calibre is of tubular form. For the greater part of its length this tube lies along the ground, but the distal end, which carries the mouth or peristome, is turned upwards. On the underside of the upturned end of the ancestrœcium a median bud arises, and forms the first ordinary zoœcium. This also is tubular, and lies for the greater part of its length upon the substratum, with its distal end and peristome tilted upwards. From this two other zoœcia may grow. These usually diverge from one another at a wide angle, and are the first beginnings of two branches, each of which extends by the addition of new zoœcia in single series, thus forming a uniserial colony. From time to time new branches are formed as just described, or by the growth of lateral buds. As these branches lie with their whole length along the ground the colony is said to be of "encrusting" habit. Each peristome faces upwards, and may be either flush with the surface, or projecting slightly above this.

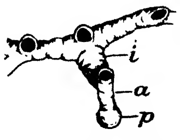


FIG. 80. — First Stages in the growth of a Colony of *Stomatopora* (based on Bassler).

p, protœcium. *a*, ancestrœcium. *i*, first ordinary zoœcium (after Bassler).

Within the limits of one asty all the zoœcia are not exactly alike, for during its growth (astogeny) differences of such magnitude may arise that two fragments of the same colony, if found separately, could be mistaken for different species. Though in some species of *Stomatopora* all the zoœcia have a primitive cylindrical form, in others they tend to become specialized, that is to say more or less club-shaped (cp. Fig. 83) between the first and the third points of branching. At a later stage they resume the cylindrical condition exhibited by the earliest zoœcia. Again the number of zoœcia, as indicated by the peristomes between any two branching points,

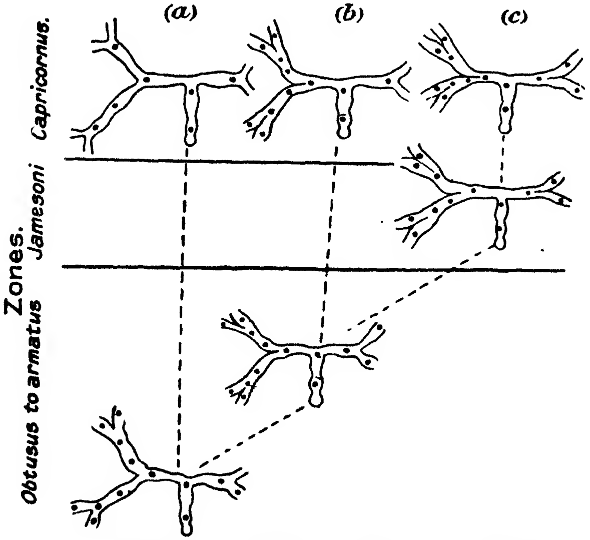


FIG. 81.—Evolution of several Lineages of *Stomatopora*.

In (*a*) there has been very little change. In (*b*) and (*c*) change has followed the lines of decrease of angle between branches and fusion of adjoining zoœcia at bases of the branches. These tendencies lead towards proboscinoid condition. [From Lang.

may increase during early life and decline later. Thus during the life of a colony, as during the evolution of a race of individuals, the phenomena of *anagenesis* and *catagenesis* may be manifested. In other phyla of the animal kingdom various ontogenetic stages have been recognized nepionic (brephic), neanic, ephebic and gerontic —each of which has its phylogenetic significance. In the Polyzoa, as already noticed, the ontogeny of the first individual of the colony has been short-circuited, and such stages cannot be recognized. Nevertheless analogous stages of like significance can be detected in astogeny (development of the asty) and these are called brephastic, neanastic, ephebastic and gerontastic respectively.

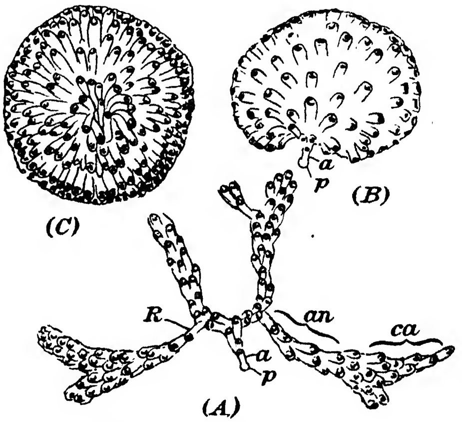


FIG. 82.—Diagrams illustrating the Proboscinoid (*A*) and Berenicoid (*B*, *C*) types of Colony formation.

an, region illustrating anagenesis from uniserial to multiserial condition. *ca*, region illustrating catagenesis from multiserial to uniserial condition. *R*, point at which rejuvenation is manifested by the origin of a branch. *p*, protœcium. *a*, ancestrœcium.

(*A*)Adapted from Bassler. (*B*, *C*) After Brit. Mus. Cat. (*B*) Cret. Bryo., Vol. 1, pl. 5, 3. (*C*) Jur. Bryo., pl. 4, 3.

Besides the two changes already described as taking place during the growth of the colony, two others can be detected, which exercise a yet more important influence upon the character of the asty as a whole. In the first case the angle between the adjoining branches tends to diminish during the growth of the colony. In the other case the zoœcia situated at the point of origin of the branches become united with one another first by their bases, but eventually by their whole length. The later phases of these changes are confined to only a part of the asty in some species. From this condition they extend until they become prevalent for the whole colony in the species that are regarded as the most advanced. The process of union between zoœcia may also affect the whole of two adjoining branches, which thus become one biserial branch. These last stages in the evolution of the colony usher in what may be described as the proboscinoid condition (Fig. 82A), which has probably arisen from a uniserial or stomatoporoid condition repeatedly.

In its more advanced stages the proboscinoid polyzoan may have a part or even the whole of each branch of considerable width, and consisting of a number of zoœcia lying alongside of and completely united with one another. With the further union not only of individual zoœcia, but also of branches, a sheet-like asty is ultimately produced, varying in outline from the shape of a kidney to that of a circle. This is the berenicoid condition (Fig. 82B) which must likewise have arisen repeatedly from proboscinoid stocks. Up to this point the asty has been of encrusting habit, but now further modifications tend to lift polypides above the substratum. Thus new berenicoid-like sheets may be formed but be superposed the one upon the other (*Reptomultisparsa*), or the colony may grow upwards either in the form of a lamina (*Diastopora*) or of a cylinder (*Entalophora*).

The phenomenon of rejuvenation is sometimes seen to great advantage among Polyzoa. Thus in uniserial forms with specialized zoœcia the first zoœcium of a new branch may revert to the more primitive condition exhibited elsewhere in the asty, only in the brephastic and neanastic stages of growth. Again in proboscinoid forms with multiserial branches a new branch may start with the uniserial condition (Fig. 82A) and become biserial and multiserial only during later growth.

The Earlier Polyzoa.

The Cyclostomata.—Twice during their long history the Polyzoa have burst into evolutionary activity, and produced numerous and widely varied types. The first outburst took place during the Ordovician and Silurian. They then produced astys exhibiting all the forms discussed above, as well as others which were sufficiently massive to play a not unimportant part in rock building. During the later Palæozoic they diminished in vigour, and at the opening of the Mesozoic, they were apparently represented by only a few cyclostomate types. The second outburst began during the late Jurassic, and attained its maximum during Cretaceous and Tertiary times. On the whole the Polyzoa were now characterized by less massive astys, and more complicated zoœcia. The passage to modern times has been marked by a diminution in vigour.

In all the Polyzoa hitherto considered the zoœcia are tubular, the mouth aperture is round, and the walls, in addition to having the usual communication pores, are minutely porous. Forms exhibiting this combination of characters are classed in the order Cyclostomata. This order ranges from the Ordovician to the Present. It embraces the more primitive Polyzoa, and probably lies close to or even includes the ancestral stocks from which the other orders have been derived.

Among the earlier Polyzoa the Cyclostomata occupied a prominent place. Even as early as the Ordovician they exhibited their maximum range of form both for the zoœcium and for the asty. Thus in uniserial types (*Stomatopora*, *Corynotrypa*) the zoœcium varied from a primitive parallel-sided tube with large terminal peristome to one that was like a club or a pear in shape, and had a peristome that was small and often situated in the front wall (Fig. 83). In addition to the forms of colony already described another type, exhibited by *Ceramopora* and its allies (Fig. 84), was produced. In this genus the zoœcia were cylindrical, and each originated from the proximal end of its parent. Instead of growing with their long axes parallel to the substratum, the zoœcia tended to rise perpendicularly to this. They all lay for the greater part of their length in close contact with one another, and consequently their apertures were close together upon the surface of the asty. These openings were obliquely placed with one lip projecting in the form of a hood. In the deeply seated (immature) portions of the zoœcia the walls were thin, in contrast to the outer (mature) portions in which the walls were thick. The ceramoporoid cyclostomes flourished up to the close of the Devonian. They then appear to have passed over into fistuliporoid types (Fig. 84) which were equally important during the Carboniferous, and were distinguished from their earlier relatives by the presence of vesicular packing material between the outer portions of the zoœcia. In both types the cavities of the zoœcia were occasionally crossed by tabulæ, the

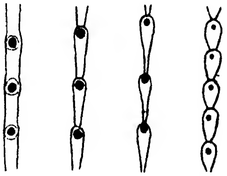


FIG. 83.—Diagrams illustrating some of the forms of Zoœcia in uniserial Polyzoa, e.g., *Stomatopora*, *Corynotrypa*.

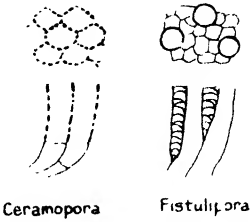


FIG. 84.—Diagrams illustrating Structure of *Ceramopora* and *Fistulipora*.

Upper line transverse sections; lower line vertical sections.

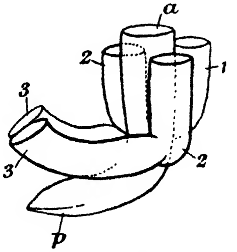


FIG. 85.—Diagrammatic restoration of the Earliest Stages in Development of Trepostome colony (*Prasopora*). (Built up from figures by Cumings.)

p, protœcium. *a*, ancestrœcium. 1. Median. 2. Lateral zoœcia formed by budding from ancestrœcium. 3. Zoœcia budded from first laterals.

presence of which is believed to indicate a succession of polypides within the same tube.

The Trepostomata.—This last mentioned feature which occurs only occasionally among the Cyclostomata became the rule among the members of the order Trepostomata. In these each zoœcium became a tube of considerable length (Fig. 86) and, having many "tabulæ," was presumably built up by a long succession of polypides. Here also mature and immature portions were differentiated. As the zoœcium elongated, that part of the thickened wall which is furthest from the aperture (Fig. 87), must have undergone reabsorption, for only thus can the much thinner walls in the interior of the asty be explained. The zoœcia were either in close contact with one another throughout their length, or they were separated to a greater or less extent by a packing of aborted zoœcia (Fig. 86) and tubular spines. The Trepostomata form comparatively massive, compact or branching astys. These often present a striking resemblance, on a small scale, to cœlentera such as *Favosites* and *Heliolites* (cp. Fig. 86 with Fig. 37). This, together with the tabulate character of the zoœcia, led earlier workers to regard them as Cœlentera; but the discovery of a protœcium and ancestrœcium (Figs. 85, 86), from which zoœcia grow by budding, definitely established their polyzoan affinities.

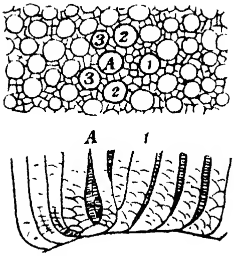


Fig. 86.—Diagrammatic Sections of *Prasopora*.

Upper, transverse. Lower, vertical. (Adapted from Cummings.)
Lettering as in Fig. 85.

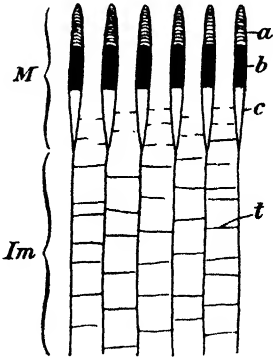


Fig. 87.—Diagrammatic Section of Trepostome parallel to length of zoœcia (modified after Lee).

Im, inner or immature zone. *M*, outer or mature zone. (*a*) Newly formed portion of zoœcial wall. (*b*) Thickest portion of zoœcial wall. (*c*) Portion of thick zoœcial wall undergoing reabsorption. *t*, tabulæ.

The Trepostomata attained their maximum development during the Ordovician, and became insignificant during the later Palæozoic. Whether they existed in later times is an unsettled question. There are certain Polyzoa, especially in the Cretaceous rocks, which resemble them closely, and are classed as Trepostomata by some investigators. Others described them as trepostomatous Cyclostomata because of the minutely porous character of their zoœcial walls. This feature is one that is wanting in the Palæozoic trepostomes but is diagnostic of the Cyclostomata.

THE CRYPTOSTOMATA.—These formed almost as important an element in the fauna of the Ordovician and Silurian as did the Trepostomata. They continued with undiminished vigour into the Carboniferous, but disappeared at the close of the Permain. As in the Cyclostomata their zoœcia were usually (Fig. 89) short and overlapped one another to only a small extent. The organism was, however, burdened with a capacity for secreting a superfluous amount of calcareous matter, which it deposited in the form of laminæ, around the peristomes and upon the exposed surfaces of the zoœcia. Thus the peristome came to be situated some distance below the surface of the asty at the bottom of a pit walled in by this deposit. Generally speaking the branches of the cryptostome asty were more slender than in the trepostomes; and they were frequently united at intervals in the form of a delicate network (cp. *Fenestella*). Such an arrangement secured a wide spacing of the peristomial openings and increased the advantage arising from a spreading of the polypides over a larger food collecting area. In the Trepostomata and *Fistulipora* the same purpose was less efficiently served by the interposition of packing material of one kind or another between the zoœcia.

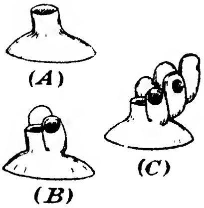


FIG. 88. — Earliest Stages in growth of a cryptostome Colony. Reconstructed from figures of Fenestella by Cumings.

(*A*) Protœcium—with tubular almost erect ancestrœcium. (*B*) Later stage when two first zoœcia have been formed by lateral budding. (*C*) Completion of first tier of zoœcia.

THE CTENOSTOMATA.—These have been only an insignificant section of the Polyzoa from the Ordovician until the Present. They are characterized by a fringe of spines around the peristome.

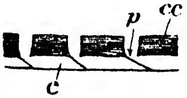


FIG. 89.—Diagram of Longitudinal Section through several Zoœcia of Cryptostome.

cc, Calcareous deposit. *p*, Peristome. *c*, Cavity of zoœcium.

The Later Polyzoa.

THE CYCLOSTOMATA.—With the exception of the Ctenostomata, and possibly also of certain trepostome-like forms, the Cyclostomata were the sole survivors into later times of the rich and varied polyzoan fauna of the Palæozoic era. During Triassic and Jurassic periods they exhibited the normal types of zoœcia and colony formation already described. In addition they developed two modifications which may be seen in the genera *Heteropora* and *Haplœcia* respectively. *Heteropora* and its allies developed along lines strikingly like those seen in the Trepostomata, and on that account are referred to either as trepostomatous cyclostomes or as heteroporoid trepostomes. *Haplœcia* and its allies on the other hand tended to develop along lines parallel to those which characterize a later and more specialized order, the Cheilostomata. Their zoœcia were on the whole tubular, but distally each became angular in outline and fitted against its fellows in a mosaic pattern. The aperture was small and situated in the frontal wall.

During the Cretaceous period the Cyclostomata rose to the acme of their development. Normal Cyclostomata still abounded, and trepostomatous forms (*e.g. Ceriopora*, *Heteropora*, *Radiopora*) were more prominent than heretofore. A new modification, however, appeared in the family Eleidæ. In them the zoœcia were similar to those of *Haplœcia*, from which they may have been derived, but the peristome now assumed a trigonal outline. Moreover, occasional zoœcia (aviculœcia) exhibit an approach to a type of adaptation which is common among the Cheilostomata. The function of these is not certain, though it has usually been regarded as protective. This similarity to the Cheilostomata is to be regarded, however, not as indicative of close affinity, but as a case of parallel development. During the Tertiary period the Cyclostomata declined in importance and to-day are represented only by isolated survivors of the order.

THE CHEILOSTOMATA.—This order represents the climax of specialization among the Polyzoa. It probably originated from cyclostomatous ancestors, possibly during the Jurassic period. It rose to prominence during the Cretaceous, but did not become dominant until Tertiary and Recent times.

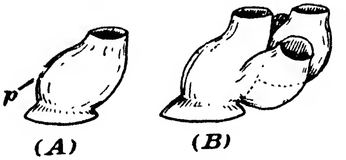


FIG. 90.—Early stages in Development of a Cheilostome (*Retepora*). (Reconstructed after Cumings.)

(*A*) Small protœcium. *p*, A large inflated ancestrœcium. (*B*) Later stage showing median and lateral zoœcia formed by buds from ancestrœcium.

In their modes of colony formation the Cheilostomata followed the same general lines already described. The earliest stages of development (Fig. 90, cp. 85, 88), are characterized by the very small size of the protœcium and by the specialized condition of the ancestrœcium which is no longer simply cylindrical but by a process of acceleration has become inflated and more like an adult zoœcium. The other distinguishing characters of the order are almost confined to the zoœcia. In the uniserial types (Fig. 91) these were club-shaped or pyriform, but in the multiserial types they were short and angular, and fitted against one another like the tiles in a tesselated pavement. The aperture was small, situated in the front wall, and provided with a trapdoor-like covering, the operculum. A number of zoœcia have been modified into organs (aviculœcia) resembling a bird's head. The apertural margin and operculum together are shaped like the beak and are constantly snapping against one another. Within the order special lines of modification affected the front wall of the zoœcia, and produced chambers for housing developing larvæ. Around the peristome and for some distance below this the front wall is flat and chitinous (Fig. 92A), and consequently it is rarely preserved in the fossil state. Beyond this area the wall is thick and calcareous and slopes away to the margins of the zoœcium. The line which marks the change of slope is called the termen, and is almost coincident with the junction between the two areas, which are called respectively the intra- and extra-terminal frontal walls.

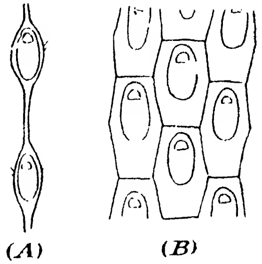


Fig. 91.—Diagram of (*A*) uniserial Cheilostome ; (*B*) multiserial Cheilostome.

Calcareous spines commonly arise from the termen and in their simplest state (in *Membranipora*) they project freely from the surface (Fig. 92A). With advancing specialization those situated below the level of the peristome lean across the chitinous area until they are in contact with one another near their tips (*Myagrapora*, B). From this point onwards they exhibit various degrees of union in the middle line leading up to the formation of a grid-like structure (*C*) in front of the intraterminal front wall (*Prodromopora*). By

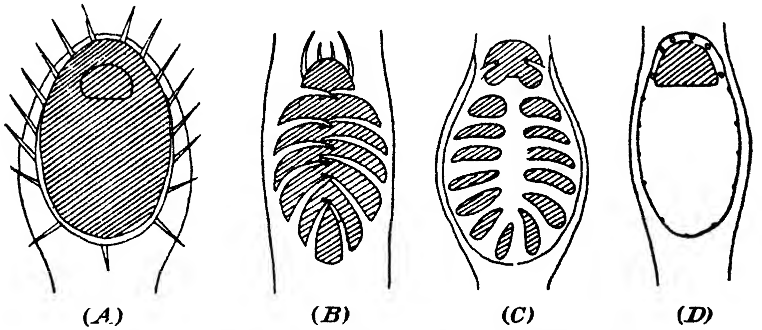


Fig. 92.—Diagrams of Frontal Walls of Cheilostomata.
(*A*) *Membranipora*. (*B*) *Myagrapora*. (*C*) *Prodromopora*. (*D*) *Holostegopora*.
[After Lang.

a continued thickening of the spines (now called costæ) the openings in the grid became reduced (*Andriopora*), and eventually quite suppressed (*Holostegopora*, D), and thus a continuous secondary wall is brought into being. Such a series of modifications is one which takes place repeatedly in many separate lines of descent.

As with other orders of Polyzoa, and, indeed, of animals generally, the problem of the disposal of superfluous calcareous matter becomes a pressing one in some lineages. The series of changes leading up to the formation of a secondary wall provide an additional area, besides the extraterminal wall and the spaces between the zoœcia where this phylogenetic rubbish may be shot. When the accumulation of this material becomes excessive it tends to interfere with the normal activities of the organism, and extinction of the lineage results.

The provision of brood chambers is accomplished, in a number of Cheilostomata, either by a specialization of the spines which lie beside and in front of the peristome, or by the modification of that part of the zoœcium which lies in front of the peristome into a more or less completely separated chamber.

SECTION IX

ECHINODERMA

As an introduction to the study of the Echinoderma, the familiar starfish, *Asterias*, may be taken as a type. It is a marine animal having a flattened star-shaped body (Fig. 93), without any sharp distinction between the central disc of the star and the five rays. Its mouth is situated in the centre of the ventral surface, and the anus at the corresponding point on the dorsal surface. It thus exhibits a remarkably regular five-rayed symmetry. It lives upon the floor of the sea, creeping about freely by means of numerous soft tubular organs provided with sucking discs, called tube feet or podia (Fig. 94). These are situated in broad grooves, which run from the mouth along the ventral side of each ray. They are arranged like an avenue of trees on either side of a walk, hence the name ambulacrum for those areas of the body occupied by the grooves. The under side of the body, occupied by the ambulacra, is called the oral (actinal) surface; the upper surface, without them, is described as apical (abactinal).

The body is cased in a tough skin in which is embedded a calcareous skeleton. This differs from that of the Cœlentera, and indeed of all other invertebrates, and resembles that of the vertebrates, in the fact that it lies beneath the epidermis, and is formed by the mesodermal tissues. Thus in spite of its close proximity to the surface it is essentially an endoskeleton. The skeleton of the dorsal side consists of a network of calcareous rods, bearing numerous small spines. These project through the skin, giving it a prickly character. This fact suggests the name Echinoderma (or hedgehog skin) for the phylum. In the meshes of the network, finger-like outgrowths of the skin project. These are called papulæ,

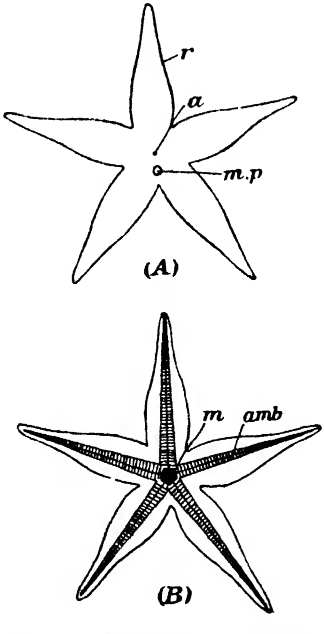


FIG. 93.—Diagrams of *Asterias*. (*A*) Apical surface. (*B*) Oral surface. *a*, anus. *amb*, ambulacrum. *m*, mouth. *m.p*, madreporic plate. *r*, ray.

and serve a respiratory function. On the ventral side the skeleton is made up of calcareous plates, systematically arranged in relationship to the ambulacral grooves. If the podia and other soft parts be removed, the roof of the groove (Fig. 94B) is seen to be supported by a paired series of long plate-like ossicles ; the ambulacral ossicles. These abut against one another in the median line, but at their outer ends they come into contact with another series of smaller plates, the adambulacrals.

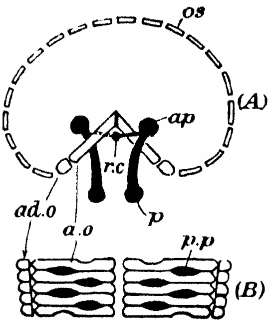


FIG. 94.—Structure of the ray of a Starfish.

(*A*) Section across the ray. (*B*) Under view of ambulacrum. *a.o*, ambulacral ossicle. *ad.o*, adambulacral ossicle. *ap*, ampulla. *os*, ossicle. *p*, podium. *p.p*, podial pore. *r.c*, radial canal.

Behind the anus and close to the angle between two rays, there is a well-defined ossicle called the madreporic plate. A close examination of this shows that its surface is minutely decorated with meandering grooves, which give to it a superficial resemblance to the madreporic coral, *Meandrina.* At the bottom of this groove are numerous minute pores, which open into the cavity of a calcareous tube called the stone canal. This hangs down into the body cavity, and opens into a circular ring (Fig. 115) or canal lying just above the mouth. From this circular canal there radiate five others, each of which runs along an ambulacral groove. These give off a series of branches on either side, each of which opens into the cavity of a podium. The upper end of the podium passes up between two ambulacral ossicles, and is swollen into a sac, the ampulla, which lies dorsal to the ossicles. This complex of canals and podia is the water vascular system. As this name implies, the system is filled with water, which gains access through the pores of the madreporic plate.

That division of the Echinoderma to which the starfish belongs is called the Asteroidea. Closely allied to it are the Ophiuroidea, or Brittle Stars. In these there is a very sharp line of demarcation (Fig. 95A) between the central disc and the arms. The podia (Fig. 114) are not provided with sucking discs, and are of little value for locomotion. The arms are, however, thin, flexible and prehensile. By their means the creature wriggles along the sea-floor, or climbs the stones and seaweeds. The madreporic plate is situated orally. These two star-like types are more closely allied to one another than to any other echinoderms. They are therefore grouped together in one class, the Stelleroidea, which dates back to Ordovician times.

The sea urchins (Echinoidea) form another important class. They have a compact body (Fig. 95B) which may be globular (Fig. 124), spheroidal (Fig. 95B), or heart-shaped (Fig. 130). In them the abactinal surface is reduced to a small patch called the apical disc (Figs. 95, 123), whilst the actinal surface occupies the remainder of the body. This actinal portion of the skeleton is called the corona, which consists of a mosaic of calcareous plates arranged in twenty vertical rows or columns (Fig. 123). These are associated together in alternating pairs called the ambulacral and interambulacral areas respectively. It is important to notice that the radial canals lie along the inner surface of the ambulacrum, and not along the outer surface, as in the starfish. The earliest echinoids occur in the Ordovician. Throughout both Palæozoic and later times this class has been well represented.

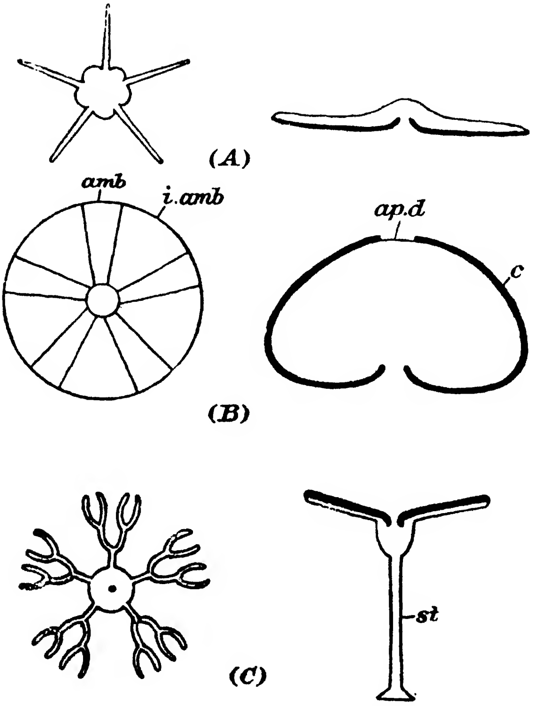


Fig. 95.—Types of Echinoderm.

Plan (Left) and Section (Right) of (*A*) Stelleroid, (*B*) Echinoid, (*C*) Crinoid. In the sections, the thick line represents that surface which carries ambulacral grooves ; the thin line that portion of the surface without these.

amb, ambulacral area. *ap.d*, apical disc. *c*, corona. *i.amb*, interambulacral area. *st*, stalk.

In the Sea Cucumbers (Holothuroidea) the body is soft, for the skeleton is represented only by isolated calcareous spicules. As with the two previous classes, the body has a radial symmetry, but the axis of symmetry lies parallel to the surface over which these creatures creep. Fossil remains of *Holothuria* are usually represented only by spicules but some remarkably preserved remains of complete individuals have been found in the Middle Cambrian of British Columbia.

Eothuria is a remarkable form from the Upper Ordovician of Girvan. At first sight it could be described as an elongated echinoid. Nevertheless it exhibits other features which give justification for describing it as a plated holothurian and for regarding these two great groups as being closely related to one another.

The Sea Lilies (Crinoidea) are the only other class represented at the present day. They bear a superficial resemblance to the ophiuroids in that they have a compact body (Fig. 95*c*) bearing clearly defined arms supported by series of ossicles. These, however, are usually either much branched, or bear parallel series of branchlets. In typical crinoids the body is borne upon the upper end of a stalk, which at its lower end is attached to the sea-floor. As the body is fastened by its aboral or abactinal surface, its oral or actinal surface, bearing the anus, the mouth and the ambulacral grooves, faces upwards. This is the most suitable attitude for an animal which, by reason of its stationary habits, is a passive feeder; that is to say is dependent for its food upon material which is brought to it by the water. The epidermis lining the grooves is provided with numerous cilia, which by their concerted movements cause currents of water, bearing particles of food, to flow towards the arms, and along these towards the mouth. This method of feeding, which to-day characterizes one class, was the predominant method, especially among the older Palæozoic echinoderms. Crinoids existed during the Cambrian. They rose to the premier position among echinoderms in late Palæozoic, and have continued, much reduced in numbers, from then until the present day.

Other classes of echinoderms occur only as fossils, *e.g.* Cystoidea, Blastoidea, Edrioasteroidea. Many of them, like crinoids, had stalks and are therefore classed along with these in one large division—the Pelmatozoa. They were all more or less addicted to a statozoic or stationary and attached mode of life. The other classes mentioned above moved freely from place to place, that is to say they lead an eleutherozoic existence. Such are grouped into another large division—the Eleutherozoa.

The Development of an Echinoderm.—During development *Asterias* passes through a free-swimming larval stage, which has many features in common with the larvæ of other types of echinoderms. These features may be regarded as inheritances from a common ancestral stock, and have furnished a basis for reconstructing the broad structural outlines of the ancestor of the echinoderms (Fig. 96). This hypothetical ancestor is called *Dipleurula*. It moved about freely. It had an ovoid bilaterally symmetrical body, with an alimentary canal opening by a mouth on the ventral side anteriorly, and by an anus situated posteriorly. It possessed two pairs of cœlomic cavities situated on either side of the straight intestine. The anterior pair, which became the water vascular system, was provided with a canal opening to the exterior by a small aperture, the hydropore.

During development the free swimming dipleurula stage often passes over into a fixed stage, in which it becomes attached at some point near its anterior end. Under these new conditions the internal organs become re-arranged in such a way that the mouth comes to lie at the free apex, and the hydropore and anus at slightly lower levels, some distance from it. Among the Crinoidea this attached condition is always maintained for a long time during development, and may last the whole of life. In all the other living types this condition is but a transitory phase, and for nearly the whole of life they are able to move from place to place freely. The attached habit, and the free habit, of life are described as being statozoic and eleutherozoic respectively.

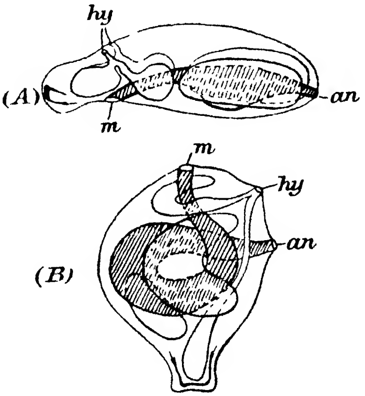


FIG. 96.—Diagram of (*A*) *Dipleurula*. (*B*) Primitive pelmatozoon.
an, anus. *m*, mouth. *hy*, hydropore.
[After T. Z., Messrs. A. & C. Black.

The existence of an attached stage in the development of several classes of echinoderms is believed to represent a statozoic stage in the evolution of the phylum. The primitive echinoderm at this stage must not be pictured as a rigidly fixed organism, but as one that on the whole favoured an attached or stationary mode of life, but when occasion required it could become detached and move elsewhere. It is a characteristic result of a stationary mode of life that classes of organisms addicted to it tend to become radially symmetrical. This has already been seen in the Cœlentera, and is abundantly illustrated in the plant kingdom.

Whilst the existence of a dipleurula stage carries the conception of the echinoderm ancestry back to a freely moving bilaterally symmetrical ancestor, the marked radial symmetry which prevails, even among the most perfectly eleutherozoic modern forms, is usually ascribed to a prolonged statozoic phase in their evolution. The assumption of the statozoic habit was frequently, but not universally, accompanied by the evolution of a stalk such as that possessed by the crinoids. Stalked echinoderms have long been grouped together in one great division as the Pelmatozoa. A number of closely allied statozoic, but unstalked, forms are of necessity included under that heading. The eleutherozoic unstalked forms are similarly grouped together as Eleutherozoa.

In view of the facts discussed above it is interesting to note that many of the earliest known fossil echinoderms, viz. these from the Cambrian, are Pelmatozoa, and that Pelmatozoa predominate throughout the Palæozoic era. On the other hand, though Eleutherozoa were in existence then, it was not until later times that they began to approach their acme.

CYSTOIDEA AND BLASTOIDEA

The Birth of the Echinoderms.—The basal beds of the Middle Cambrian of Queensland have yielded abundant remains of two forms (Fig. 97), *Peridionites* and *Cymbionites*, which led an unattached mode of life and appear to be the simplest echinoderms hitherto discovered. The skeleton of the former is laterally compressed and consists of one apical, two end and two lateral plates symmetrically disposed about the longitudinal and transverse planes. Its under surface bears markings closely consonant with the structure of dipleurula. The skeleton of the latter is on the other hand radially symmetrical and consists of five plates which sometimes enclose a central one. In these respects it bears comparison with the earliest skeleton-bearing stage in the development of modern Eleutherozoa (cp. Figs. 115, 116).

The small number of plates in these early forms is in striking contrast to the condition of other very primitive echinoderms such as *Aristocystis* from the Ordovician of Bohemia. It had a pear-shaped body (Fig. 97), and though it was usually attached by its narrow end, it probably lay full length upon the sea-floor. Some individuals, however, do not show traces of any place for attachment. The mouth was situated at the apex of the free end, and the anus was placed about one-third of the distance from the mouth to the aboral pole. Two other openings, regarded as the apertures of the water vascular and genital systems, occupy an intermediate position between the mouth and the anus.

It is evident that a remarkable similarity exists in the shape of the body in the arrangement of the apertures and presumably, therefore, of the internal organs between this type and the attached dipleurula stage in the development of modern forms. It is not unlikely, therefore, that *Aristocystis* and its allies, some of which are of Cambrian age, represent, as far as structure is concerned, that stage in evolution which is reflected by the transitory statozoic stage in the development of living echinoderms. From the standpoint of time, however, they existed too late to be the actual ancestral stock. For that it will be necessary perhaps to go back to pre-Cambrian times.

Aristocystis differs from the attached dipleurula, among other respects, in the presence of a test or theca made up of numerous polygonal plates. Their absence in this early developmental stage of living forms furnishes a good illustration of what may be called the imperfection of the embryological record. The statozoic habit of this lowly type was evidently a comparatively fresh acquirement; for it had not been in existence long enough to lead to the formation of a stalk, or to the appearance of any traces of radial symmetry; except, perhaps, in the arrangement of the plates at the point of attachment. In all probability, in the living state, the epidermis was traversed by grooves converging on the mouth. Currents of water, actuated by cilia and bearing particles of food, would flow along these towards the mouth. These food grooves left no impression upon the test.

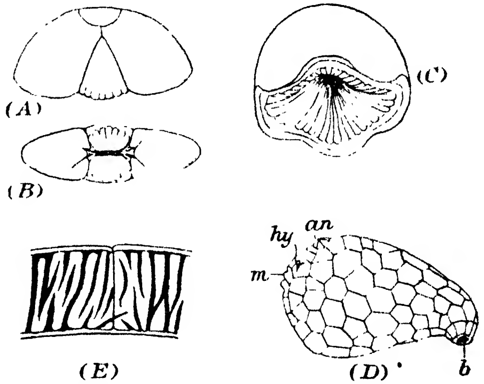


FIG. 97.—Primitive Echinoderms.

(*A*) *Peridionites*, side view. (*B*) Ventral view. (*C*) *Cymbionites*. (*D*) *Aristocystis*, side view of restoration of complete test. (*E*) Section of plate.

an, anus. *b*, base of attachment. *m*, mouth. *hy*, hydropore.

[*A–C*, after Whitehouse. *D*, after Brit. Mus. Guide.

Aristocystis and other allied genera may be spoken of collectively as the Amphoridea (Cam.-Sil.). Though they bear very little resemblance to modern echinoderms, their affinity with these is indicated by such facts as those just discussed, and by the existence of fossils, which exhibit various grades of structure tending to fill up the gaps between them and typical echinoderms. Their relationship to these is not to be regarded as that of an ancestral stock, but as that of survivals of such a stock; for by the Ordovician the main groups of echinoderms had nearly all become clearly differentiated, and easily recognizable representatives of some are found in Cambrian rocks. Evidently the birth period of the echinoderms could not have been later than the early Cambrian, and much more probably goes back to late pre-Cambrian. In the absence of fossil remains of the actual ancestral stock the well-preserved remains of these Ordovician survivors, or—as they may be called—collateral ancestors, serve as a good substitute. It must not be assumed that these survivors, simple as they are, had undergone no change. It is quite conceivable, for example, that they had progressed in the direction of the multiplication of plates, and that the earliest representatives of the stock were small and enclosed in only a few plates.

Flowlines of Structural Change in Attached Forms.—Starting from some such unspecialized condition as that seen in *Aristocystis* the various structures, which taken together make up what is called an echinoderm, underwent a number of modifications which produced the wonderful variety of known genera and species. These modifications were for the most part associated with only a very few factors. First among these was the statozoic habit. This necessitated a second factor, namely, a passive mode of feeding. A third and minor factor, as far as influence upon structures which were preserved was concerned, was the aeration of body fluids.

The organ of attachment to the sea-floor was, in its simplest form, no more than a slightly modified patch on the simple sac-like theca. In the vicinity of this patch the plates took on a definite arrangement (Figs. 97D, 98A). The next step (Fig. 98B) was the oncoming of a tendency towards the elongation, either of the whole theca or only of its lower portion (Fig. 98C), giving rise in the latter case to a stalk. At this early stage of its evolution, the stalk was merely a narrow prolongation of the theca, and like that it was enveloped in a number of irregularly arranged plates. At a later stage (Fig. 112) these became regularly or even radially arranged in a few vertical rows. Eventually those plates which lay near the same level became united, and formed ring-like ossicles or columnals. Meanwhile the cavity of this part of the body became reduced.

In the most primitive Pelmatozoa the plates (Figs. 97D and 100D, E) are numerous, small and irregular, both in size and arrangement. Specialization usually proceeded along the lines of a reduction in the number of plates, and a relative increase in the size of those plates that remained. These few plates became regularly arranged according to some plan of symmetry, sometimes bilateral but more usually radial. In the most advanced forms (Fig. 100B, C) the theca consisted of only three or four circlets with only five plates in each. In association with the attached habit the establishment of radial symmetry set in first near the point of attachment (Fig. 97D) and extended thence upwards. Meanwhile the necessity for an adequate supply of food was met by the evolution of various devices for carrying the food grooves, and extending their range.

Primarily there appears to have been only three food grooves (cp. Fig. 100D), a median anterior one, and a pair of posterior ones lying on either side of that sector of the theca in which the anus was situated. As a rule only traces of this triple arrangement can be detected (Edrioasteroidea) for each of the posterior grooves bifurcates close to its origin and thus a quintuple arrangement arises. With this there may be associated a radial arrangement of some of the thecal plates. Increased food supply could be obtained only by the extension of the main food grooves, and by the formation of minor tributary grooves. These two processes lend themselves naturally to a serial development of the grooves from short to long, and from few to many.

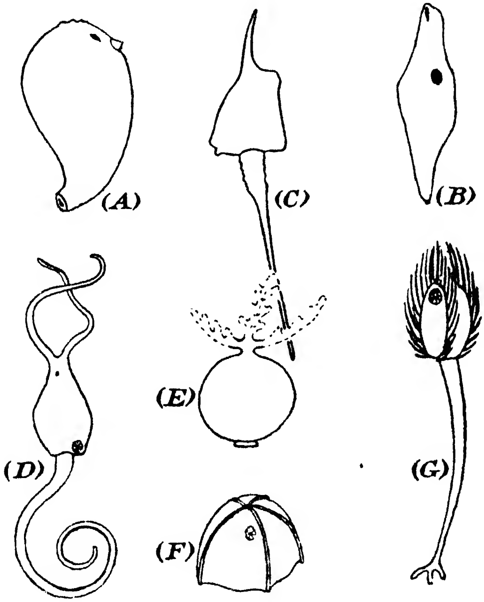


FIG. 98.—Adaptational Forms among Cystoidea.

(*A*) *Aristocystis.* (*B*) *Caryocystis.* (*C*) *Dendrocystis.* (*D*) *Pleurocystis.* (*E*) *Echinosphæra.* (*F*) *Mesocystis.* (*G*) *Lepadocrinus.*

[*G*, after Brit. Mus. Guide.

In some cases (Amphoridea, Fig. 99B) the food grooves rested on the surface of the theca, and merely elongated from the mouth towards the aboral pole, giving off short minor grooves at intervals (Fig. 100D). The thecal plates which underlay the grooves then became regularly arranged on either side of each groove, thus definite ambulacral areas (Fig. 98F) in the theca were instituted. The interambulacral plates remained numerous and irregularly arranged (Fig. 100D, E) for a much longer time (Edrioasteroidea). The acme of this line of development was attained, when, from the margins of the ambulacral areas, armlets or brachioles (Fig. 100C), consisting of single series of small ossicles, grew; and carried extensions of as many tributary grooves (*e.g.* Blastoidea). When these were spread out the area from which food could be drained was greatly increased.

In other cases (*e.g.* Rhombifera) (Fig. 98E, 99A) no part of the food grooves rested upon the theca, for they were carried above it by outstanding arms, supported by ossicles, which grew out from the immediate vicinity of the mouth. There again the acme of development was reached by the production of brachioles from the margin of the arms. Between these two arrangements of the food grooves there can be no transition. They are fundamentally different, and mutually exclusive; and therefore differentiate the stocks concerned from one another at the outset. Such characters are valuable for classificatory purposes, and may be referred to as differential characters. Once established they enter upon a progressive series of changes, and furnish a series of progressive characters.

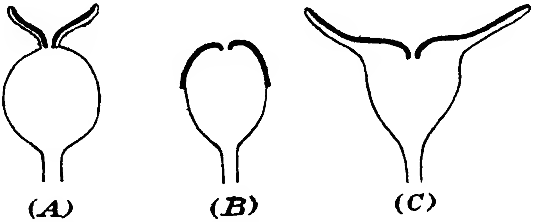


FIG. 99.—Diagrams showing different types of Relationship of Food Grooves (thick lines) to Theca in Pelmatozoa.

(*A*) Rhombifera. (*B*) Amphoridea, Diploporita and Blastoidea. (*C*) Crinoidea.

The most successful arrangement was that attained by the crinoids (Fig. 99C). Fundamentally it was a combination of the other two. The main food grooves extended for a portion of their course over the upper surface of the theca, and then passed on to strong arms or brachials which grew out from the uppermost row of plates of the abactinal surface. These arms were capable of

TABLE VI.—Distribution of Structural Elements among Pelmatozoa.

<table>
<tr><th></th><th colspan="8">Cystidea.
(Amphoridea, Rhombifera & Diploporita)</th><th colspan="2">Blastoidea.</th><th colspan="2">Crinoidea.</th></tr>
<tr><td>Stalk.</td><td colspan="2">Absent⁕</td><td colspan="10">Present.</td></tr>
<tr><td>Arrangement of thecal plates.</td><td colspan="3">Irregular.</td><td colspan="4">Regular along certain lines.⁕</td><td colspan="5">Quite regular.</td></tr>
<tr><td>Course of the main food grooves.</td><td colspan="5">On arms only.</td><td colspan="5">On thecal plates only⁕</td><td colspan="2">Partly on thecal plates and partly on arms.</td></tr>
<tr><td>Course of the minor food grooves.</td><td colspan="5">On theca only.⁕</td><td colspan="5">On Brachioles.</td><td colspan="2">On branching arms.</td></tr>
<tr><td>Types of symmetry.</td><td>None</td><td colspan="3">Bilateral</td><td colspan="2">Other than Pentameral.</td><td colspan="6">Pentameral.⁕</td></tr>
<tr><td>Provision for respiration.</td><td colspan="9">Stereom canals.</td><td colspan="2">Hydrospires.</td><td>Podial outgrowths of radial canals.⁕</td></tr>
</table>

⁕ shows the stages exhibited by the Edrioasteroidea.

branching indefinitely (Fig. 107), and when spread out extended the food-collecting area beyond that attained by either of the other two arrangements.

The establishment of a definite plan of symmetry did not extend to the whole body at once, but advanced concurrently with the perfecting of the means of attachment and of getting food. Nor was the actual plan of symmetry the same for all lines of descent. In a few, a more or less perfect bilateral symmetry was established. In the majority, however, the symmetry became radial, sometimes upon a three or six rayed plan, but more usually it became five rayed or pentameral.

The enclosure of the organism in an armour of calcareous plates naturally tended to interfere with the function of aeration of the body fluids. The minute structure of the plates seems, however, to have furnished a way out of the difficulty, in that it provided means whereby the inner fluids could come into close relation to the water outside. Whilst the plates were covered internally and externally by a thin calcareous layer, the main mass of the plate, consisting of stereom, was traversed by canals (Fig. 97E). In the most primitive forms (Amphoridea) these had no definite arrangement, but in more advanced forms they tended to lie parallel with the surface (Rhombifera) or to become perpendicular to the surface. In the latter case they were connected in pairs called diplopores (Diploporita). At first these pores were scattered indiscriminately over the body, but eventually (*e.g.* primitive blastoids) they became concentrated in the vicinity of the food grooves, where of necessity there was a constant flow of water. These diplopores next gave place (in typical blastoids) to a more complicated device (Fig. 101), the hydrospire. In this the stereom was thrown into a series of folds with their axes practically parallel to the food grooves. This system also became obsolete; and was replaced functionally by radial outgrowths from the water vascular system which lay in the grooves themselves (*e.g.* Crinoidea).

The Radiation of Attached Forms.—At such an early stage in the evolution of the echinoderms as that represented by the Amphoridea, the organization was in a very plastic state; and, during the Cambrian and Ordovician periods, gave rise to a wonderful variety of lines of descent. Some of these were limited in range and in the number of members, and soon became extinct. Others flourished vigorously, specialized rapidly, and died out, leaving no issue. Others, again, advanced more steadily, rose to predominance slowly, and ranged through vast periods of time and even on to the present day. Such a period of experimentation in the history of a race may be described as a period of radiation. Already during the Cambrian and Ordovician periods all the main types of echinoderms had come into being; and though about as many as 350 genera of attached forms are known, nearly one-third of these had already appeared. The Cystoidea, of which the Amphoridea are the most primitive representatives, were the dominant echinoderms during these two periods of time; and they reached their acme in the Ordovician. After that they declined in importance, and eventually became extinct in late Palæozoic times. (See Table VII, p. 121.)

The plasticity of this group of primitive forms is manifested by the fact that amongst them there was no settled mode of adaptation (Fig. 98) to the attached habit. Some, having a spherical or oval form, appear to have floated about. Others were attached only temporarily by cementation of some part of the theca to a fixed object. Others exhibited the various grades of column formation described above. In those which had this organ most perfectly developed, its terminal portion could be either coiled and used as a prehensile organ, or it could be rigidly cemented to stones or other objects. Perhaps the most extraordinary modification was that (Fig. 100A) shown in various degrees by *Trochocystis* (Camb.), *Mitrocystis* (Ord.) and *Placocystis* (Sil.). In these the body was compressed to a biconvex or a concavo-convex form. The mouth and other openings, together with a pair of spines, were situated on one margin, and the column was articulated to the opposite margin.

The majority of Cystoidea, however, exhibit a tendency towards a radially symmetrical plan of structure. Among these the chief differentiating tendency was associated with the food-gathering apparatus. This was either carried upon arms arising from the immediate vicinity of the mouth (Fig. 99), as in the Rhombifera, or it extended over the surface of the theca, as in the Diploporita.

With each of these became associated one of two arrangements of the stereom canals. In the former they generally ran parallel to the surface, in the latter they were usually at right angles to this.

The Rhombifera appear to have had their origin in some such simple form as the amphorid genus *Eocystis* (L. and M. Camb.). In this simple sac-like organism ten arms bearing food grooves arose near the mouth. The thecal plates were still very numerous and irregularly arranged, and many of them showed a radial marking or folding of the surface. Though not represented by many fossils from British rocks, the Rhombifera exceeded all other Cystoidea in numbers and variety of genera. The two familiar British genera, *Macrocystella* (Trem.) and *Lepadocrinus* (Sil.) illustrate the advanced stage of specialization which might be attained in some members of this order.

In *Macrocystella* (Fig. 100B) almost perfect radial symmetry had been attained. The thecal plates were large, but were reduced in number to four circlets with five plates in each. The individual plates showed the strong radial folding characteristic of Rhombifera. The theca bore, at its upper end, five bifurcating arms ; and its lower end passed into a long stalk, which tapered gradually, and which, during life, was either anchored in the mud or coiled round some object. *Lepadocrinus* (Fig. 100C) differed from *Macrocystella* mainly in the fact that the arms carrying food grooves, of which there were only four, lay down in contact with the theca ; and each bore two parallel series of armlets or brachioles, which in turn carried tributary food grooves. Moreover, the lower end of the stalk was attached by cementation to the sea-floor. Having attained such an advanced stage of specialization in so many characters, it is not surprising that the Rhombifera, which had already reached their acme in the Ordovician, became extinct at the close of the Silurian, and do not appear to have given origin to any new types.

The Diploporita on the other hand retained the simple sac-like form, undifferentiated stalk, and numerous thecal plates of the Amphoridea. Even in the more advanced forms, such as *Mesocystis* (Fig. 98F) and *Proteroblastus*, it was only those plates which were associated with the food grooves that became regularly arranged. It is probable that tubular outgrowths of the water vascular system extended along the food grooves, and produced podia which would serve the purposes of respiration or even of the prehension of food. This race attained its acme in the Ordovician, but isolated genera occur as late as the Devonian. Not later than the close of the Ordovician some portion of this diploporitid stock entered upon a career of specialization, which ran parallel to that already described for the more advanced Rhombifera. They developed a stalk, their plates became reduced in number, of increased size and arranged upon a radially symmetrical plan. The food-collecting apparatus was improved by the appearance of a fringe of brachioles on either side of the food groove. In this case, however, this specialized section of forms attained such stability and importance that it has been placed in a separate class, the Blastoidea, of equal classificatory importance with the Cystoidea.

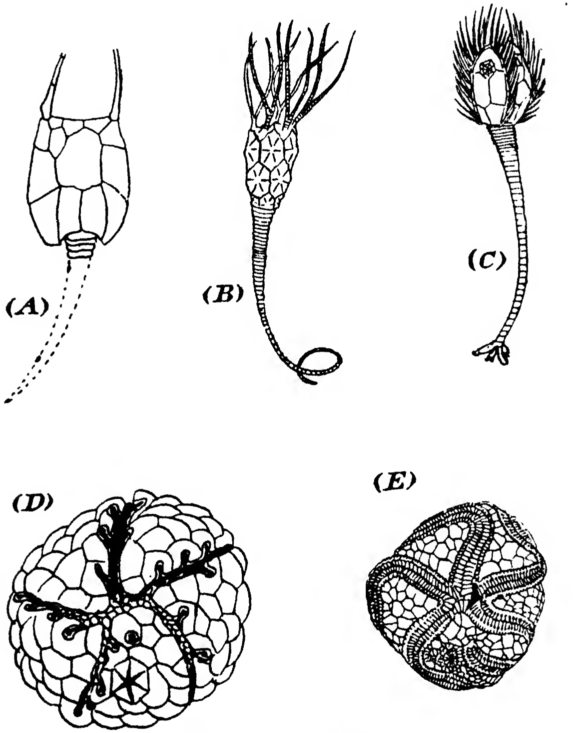


FIG. 100.—Various Pelmatozoa.

(*A*) *Placocystis*. (*B*) *Macrocystella*. (*C*) *Lepadocrinus*. (*D*) *Prolocrinus*. (*E*) *Edrioaster*.
[*A*, *B*, *E*, after T. Z., Messrs. A. & C. Black. *C*, after Brit. Mus. Guide.

Some idea of the mode of transition from the Diploporita to the Blastoidea may be gained from the study of such a lowly blastoid as *Asteroblastus* (Ord.). In this the usual five food grooves radiated from the mouth and extended on to the theca; but, as in typical blastoids, the thecal plates, between which these grooves ran, became regularly arranged and alternated with one another on either side of each groove. Thus a clearly defined ambulacral area consisting of side or adambulacral plates was established. The three circlets of plates, which constituted the remainder of the theca in any typical blastoid were recognizable. They were the five deltoids around the mouth, the four basals around the aboral pole, and the five radials in between. Between the latter two circlets, however, there were from twenty-five to fifty polygonal plates, the presence of which gave to the theca a cystidean appearance. This resemblance was further emphasized by the presence of diplopores in most of the plates. These were especially numerous upon a few plates situated between the radials and the deltoids.

Typical blastoids (Fig. 101) existed during the Devonian, became abundant during the Carboniferous and disappeared before its close. In them the thecal plates settled down to a definite arrangement and number, viz., five deltoids, five radials and three basals. Early development shows that these last did not arise by fusion. Each radial plate forks at its oral end, and has a deep notch or sinus between the prongs. This notch is occupied by a plate, peculiar to this class, which by reason of its shape is aptly called the lancet plate. The adambulacrals or side plates carrying brachioles upon their edges, constitute the ambulacral areas.

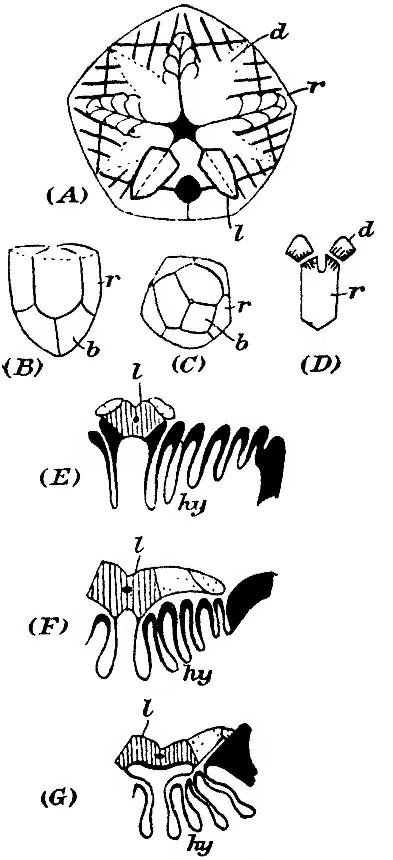


FIG. 101.—Structural Features in the Blastoidea.

(*A–E*) *Codaster*. (*A*) Oral aspect. (*B*) Lateral aspect of theca. (*C*) Aboral aspect. (*F*) *Phænoschisma*. (*G*) *Pentremites*.

b, basal. *d*, deltoid. *hy*, hydrospire. *l*, lancet plate. *r*, radial.

[After T. Z., Messrs. A. & C. Black.

A very distinctive feature of the typical Blastoids is the absence of diplopores, and their functional replacement by a new device called the hydrospire. The hydrospire is confined to the prongs of the radials, and to the adjoining portions of the deltoid plates. It is formed by a remarkable folding of the stereom of these plates. The axis of folding is, roughly, parallel to the food grooves. The lancet plates lie between the members of each pair of hydrospires. In more primitive genera, such as *Codaster* (Fig. 101E) (Carb.) they are visible on the outer surface of the fossil. Specialization proceeds in two main directions. The one affects the ambulacral structures themselves which may widen and, by extending over the outer surface of the hydrospire, may shut it off from external view. In this case a series of small apertures is left along the margin of the ambulacrum, through which water may have passed to the hydrospire, and gained exit by a larger aperture at the oral end of the ambulacrum, or *vice versa*. In the other line of specialization the outer margins of each hydrospire area come closer and closer together, and the hydrospire itself tends to hang down into the thecal cavity. Various stages of specialization are shown by the Carboniferous genera *Codaster* (Fig. 101E) *Phænoschisma* (Fig. 101F), *Pentremites* (Fig. 101G) and *Orbitremites*).

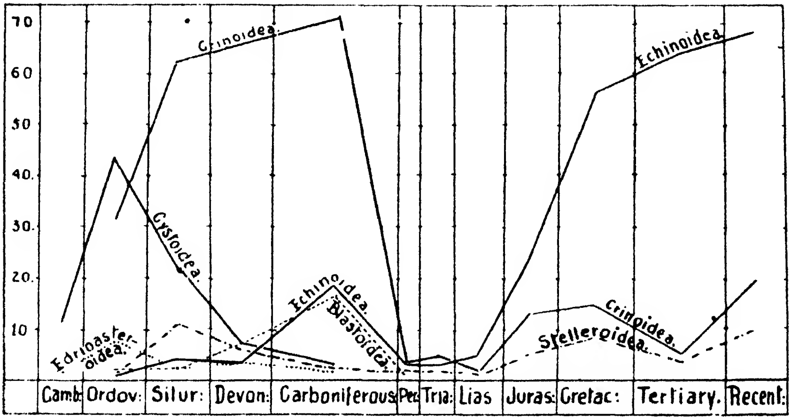
In common with other groups of attached echinoderms there are indications that some of the blastoids regularly resorted to eleutherozoic habits. Thus in *Pentremites* the stalk often tapers off to a point distally. *Eleutherocrinus* has lost its stalk completely. Moreover, whilst four of the ambulacral areas extend almost to the oral pole, one is so short that it is confined to the oral surface. The creature was thus able either to lie or slide freely upon the corresponding side of the theca.

Whilst it is possible to trace the relationships to one another of many different types of attached echinoderms with some degree of certainty, this cannot be done for the longest ranged and most important class, the Crinoidea. These were already represented by one species which was in every respect a typical crinoid as early as the Lower Cambrian. During the Ordovician, representatives of all the Crinoid orders were in existence. Even in present-day seas many species of crinoids, and multitudes of individuals, are still found and will be considered more fully subsequently.

Contemporaneous with the Cystoidea was a small group of forms, the Edrioasteroidea, having structural features in common with that class on the one hand, and with Asteroidea on the other. The test (Fig. 100E) which consisted of an indefinite number of irregularly arranged plates, was of depressed shape, and rounded or pentagonal outline. It was attached by some indefinite point on the aboral surface, which in some cases, *e.g. Edrioaster*, was modified into a sucker-like apparatus. The mouth, anus and five radiating food grooves, were situated on the upper surface. Already in Cambrian times the plates adjoining the grooves had become regularly arranged, and were related to one another like the ambulacral ossicles of the

TABLE VII.—Showing distribution of different Types of Echinoderms in time, and the relative abundance of each during the various periods.

Vertical height represents approximately the number of known genera.



starfish; and, as in that type they formed a wide ambulacral groove. Along the centre of this there ran a radial canal with branches and podia as in the starfish. The presence of pores between the ossicles points to podia having been connected with ampullæ within the theca. The ambulacral groove was roofed over by a similar double series of plates, the roofing or cover plates, attached at their outer ends to the ambulacral ossicles. They could be lifted up, thus exposing the ambulacral apparatus with its podia and ciliated food groove. The flattened, almost disc-like, shape of the body and the curvature of the ambulacra secured a maximum of extension of the food-collecting apparatus.

CRINOIDEA

The Structure and Life History of Antedon.—The genus *Antedon* is a free-swimming crinoid, having a world-wide distribution in modern seas. Those species which live around the British Isles occur at a depth from ten to twenty fathoms. The animal has an almost hemispherical body (Figs. 102, 104); the flat side being the ventral or oral surface; and the convex being the dorsal or apical surface, which is made up of calcareous plates or ossicles. From the junction of the two surfaces there arise ten long arms, consisting of series of calcareous pieces or ossicles, each of which usually bears a small arm or pinnule. The mouth is situated in the centre of the ventral side (Fig. 104), which is covered by a soft skin or integument unprovided with calcareous plates. Five food grooves radiate from the mouth, and presently bifurcate sending one branch to each of the arms. These grooves run along a channel on the ventral side of the arms, and give off branchlets to the pinnules.

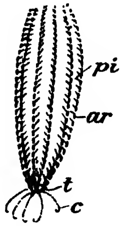


FIG. 102. Adult, *Antedon*.

ar, arm. *c*, cirrus. *pi*, pinnule. *t*, theca.

Close to the centre of the dorsal surface twenty to thirty unbranched arm-like structures arise called cirri (Fig. 102). These have a dorsal curvature and each bears a claw-like ossicle. These cirri function as prehensile organs whereby the animal attaches itself to shells, pebbles and other suitable objects. The animal spends most of its time attached thus, but when occasion requires, as for example at the breeding season, it may release itself and swim away, propelling itself by gentle movements of its long pinnule-bearing arms.

The eggs of *Antedon* like those of other Echinoderms give rise to free-swimming larvæ, which eventually attach themselves to some solid object by their anterior ends. The period of attachment in this case is much longer than for any other of the Echinoderm types, and the anterior end becomes drawn out into a long stalk. Meanwhile, the vital organs shift their position in the body until the mouth, anus and hydropore come to be situated at the free end. Already at this early stage (Fig. 103A) the calcareous skeleton has begun to appear and consists of two sets of ossicles. One set (columnals) is in single series along the axis of the stalk. The other set consists of three circlets having five ossicles in each. These enclose the vital organs and constitute the theca. One circle of ossicles (orals) lies round the mouth. Another (basals) surrounds the main mass of the vital organs. The third lies close to the upper end of the stalk, and includes the infrabasals.

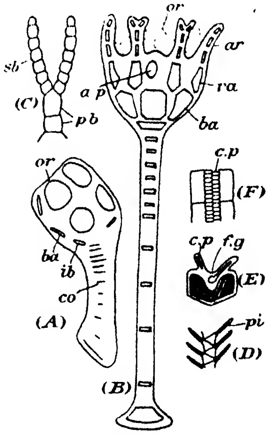


FIG. 103.—Development and detailed Structure of *Antedon*.

(*A*) Larva soon after attachment. (*B*) Later but still attached stage. (*C*) Young arm. (*D*) Structure of adult arm. (*E*) Section across arm. (*F*) Oral view of portion of the arm.

ar, arm. *a.p*, anal plate. *ba*, basal. *co*, columnal. *c.p*, cover plate. *f.g*, food groove. *i.b*, infrabasal. *or*, oral. *p.b*, primibrach. *p.i*, pinnule. *ra*, radial. *sb*, secundibrach.

During further development the new columnals (Fig. 103B) are added below the top one which joins the theca later. In the latter another circlet of six plates puts in its appearance between the orals and the basals, and these plates grow until they are equal to the latter in size. Five of these new plates (radials) alternate with the basals. The three circlets—radials, basals and infrabasals—together are called the patina. From each radial plate a series of ossicles, or brachials, grows out to form the incipient arms. The sixth plate (anal), which is smaller than the others, is associated with the anus, and marks the posterior interradius. Thus at this stage the young *Antedon* exhibits all the essential characters of a typical crinoid, having its body enclosed dorsally as well as ventrally by plates. That portion of the theca which lies on the oral surface is called the tegmen. That which lies below the level of the arms, that is to say, which is dorsal or apical, is the calice or cup, and consists up to this stage only of the patina.

During the further growth in the size of the animal the orals remain small and near the mouth, whilst the tegmen extends and becomes covered by integument. The anal aperture, which opens on the posterior interradius, is borne upon a projecting tube. In association with the growth of this the anal plate rises out of the circlet of radials for a while and then degenerates and disappears. The arms increase in length by the addition of fresh ossicles at the end. These brachial ossicles (Fig. 103C–F) are like short rods with a channel running along the oral side. The two first formed ones are called primibrachs. Beyond these the arm bifurcates, and the ossicles which make up the two branches thus formed are the secundibrachs. In *Antedon* these constitute the main portion of the arm, so that the animal appears at first sight to be provided with ten arms. The pinnules arise alternately on opposite sides of the arm on successive ossicles. They carry extensions of the food grooves, and also bear fertile portions of the sexual organs.

The formation of new columnals (Fig. 103B), which takes place at the junction of the stalk and the patina, ceases when about twenty to twenty-four have been formed. At the same time the topmost columnal (proximale) increases in size, becoming convex below and concave above. It thus comes to cover up first the infrabasals, and eventually the basals also. It may also extend over the radials. Meanwhile the apical elements fuse with it and a compound structure is formed which, when it bears cirri, is called the centrodorsal. Shortly after the stem has ceased to grow, the body with its arms breaks off below the centrodorsal, and henceforth the creature leads a free existence. During all these changes there has been going on a morphological extension of the calice (Fig. 104A) or theca, which has led to the incorporation of the lower portions of the arms, including the bifurcation and several of the secundibrachs. The apical portion of the body now no longer consists merely of the patina. The food grooves become similarly incorporated in the tegmen (Fig. 104B). The interradial spaces of this extended theca are occupied both dorsally and ventrally by integument.

The Simplest Crinoids.—It has been already noticed that the theca of *Antedon* is more simply constituted in the early stages of development than in the adult. Indications of a like simplification are shown as the development of some of the more complicated Palæozoic crinoids is traced back to its early stages. These embryological facts seem to indicate that the most primitive crinoids are those in which the theca consisted only of the patina and orals. Though the early stages in the evolution of the crinoids from a previous stock are quite unknown, some crinoids are known which in the adult state show a type of theca practically as simple as that of the larva of *Antedon* and of some fossil forms. On this account they are described as larviform. Except for its tegmen, *Hybocrinus* (Fig. 105A) (Ord.-Sil., N. Amer.) is such a larviform crinoid. Its arms are unbranched, uniserial, and devoid of pinnules. The tegmen (Fig. 110) has advanced beyond the larviform condition since, in addition to the five orals, it has a series of plates covering the food grooves and overlapping the edges of the orals. Moreover, the posterior interradius is larger than the others and contains a number of small plates which have, as it were, pushed the corresponding oral more towards the centre. The patina (Fig. 105) consists of only two circlets, namely the radials, occupying the sides of the cup, and the basals occupying the floor. It thus differs from the larval *Antedon* in the absence of infrabasals, and in the fact that the anal plates lie above the radial circlet.

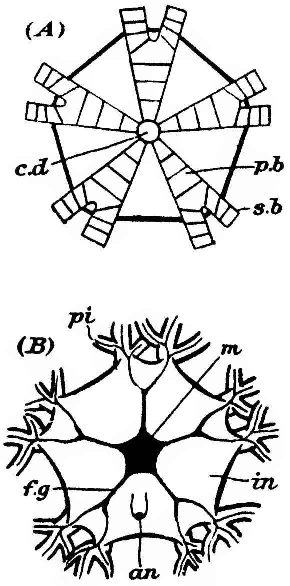


FIG. 104.—The Theca of *Antedon*.

(*A*) Apical aspect. (*B*) Oral aspect. Note the extension of theca to include the proximal portions of the arms and food grooves.

an, anus. *cd*, centrodorsal. *f.g*, food groove. *in*, integument. *m*, mouth. *p.b*, primibrach. *pi*, pinnule. *s.b*, secundibrach.

Mysticocrinus (Fig. 105B) (Sil., N. Amer.) belongs to a similar grade. Its arms are very short and each consists, like that of a larval *Antedon*, of two primibrachs and of a pair of uniserial branches with only three secundibrachs. The tegmen is unknown. The patina, like that of the very early stages of *Antedon*, consists of three circlets, the upper with five radials and an anal, the middle of five basals, and the lower of three infrabasals. Two of these last are larger than the third and have probably each been formed by the fusion of two plates.

Some larviform crinoids occur also in the later Palæozoic rocks. The best known among these is *Cupressocrinus* (Dev.). This is a massive-looking form which, like *Mysticocrinus*, has infrabasal elements, but unlike that has no anal among the radials. Its arms are very stout, unbranched, and with but few ossicles. The food grooves are covered by large plates which have occasionally been mistaken for pinnules. The tegmen consists of five orals, of which the posterior one has its hinder margin notched for the passage of the anus.

A fundamental difference shows itself among these lowly types, as in the first named genus the floor of the calice is made up of only one circlet of plates (basals), whilst in the other genera mentioned there are two circlets (basals and infrabasals). The former condition is described as monocyclic (Fig. 105A), the latter as dicyclic (Fig. 105B). This same difference can be detected among crinoids in general, and appears to be associated with two quite divergent arrangements of the thecal nervous system. As yet no satisfactory evidence has been forthcoming to show the way in which one condition can be converted into the other. This difference is, therefore, to be regarded as a differential character of some importance. On this account the crinoids are divided into two great classes—the Monocyclica and Dicyclica respectively. It is unfortunate that the dicyclic condition is not always easy to detect, and that in some cases the infrabasals degenerate and disappear (*e.g. Antedon*). In the latter case the nervous system is still dicyclic in character though the organism appears to be monocyclic externally. Such forms are described as being pseudomonocyclic.

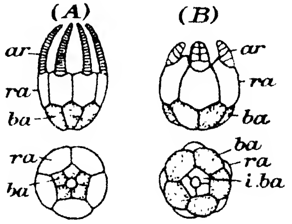


FIG. 105.—Structure of Theca in (*A*) *Hybocrinus* (monocyclic); (*B*) *Mysticocrinus* (dicyclic).

Upper row, side view. Lower row, apical view. *ar*, arm. *ba*, basal. *i.ba*, infrabasal. *ra*, radial.

The origin of the crinoids is still an unsolved mystery. There can be little doubt, however, that they have ascended through a larviform grade of structure similar to that retained by the types described above. A few isolated facts throw some light upon the probable prelarviform stage. Of especial interest, in this connection, are the facts that the orals of *Hybocrinus* are known to bear traces of hydrospires, and that in the closely allied *Hybocystis* the food grooves extend beyond the oral surface on to the radials or even the basals. These facts, together with the small number of plates and their symmetrical arrangement, point back to a blastoid-like stage in evolution. The existence, however, of typical crinoids in the lower Cambrian renders it improbable that the blastoids already described belonged to that ancestral stock. On the contrary, it is more likely that the crinoid stock lay upon another line of descent, which in its earlier phases developed along lines parallel to those of the blastoid series. The Rhombifera appear to fulfil the conditions.

In some Crinoids (*Botryocrinus*, *Iocrinus*) a part, or all of the stem (Fig. 112) may consist, not of bead-like columnals, but of five vertical rows of hexagonal plates. It is not difficult to imagine how such a stem could have been derived from such a condition as that exhibited by some cystids in which the stem is merely a constricted extension of a many-plated theca. If this fact has any phylogenetic significance it points back to a cystidean predecessor of the blastoid-like ancestor already discussed.

The Arms of Crinoids.—In the development of *Antedon* the changes in structure which marked the passage from the larva to the adult, consisted mainly in an increase in the complexity of the arms, and in an extension of the theca. These are likewise the two main types of change manifested by crinoids in their evolution. Both were, however, expressed in a number of different ways.

The simplest form of arm was that already described for *Hybocrinus* (Fig. 105) and *Cupressocrinus*, in which it consisted of a single series of ossicles. In the former genus the number of these exceeded twenty, in the latter it was from three to fifty. These bore upon their upper, or ventral, surfaces food grooves protected by a paired series of "cover plates." During life the food grooves, like those of living crinoids, must have been provided with numerous cilia which by their concerted movements set up currents of water flowing along the grooves from the apex of the arms towards the mouth. Minute organisms caught in this current furnished a supply of food which was thus drawn from an area (food area) enclosed by a circle, passing through the extremities of the arms. The series of structural changes exhibited by the arms of crinoids appear to have followed lines leading to ever-increasing efficiency in the draining of this area. In the simple type of arm mentioned above, increase of food supply was secured by mere elongation of the arms. The food area was thus extended, but between the arms wide interradial spaces were left undrained.

In the larval *Antedon*, after the formation of the two first primibrachs, the end of the arm swelled and bifurcated giving rise to two branchlets with several secundibrachs. This condition was apparently permanent in *Mysticocrinus*. In other crinoids bifurcation was repeated. In *Ichthyocrinus* (Fig. 109) it took place twice, giving rise to four branchlets, consisting of tertibrachs. In *Cyathocrinus* (cp. Fig. 107A) the number of bifurcations rose to as many as five, six, or even seven. As the result of such complex branching the food area was occupied by a network of food grooves, and was therefore drained with great efficiency. In certain forms having this arrangement of food grooves there was an exceptional shortening of the proximal portions of the arms (Fig. 111). The outcome of this was that the more distal branches were drawn towards the centre, and became crowded together. In *Crotalocrinus* they even became fused or intimately united with one another in the form of fan-like nets.

This food-collecting system was by no means perfect. The spreading of the numerous terminal branchlets around the whole periphery (Fig. 107) tended only to set up a drift of water towards the food area, which moved too slowly to prevent the escape of many minute organisms. Other modifications tended towards an arrangement of the armlets which concentrated the flow of water along a few definite lines, converging radially upon the mouth, and thus to produce stronger currents. In the cases considered above, the branching system was isotomous (Fig. 106), that is to say the branchlets produced at each bifurcation were equal. In another, the heterotomous system of branching (Fig. 106, 107B), the twin branchlets were of unequal size (*e.g. Taxocrinus*). The shorter branchlets drained the centrally placed and larger meshes of the food collecting network. The longer members on the other hand bifurcated more frequently and thus extended the food area at its periphery (*e.g. Calpiocrinus*).

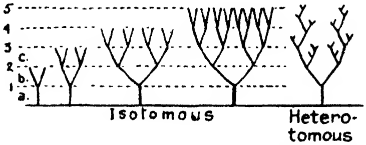


FIG. 106.—Types and Degrees of Bifurcation of the Arms.

1–5, Degrees of bifurcation. *a*, primibrachs. *b*, secundibrachs. *c*, tertibrachs.

Perhaps the most effective improvement was the production of pinnules (Figs. 107C, 108). These were miniature branches, consisting of a single row of ossicles which had lost the capability of bifurcation. Each ossicle in an arm was capable of producing one pinnule, and successive ossicles bore them alternately upon opposite sides (Fig. 108). Pinnules were borne most abundantly upon the distal branches. By reason of their superior numbers they were functionally more efficient than mere terminal branchlets. The latter were frequently no longer produced and so pinnulate arms bifurcated only a few times (*e.g.* *Tanaocrinus*). With a more advanced state of pinnulation branching ceased sometimes at the second (*Hapalocrinus*, *Marsipocrinus*), more frequently at the first, bifurcation (*Botryocrinus*). The terminal branches, which now numbered only twenty or ten, were much elongated and, with their pinnules, looked like feathers. When spread out and extended they drained the food area very efficiently ; when not spread out they closed compactly (*Eucalyptocrinus*, *Encrinus*). Further progress now lay in the direction of an increase in the number of pinnules for a given length of arm. This was brought about by a modification of the pinnule bearing ossicles (Fig. 108). These shortened and became wedge-shaped. The points of the wedges

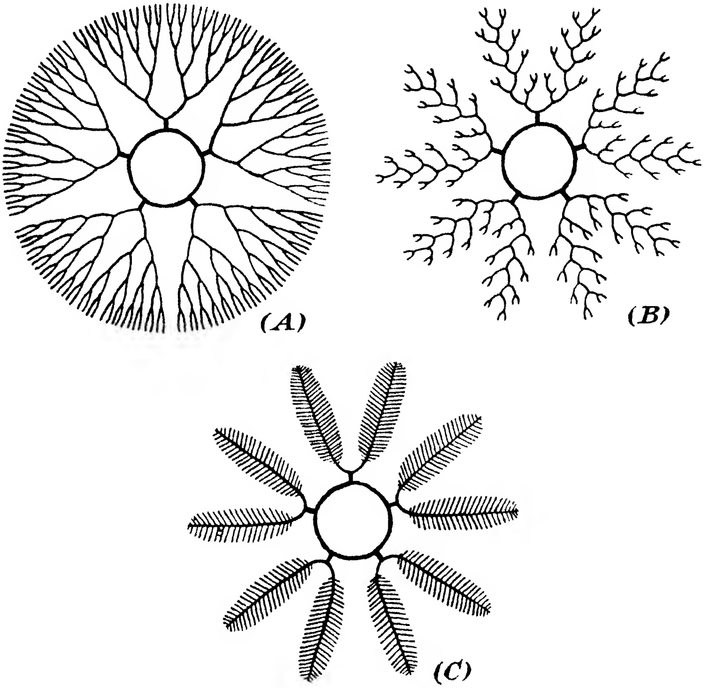


FIG. 107.—Types of Branching System in Crinoid Arms.

(*A*) Isotomous. (*B*) Heterotomous. (*C*) Pinnulate.
Circle = theca, thick line = base of arm consisting of primibrachs.

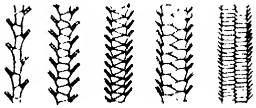


FIG. 108.—Evolution of Biserial from Uniserial type of Branch.

(After T. Z., Messrs. A. & C. Black.)

were then withdrawn from the margin of the centre of the arms and thus ossicles, which once followed one another in succession, now lay alongside of one another, that is to say were biserially arranged. The corresponding pinnules likewise came into line with one another. This process set in at the apices of the arms, and extended downwards towards the base.

The changes in the arms discussed above, though they introduced an extraordinary variety of form and pattern, do not furnish differential characters of great diagnostic value for larger groups. The marked shortening of the proximal portions of the arms, which set in during the Silurian, and which was manifested in its fullest development by *Marsipocrinus* and *Crotalocrinus*, played an important part in the adunate modification dealt with more fully later. The presence or absence of pinnulation was already manifested by Ordovician crinoids and has been found of diagnostic value in some divisions larger than families. Generally, however, large sections of these changes took place within the limits of a family and therefore serve only the purposes of specific and generic identifications.

The Theca of Crinoids.—In many crinoids, as in the simple forms (Fig. 105) already considered, the dorsal portion of the theca is confined within the limits of the patina, whilst the ventral portion is closed in by the five oral plates alone or with a number of small plates added (Fig. 110A, B). Such forms as these are described as the Inadunata to distinguish them from several not less important assemblages in which the theca extends beyond the limits of the patina. The physiological necessity for this extension is not so evident as for the modifications of the arms. It is possible, of course, that the increased efficiency of these created a necessity for greater storage capacity to cope with the more abundant supply of food.

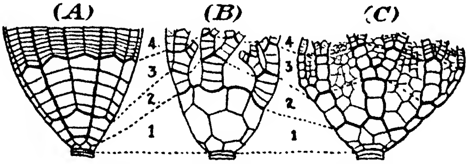


FIG. 109.—Methods of incorporating the proximal portions of the Arms in an extended Theca.

(*A*) *Ichthyocrinus* (incorporation unaccompanied by formation of interbrachials). (*B*) *Cyathocrinus* (condition before incorporation) (after Bather). (*C*) *Sagenocrinus* (incorporation accompanied by formation of interbrachials). 1, patina. 2, primibrachs. 3, secundibrachs. 4, tertibrachs.

The extension of the theca involved several changes. First and foremost among these was the incorporation of the proximal portions of the arms in varying degrees up to and including the second bifurcation (Fig. 109). The corresponding portions of the food grooves passed on to the tegmen, so that each food groove as it ran from the mouth to the free parts of the arm bifurcated once or twice also (Figs. 104, 110). When this extension involved only the arms, the latter widened sufficiently to come into flexible union with one another (Fig. 109A). In the majority of cases, however, the arms remained separate, and the interval between them, which in *Antedon* is occupied by membrane, was filled by the formation of new plates (Fig. 109C), the interbrachials. These varied in number from one upwards. When secondary and tertiary sections of the arms were included additional interbrachials appeared between the branches. The posterior interradius, in which the anus lay, was frequently wider than the others, and had a correspondingly larger number of plates, of which the lowest is called the anal plate. This either rested upon the shoulders of a pair of radials, or sank between them and formed a sixth plate within the radial circlet. Among some of the more specialized Dicyclica the lowest plate in each of the other interradii followed suit, and thus the number of plates in the radial circlet was doubled.

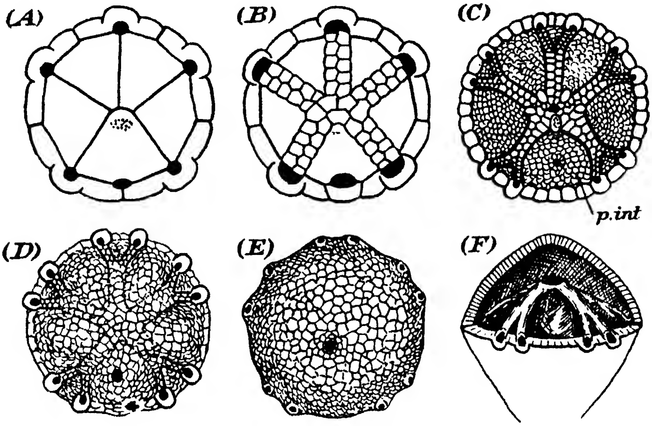


FIG. 110.—Types of Tegmen in Crinoids.

(*A*) With orals only and food grooves open. (*B*) Orals prominent, food grooves covered with ambulacral plates. (*C*) Orals reduced, food grooves incorporated beyond their first bifurcation and covered with plates, numerous interambulacrals. (*D*) Food grooves partly sunk below the surface. (*E*) Food grooves completely sunk below the surface. (*F*) Diagram illustrating internal structure of *E*.

A, *B*, from Bather. *C*, *D*, modified after Wachsmuth and Springer.

Whilst such changes took place in the dorsal region, similar ones affected the tegmen (Fig. 110). In this case, however, the primary elements, namely the five orals, tended to decrease in importance (Fig. 110C) and even ultimately to vanish. On the other hand the ambulacral elements remained and many interambulacral plates were formed. Here again, as with the dorsal region, the posterior interradius tended to become more extensive than the other interradii. The numerous interambulacral plates which covered it bulged upwards thus giving rise to the fistulate condition. This bulge often bore the anus at its apex. In this case it is called the anal tube. This was sometimes so high that it carried the anus upwards on to a level with the tips of the arms when these were closed (*Eucalyptocrinus*). The animal was thus able to extrude the indigestible portions of its food without polluting the food-collecting surface of its arms.

In the most specialized crinoids the mouth and food grooves, with their accompanying oral and ambulacral plates, which had hitherto been exposed at the surface, now sank below, and became hidden from view by the overgrowth of the interambulacrals (Fig. 110D, E, F). The ambulacrals formed tubes or tunnels from the bases of the free arms to the mouth. During the extension of the theca to include brachials, interbrachials, ambulacrals and interambulacrals, the plates at first were all loosely connected with one another and the theca was consequently flexible (*e.g. Ichthyocrinus* (Fig. 109A), *Tanaocrinus* and *Sagenocrinus* (Fig. 109C). This condition, together with the exposed food grooves, was retained by a number of lines of descent which are grouped together as the Flexibilia. Along other lines of descent the plates became fixed and the tegmen, which now hid the food grooves from the surface, formed a firm roof to the body cavity, which no longer bulged up or flattened down with the closing and opening movements of the arms. Forms exhibiting this modification are grouped together as the Camerata.

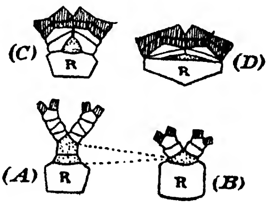


FIG. 111.—Evolution of the Adunate condition.
(*A*) *Hapalocrinus*. (*B*) *Platycrinus*. (*C*) *Marsipocrinus*. (*D*) *Crotalocrinus*. (is a homœomorph and not a derivative of *Marsipocrinus*).
Dotted area = Primibrachs.
Lined area = Tertibrachs.

Certain genera with camerate tendencies are characterized by an exceptional amount of shortening of the proximal portions of the arms (Fig. 111). This combination of shortened arms with some degree of extension of the theca appears to be a differential feature of some importance and is described as the adunate condition. The assemblage of forms which exhibits it is classed as the Adunata, and ranged from the Silurian to the Carboniferous. In *Hapalocrinus* (Sil.-Dev.) only the primibrachs were incorporated. In *Platycrinus* (Dev.-Carb.) the secundibrachs, and in *Marsipocrinus* (Sil.) and *Crotalocrinus* (Sil.) the tertibrachs also were involved.

Crinoid Stems.—Reference has already been made to the possible origin of the crinoid stem as a many-plated outgrowth of a cystidean-like theca. Among lower palæozoic crinoids these stem plates, like thecal plates, had settled down to a pentameral arrangement, that is to say they were arranged in five vertical rows around a moderately spacious central cavity or lumen.

In such a form as *Botryocrinus* (Sil.) the steps by which this primitive type of stem was converted into the more familiar later type with ring-like columnals and small lumen, are illustrated within the limits of one stalk (Fig. 112). This stalk consisted at its lower end of five vertical rows of hexagonal plates which alternated with one another. Higher up, the plates changed their position in such a way that those which adjoined one another lay at the same level. Here then the stem consisted of five pieces, *i.e.* it was quinquepartite. Half-way up the stem these pieces fused with one another, and thus gave rise to typical ring-shaped columnals. Meanwhile, the lumen was reduced in diameter, but was still large enough to allow of the passage through it of extensions of the nervous system and of other organs. The presence at different levels of columnals representing successive phases in the evolution of these structures furnishes an illustration of the phenomenon known as "localized stages in development" which recurs frequently in other animals (*vide* Figs. 131, 182–184), and which often supplies clues to the stages in the evolution or development of structural elements.

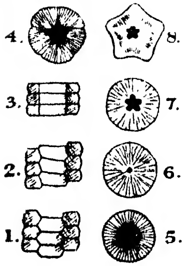


FIG. 112.—Stages in the Evolution of the Columnal.
1–4, *Botryocrinus.*
5–8, Typical Columnals.
(After T. Z., Messrs. A. & C. Black.)

In later Palæozoic crinoids (Fig. 112) the columnals are usually ring-shaped, with radiating striæ upon their upper and lower articular surfaces. Among Mesozoic crinoids the columnals exhibited a greater variation in shape. Isolated columnals are common as fossils, but as yet the information relating to them has not been sufficiently systematized to give them much value for stratigraphical purposes. The crinoid stem grows in height by the addition of new columnals at its junction with the theca. New ones may also be intercalated between previously formed columnals, which then assume a nodal character, and bear such cirri as may be present upon the stem. In a number of crinoids, in later life, new columnals put in their appearance below instead of above the topmost columnal which is called the *proximale.* This latter may fuse with the lower elements of the patina, which become reduced. This columnal is then referred to as the centrodorsal and may bear cirri.

The life history of *Antedon*, taken as a whole, illustrates the fact that the crinoid organization is not necessarily limited to a fixed mode of existence. Though the lower end of its stalk was immovably attached to the sea-floor, nevertheless at an early stage the animal broke away from the stalk below the topmost columnal. It then developed cirri upon this element and used them as a means for temporary attachment at any suitable spot it discovered. At times, especially during the breeding season, it swam about freely in the open water.

There are many modifications among fossil forms that, despite the predominance of well-developed stalks, show that lifelong fixation was by no means universal. Indeed, there are some which possess neither stalk, nor any other apical means of attachment, and which could only have led a free swimming or floating mode of life. The nature of the sea-floor mainly determined the method of fixation. When it consisted of mud the lower end of the stalk ramified (Fig. 113B) like the root of a tree, and thus gained a hold upon the loose ground. On harder floors a deposit of calcareous cementing material (Fig. 113A) was secreted around the base of the stalk, which was thus held rigidly in position. Under both circumstances accidental breakages must have occurred, as they do to-day among living crinoids. In other cases, however, the organism liberated itself of its own accord by resorbing the columnals at some point of the stem. In any case the creature could still live. It either drifted with its crown upwards, and its stalk dangling below; or it turned turtle and moved along the floor by means of its arms. Some instances are known of the secretion of stereom over the fractured end of the stalk and these throw light upon the possible mode of origin of such forms as *Myrtillocrinus*, in which the free lower end of the stalk is swollen and bears grapnel-like processes (Fig. 113C).

The presence of prehensile cirri in *Antedon* has been already noticed. In the living *Isocrinus* (Fig. 113D), as in the extinct and allied *Pentacrinus*, such cirri occur in clusters at regular intervals along the stalk. Similar cirri are present also in some Palæozoic genera. From analogy with living crinoids it may be assumed that these enabled the animal to attach itself temporarily to any object with which it came into contact as it drifted along. The Liassic pentacrinoids frequently occur preserved in such a relation to pieces of lignite as to suggest strongly that numbers grew upon the undersurfaces of floating pieces of wood. Such a mode of life is described as epiplanktonic. The Devonian genus *Edriocrinus* was apparently epiplanktonic in youth, but free floating in adult life.

In many Palæozoic crinoids (*e.g. Woodocrinus*) the stem tapers to a point at its distal end. This shape precludes it from fixation by cement. On the other hand, there are indications that the stem was flexible, and could be coiled around thin objects. This was certainly the mode of attachment for many species. The acme in coiling capacity of the stem was attained by *Herpetocrinus* (Sil.) (Fig. 113F). In it the crown could be bent back to lie along the upper part of the stem, whilst the remainder of the stem coiled up like a watch spring around it. The presence of cirri in great numbers in this genus afforded further means for attachment.

In the cases hitherto considered, though the organisms must have been free for periods of time during life, the stem was retained fully developed, and still functioned as an organ for temporary attachment. *Millericrinus* (Lias.-L. Cret.) serves to introduce the consideration of a different mode of life (Fig. 113E). Within the limits of this genus the stem varied greatly in length, from one having some seventy ossicles, to another in which it had only one. This crinoid was evidently attached for part of its life, for the stem at times shows a clearly fractured end; sometimes, however, the broken columnal is partly reabsorbed. During the later portion of its life it must have led a free existence, for the reduced stems show no indication of having been attached to any object.

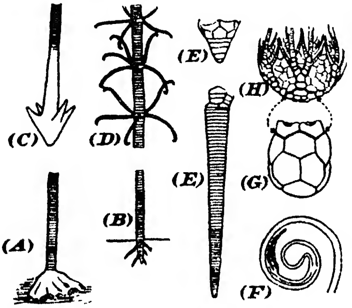


FIG. 113.—Adaptive Modifications of Crinoid stems (all except *A*, *B*, based on Bather).

(*A*) Base cemented to hard substratum. (*B*) Base branching in soft substratum. (*c*) Base with grapnel-like form (*Myrtillocrinus*). (*D*) Stem with cirri for grasping (*Isocrinus*). (*E*) Extremes of variation in the stem of a form that has lately adopted a free habit (*Millericrinus*). (*F*) Stem which can be spirally coiled around the theca (*Herpetocrinus*). (*G* and *H*) Stemless free-swimming or floating crinoids (*G*, *Marsupites* ; *H*, *Uintacrinus*).

Apart from those crinoids which have been referred to as epiplanktonic in habit the free forms hitherto dealt with appeared to have been wanderers upon the sea-floor (vagile benthos). There were some, however, that had become adapted for life in the open sea. The best known of these is the Upper Cretaceous genus, *Marsupites* (Fig. 113G). The theca of this was made up of a dicyclic patina in which the plates were all greatly enlarged. At the apex, where in normal crinoids the stem joins the theca, is a single large plate of uncertain origin. The arms were short and bifurcated. The thickness of the thecal plates indicates that the assumption of the perfectly free habit was phylogenetically a recent acquirement. *Uintacrinus* (Fig. 113H) (U. Cret.) was even more perfectly adapted to a free pelagic life. In it the patina was reduced to insignificance and was pseudo-monocyclic. The theca had extended some distance along the arms and even involved a number of pinnules as well as the main brachials. Numerous interbrachials were also present. In both tegmen and cup the plates were thin and walls flexible. Both genera have a spherical form of theca suggestive of a floating existence.

The Later History of the Crinoids.—Already in the chapter upon the simplest crinoids (p. 124) an attempt has been made to gather together some shreds of information upon the early history and primeval origin of the crinoids. The broad outlines of their history from the Ordovician down to the present day must now be traced.

Typical crinoids of both the monocyclic and dicyclic plan of structure appear to have been already established before the close of the Cambrian, for all later forms belong to one or the other of these categories. From that time onwards further evolution proceeded so rapidly that complexly branched and pinnulate arms, inadunate flexible and camerate thecæ, and normal bead-like columnals were all exhibited by crinoids during the Ordovician. At this time the two great sub-classes, Monocyclica and Dicyclica, were of equal importance, and in both it was the inadunate orders which predominated. The camerate order came next in importance. The Flexibilia were insignificant and the Adunata non-existent.

From the Silurian to the Carboniferous, crinoids were the dominant echinoderms and exceeded all other classes of these organisms in numbers and variety. The remains of their stems were often so abundant that they formed thick masses of limestone (*e.g.* Derbyshire marble). The Monocyclica were now less important than the Dicyclica. Among the former the adunate order put in its first appearance and eventually rivalled the Inadunata which in the meantime had begun to wane. The Camerata, however, already exceeded these two orders in the Silurian and increased to an acme in the Carboniferous. The Dicyclica evolved along similar lines, but at different relative rates. Thus the adunate modification affected so few forms (*Crotalocrinus*) that it has not yet been thought necessary to create a separate order for their reception. The Camerata remained insignificant. The Flexibilia with branching impinnate arms rose to considerable importance in the Silurian, but never afterwards formed so important a section of the fauna. The Inadunata, however, advanced so markedly that in Carboniferous times they outnumbered every other order. It is more than probable that they with their simple and still plastic organization provided the stock from which the great majority of Mesozoic crinoids arose. The Encrinidæ, of which *Encrinus*

(Trias.) is a familiar representative, were the only family which survived the close of the Palæozoic era, and they belonged to this order.

For the crinoids, as for so many other types of marine organisms, the close of the Palæozoic proved to be a period of rapid decline. This was so emphatically the case that no genus is known to have survived from the Palæozoic into the Mesozoic seas. The Mesozoic crinoids must, of course, have descended from Palæozoic ancestors, but the lines of descent have not yet been traced. With the exception of several apparently monocyclic genera, all these crinoids are so essentially similar in structure that they can only be regarded as the derivatives of one Palæozoic stock, probably the dicyclic Inadunata, possibly allied to the Encrinidæ. This fact furnishes yet another indication of the extraordinary mortality suffered by the earlier types during the interval represented by the Upper Carboniferous and Permian rocks. The thin strain which survived that period of heavy mortality was apparently very well suited to the conditions of life in the Mesozoic and later seas, for before the close of the Cretaceous it had exhibited just as varied adaptations to different modes of life as had arisen in previous ages. This is well illustrated by the wide range of peculiarities exhibited by the genera *Apiocrinus*, *Pentacrinus*, *Millericrinus*, *Marsupites*, *Uintacrinus*. all of which lived during the Mesozoic.

The crinoids thus entered upon a new lease of life, but they never again exhibited that wide range in variety of structure indicated by the several orders of crinoids of Palæozoic age. Close upon seven hundred species are known to exist in modern seas. Nevertheless, the majority of these conform to the plan of structure presented either by *Pentacrinus* or by *Antedon*. Both these, in their larval stages, possessed stalks with columnals not unlike those of *Bourgueticrinus*. Both shed this larval stalk, but whilst *Antedon* never grows another, and enters on a free existence, *Pentacrinus* produced new star-shaped columnals in considerable numbers, and a stalk of extraordinary length.

STELLEROIDEA

The Stelleroids—Structure and Development.—As already indicated the Stelleroidea include two great divisions, namely the Asteroidea and the Ophiuroidea. These are sometimes referred to as crawlers and wrigglers respectively, on account of their dominant mode of progression. Superficially they are distinguished from one another by the fact that in the asteroids (Fig. 93) the arms merge into the central disc or body, whereas in the ophiuroids these two sets of parts (Fig. 95A) are quite sharply marked off from one another. There are, however, many other less obvious structural differences.

The arms of the asteroids are relatively much stouter than those of the ophiuroids. This is due to the fact that they enclose spacious prolongations of the body cavity (Fig. 94) which contain bulky digestive glands and other organs. In the ophiuroids (Fig. 114) there is a corresponding prolongation of the body cavity, but it is very attenuated. As already noticed in the description of the starfish the integument of the apical side of the body and arms is supported by rod-like ossicles, which are united at their ends to form a skeletal network. On the oral side (Fig. 94), however, these rods are arranged in two paired series, the ambulacra and adambulacra. In many living and fossil asteroids the ambitus, or boundary between the apical and oral surfaces, is occupied by two series of larger ossicles, the marginals (Figs. 120, 121). Those of the upper row are called the supra-marginals ; those of the lower, the infra-marginals.

In the ophiuroids the arms are long and slender, and the axis of each (Fig. 114) is occupied by a series of large ossicles (vertebral ossicles), which articulate with one another like the vertebræ of a backbone animal. The arms are therefore so flexible that they can be coiled around slender objects, and used as prehensile or climbing organs ; or they can be thrown into flat loops, like the body of a snake that is wriggling along the ground. These vertebral ossicles differ in detail in the various members of the order, and furnish a basis for classification into minor divisions. The radial canals, with their podial outgrowths (Fig. 114), have the same close relationship to each vertebral ossicle that they have to the successive pairs of ambulacra in the asteroids. For this reason each ossicle is regarded as the homologue of a pair of ambulacral ossicles. This view is confirmed by the fact that in the development of an ophiuroid each vertebral ossicle first appears as a pair of ossicles lying side by side.

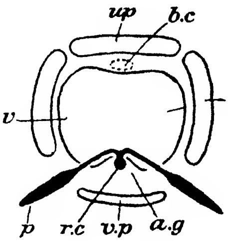


FIG. 114.—Structure of Ophiuroid arm as seen in cross-section.

a.g, ambulacral groove. *b.c*, extension of body cavity into arm. *l.p*, lateral arm plate. *p*, podium. *r.c*, radial canal. *up*, upper arm plate. *v*, vertebral ossicle. *v.p*, ventral arm plate.

Surrounding this axial series of ambulacral ossicles (Fig. 114) there are at least four rows of plates. Those which lie along the sides of the arms (the lateral arm plates) may be regarded as the homologues of the adambulacral ossicles of the starfish. Those which rest upon the apical side of the arm are the upper arm plates. Those which lie upon the oral side are the lower arm plates. Owing to the presence of the latter, the ambulacral grooves, which are wide open in all starfishes, are completely closed in all ophiuroids. In both types of stelleroids, the outer extremity of each ambulacral series of ossicles is occupied by an unpaired plate (the terminal plate), which has an intimate relationship to the extremity of the corresponding radial canal. At the inner extremity each ambulacral groove passes into the mouth, and the corresponding ossicles of all the radii become closely associated with one another to form a framework called the mouth frame.

A marked difference exists between the two great divisions of stelleroids in the position of the madreporic opening. In the asteroids this is situated on the apical side, and not far from the apex of the disc. Moreover, the madreporic plate is large and conspicuous. This fact has been correlated with the great functional activity of the podia, as organs of progression, as well as of respiration. Water has to be continually drawn into the water-vascular system to make up for that lost from the system in other ways, and to keep the tube sufficiently turgid. The position of the plate as near the highest point of the body as possible secures a supply of water with a maximum freedom from sediment. In the ophiuroids the water pore is on the under surface and close to the oral margin. It is usually quite inconspicuous, and a clearly recognizable madreporic plate is not usually present. This fact may be correlated with the minor functional importance of the podia, which serve the purposes of respiration, but not of locomotion. This difference in the position of the water pore in these two types does not exist in the young stelleroid (Fig. 115). In both cases, at that stage of development, the pore is close to the margin on the apical side.

The young stelleroid (Fig. 115), just metamorphosed from the larval state, conforms in many respects to a common plan in both asteroids and ophiuroids. Only the water-vascular and skeletal systems need be taken into account here. The vascular system consists of a circular canal, with short radial canals, bearing a few rudiments of tube feet. The hydropore is connected with the main system by a thin tube, and is situated on the apical surface close to the margin. At a very early stage the rudiments of sixteen regularly arranged plates are present on the apical surface. One, the centrodorsal, is situated close to the anus at the apex of the body. Five plates are situated in close relation to the ends of the radial canals, these being the terminal plates. Some distance from the margin is a ring of ten plates: five radial and five interradial in position. Later (Fig. 116) another ring of five accessory plates appear between this and the centrodorsal. The growth of the arms is accompanied by the appearance of a linear series of secondary radials between this ring and the terminal plates. In the interradial region, however, development follows divergent directions. In the asteroids growth takes place more rapidly between the ambitus and the hydropore, which therefore remains on the apical side. In the ophiuroid it takes place more rapidly between the apex and the pore, with the result that ultimately the interradial portion of the apical side extends over the ambitus on to the oral surface, and thus the water pore is carried into the position it holds in the adult.

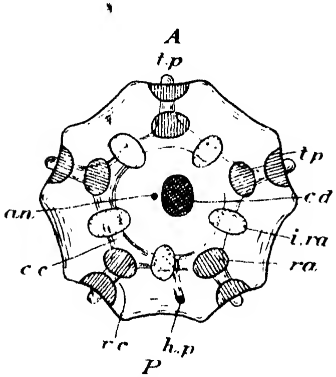


FIG. 115.—Very young Stelleroid, aboral view.

A, *P*, median plane. *an*, anus. *c.c*, circular canal. *c.d*, centrodorsal. *h.p*, hydropore. *i.ra*, interradial. *ra*, radial. *r.c*, radial canal, projecting beyond *t.p* as an unpaired tube foot. *t.p*, terminal or ocular plate.

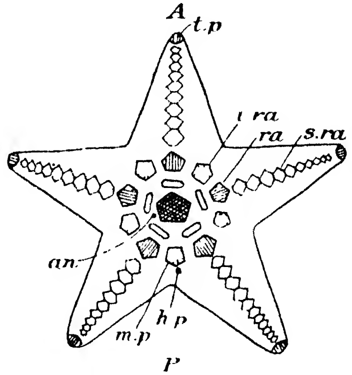


FIG. 116.—Young Stelleroid, aboral view.

m.p, madreporic plate. *s.ra*, secondary radial. Other letters as in Fig. 115.

The General History of the Asteroids.—The simplest and, at the same time, one of the earliest asteroids known is *Hudsonaster* (M. and U. Ord.). This is a small starfish-like organism (Fig. 117) about half an inch in diameter. The centre of the apical surface is occupied by a system of plates bearing a striking resemblance to that already described for the young starfish. It consists of a central plate and two rings of plates, the inner having five accessory radials and the outer with five radials and five interradials. The apical view of each arm exhibits five rows or columns of plates, a central or radial row comparable with the secondary radials already described for the developing asteroid, and two outer or marginal rows. The inner or upper one of these two is the supramarginal, and the outer or lower is the inframarginal. A madreporic plate lay near the margin of the disc, and interradially between the proximal elements of two adjoining rows of supramarginals.

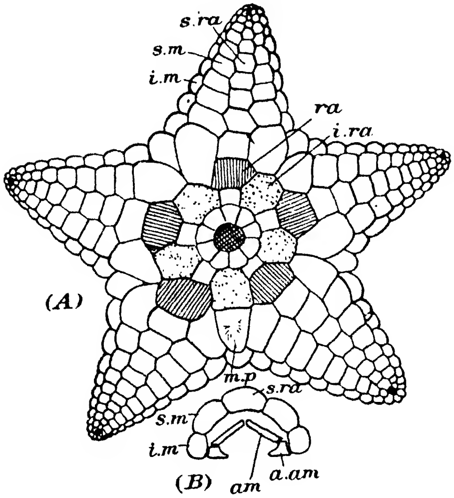


Fig. 117.—Reconstruction of *Hudsonaster*.

(*A*) Aboral view. (*B*) Section of arm. (Based on Schuchert.)

a.m, ambulacral. *a.am*, adambulacral. *s.m*, supramarginal. *i.m*, inframarginal. Other letters as in Figs. 115, 116.

The oral surface of *Hudsonaster* (Fig. 118) is furnished with the usual open ambulacral grooves, having both ambulacral and adambulacral plates, but without podial pores. Alongside of these the inframarginals may be seen. At their proximal ends, adjoining rows of inframarginals end against a single large interradial ossicle, the axillary. The main changes which took place among forms allied to *Hudsonaster* consisted of an increase in the size, an extension of the central disc, an elongation of the arms, and an enlargement of the internal capacity of the body as a whole. These same changes were also exhibited in their various stages by the members of divergent lines of descent.

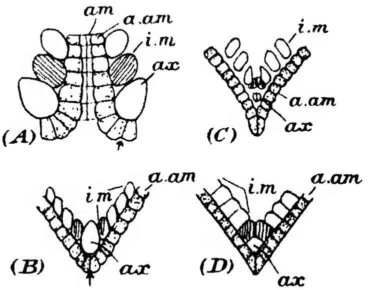


Fig. 118.—Diagrams showing progressive incorporation of proximal portion of Arms into Central Disc. (Based on Schuchert.)

(*A*) Oral aspect of ambulacrum and associated ossicles in *Hudsonaster*. Oral aspect of interradial region in (*B*) *Hudsonaster*. (*C*) *Promopalæaster*. (*D*) *Mesopalæaster*.

a.am, adambulacral. *am*, ambulacral. *ax*, axillary. *im*, inframarginal.

The extension of the disc was accomplished by the progressive incorporation (Fig. 118) of the proximal portions of the arms. This process is most clearly recognized by studying the proximal ends of adjoining rows of inframarginal plates. At first these are separated by the axillary, which thus lies on the actual margin of the disc. In more advanced forms, however, the axillary becomes cut off from the margin by the coming together of the proximal elements of adjoining rows of inframarginals, *e.g.* *Mesopalæaster* (Ord.-Dev.) and *Promopalæaster* (Ord.). A similar incorporation of adambulacrals also takes place.

Increased internal capacity is attained by the intercalation of secondary ossicles between the primary series described for *Hudsonaster* (Fig. 117B, cp. 94A). This is most marked between the secondary radials and supramarginals, less marked between the supra- and infra-marginals, and is only occasionally seen between the inframarginals and adambulacrals. In *Promopalæaster* this process has gone so far that as many as twenty-six or twenty-eight ossicles may be counted in a transverse line on the apical surface of the arm. Accompanying this increase in the number of plates was the appearance of spaces between them which in life were probably closed only by integument. No doubt this provided added facilities for the improvement of the respiratory system by the development of papulæ. There was also a tendency for the marginals to become less conspicuous, and even to lose their identity among the numerous accessory plates that develop. The condition in which the marginals can be easily recognized is described as being phanerozonate. That in which their identity is lost is cryptozonate. The passage from the former to the latter condition took place frequently in distinct series both of Palæozoic and later asteroids. The increase in length of the arms was accomplished by the multiplication of ambulacral and all other elements of the radially arranged rows of ossicles. Thus in *Hudsonaster* there were about fifteen adambulacrals in a row, in *Mesopalæaster* nineteen, in *Promopalæaster* thirty and in *Xenaster* (Dev.) thirty-eight. This implies an increase in the number of podia, and therefore of ambulatory and respiratory efficiency.

The above described types do not depart greatly from the general form of *Hudsonaster*. During the same great period of time (Ord.-Dev.) other asteroids existed in which the general form underwent considerable modification, perhaps in association with special modes of life. Some of these may now be briefly described.

In *Lepidaster* (Fig. 119B) (Sil.) the number of arms or rays was increased from the usual five up to as many as thirteen. At the same time the central disc became greatly extended. There is good evidence which indicates that *Lepidaster* lay with its apical surface resting upon the sea-floor and with its oral surface facing upwards. In this position food particles would be collected in the same passive manner as among Pelmatozoa. *Schœnaster* (Fig. 119D) (Carb.) is typical of another group of asteroids in which there was a great increase in the size and extent of the disc, whilst the number of rays remained five. This extension of the disc was not brought about by the fusion of the arms, but by the excessive growth of the interradial regions.

In forms like *Urasterella* (Ord.-Carb.) the asteroid organization (Fig. 119C) mimicked that of the ophiuroid. The disc remained very small, whilst the arms became very long, flexible, and well adapted to a wriggling habit. The ambulacral ossicles, however, remained typically asteroid in character, and though the ambulacral grooves were almost closed, the plates which shut them were adambulacrals and not ventral arm plates as in ophiuroids. The urasterellid branch of the asteroids is of special interest because in the earlier members the apical system of plates exhibits a more primitive condition even than that shown by *Hudsonaster.* There was the usual central plate. Around this there was only one ring of plates, and that consisted only of five radials and one interradial, which last functioned as the madreporic plate. This condition is more strictly comparable with the earliest stage seen in the development of the asteroid than that shown by the apical system of *Hudsonaster.*

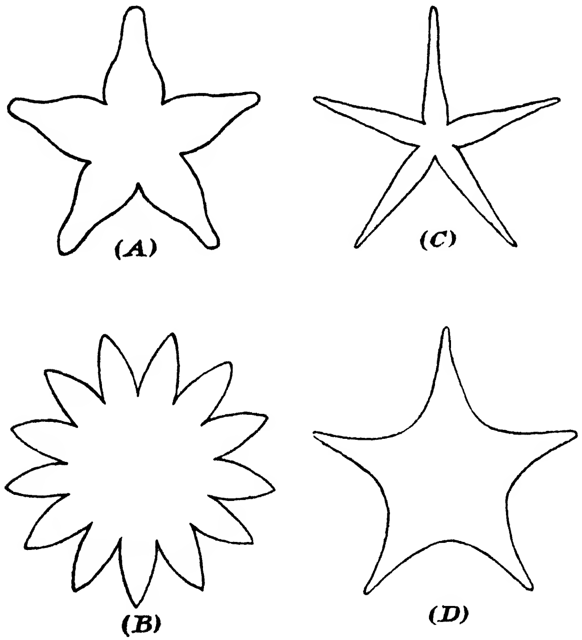


FIG. 119.—Adaptation forms among Palæozoic Asteroidea.
(*A*) *Hudsonaster.* (*B*) *Lepidaster.* (*C*) *Urasterella.* (*D*) *Schœnaster.*

But whilst some asteroids merely mimicked the ophiuroids, others, *e.g. Schuchertia* (M. Ord.-M. Sil.), showed a tendency to develop in a direction leading towards these. In this genus the interbrachial regions were occupied by downgrowths from the apical interradii, and the madreporic plate was situated on the oral surface. In all other respects, however, it was a typical asteroid.

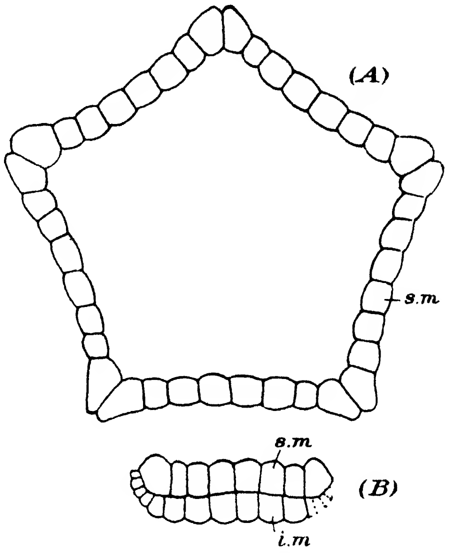


FIG. 120.—Pentagonaster type of Asteroid.
(*A*) Apical view of reconstruction of *Metopaster tumidus* (Spencer). (*B*) Side view of same.
i.m, inframarginal. *s.m*, supramarginal.

Little need be said about the Mesozoic and later history of the asteroids, but those which occur in the Cretaceous rocks demand some notice. These frequently belong to the *Pentagonaster* type (Fig. 120), which is similar to *Schœnaster* in outline, but unlike in that it is phanerozonate. Careful work upon the various species, series or lineages, shows that during the Upper Cretaceous period there was a general tendency towards increasing the internal capacity of the body by increasing its depth (Fig. 121). This was accompanied by a corresponding increase in the height of the individual marginal ossicles. In any lineage a certain height of ossicle accompanied by a particular phase of ornamentation is characteristic of a definite horizon. The isolated marginal ossicles have, therefore, a distinct stratigraphical value.

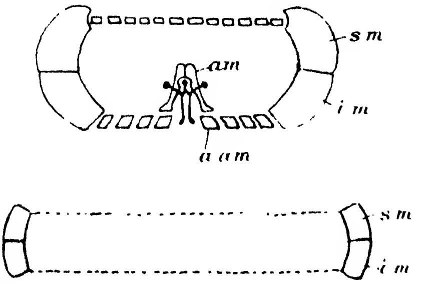


FIG. 121.—Diagrammatic section across two extreme examples of the Pentagonaster type, showing primitive shallow-bodied form below and advanced deep-bodied form above.

a.am, adambulacral. *am*, ambulacral. *i.m*, inframarginal. *s.m*, supramarginal.

On the whole, the Asteroidea have been a stable slowly evolving group. Even in Palæozoic times they appear to have been as virile and varied as they are to-day, and the modifications of shape assumed by them then can be paralleled among living forms.

The General History of the Ophiuroids.—It has been already seen that some asteroids, during the Palæozoic, manifested indications of an approach towards the ophiuroid type of organization. On the other hand the early development of the living ophiuroids so closely resembles that of the asteroids that descent from the same ancestral stock must be postulated. Though palæontological evidence does not fill the gap between these two types of stelleroids, it is sufficiently ample to provide indications of the kind of relationship which exists between them.

Among Palæozoic ophiuroid-like organisms such as *Lapworthura* (Sil.) the great majority differ from typical modern ophiuroids in features which bring their constitution closer to that of the asteroids. Indeed, the difference is sufficiently great to render it necessary to place them in a sub-class, the Auluroidea, by themselves. Like the modern ophiuroids, the auluroids had a clearly defined central disc, and long slender flexible arms without a recognizable extension of the body cavity into the ray. Whilst the ambulacrals are flanked by adambulacrals (Fig. 122), upper and lower arm plates are absent, and thus the ambulacral groove lies open as in asteroids. The ambulacral ossicles are not fused with one another to form a "vertebra." In the proximal portions of the arms in *Lapworthura* the ossicles are broader than they are long. Towards the distal ends, however, they become proportionally longer, until they are like cylindrical rods, closely resembling the earliest stages in the development of these ossicles in modern ophiuroids.

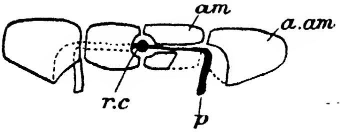


FIG. 122.—Diagrammatic section of the Arm of an Auluroid. (Based on Schuchert.)
a.am, adambulacral. *am*, ambulacra. *p*, podium. *r.c*, radial canal.

The earliest auluroids, which occur in the Ordovician, resemble *Urasterella*, rather than *Hudsonaster*, in the number and arrangement of the apical plates. They must therefore have branched off from the asteroid-like stock at an earlier and more primitive stage than any represented by known fossils. Though the auluroids existed as early as the Ordovician, it was not until Carboniferous times that typical ophiuroids, *e.g. Onychaster*, put in an appearance, so that the former fulfil the requisite conditions, both from the standpoint of time and of structure, required for the stock out of which the latter must have originated. In *Onychaster* the opposing ambulacral ossicles fused with one another, and formed typical, deep, broad vertebral ossicles, whose articular surfaces were only less complex than those of later times.

The ophiuroids did not become at all common until after the Triassic period. To-day they live in very varied depths, shallow and abyssal. Where they do occur they are often found in vast numbers.

ECHINOIDEA

The Structure of an Echinoid.—The sea urchin, *Echinus*, may be taken as a type for echinoids. Its test, except for the slightly flattened under surface (Fig. 95B), is almost globular, and is covered with spines, which must be removed in order that the test may be studied. The mouth is situated in the centre of the under surface, and the anus at the corresponding point of the upper surface (Fig. 123A). The anus is a minute opening surrounded by the periproct, a limited area occupied by small irregularly arranged plates. Around the periproct is a ring of ten plates regularly arranged in an inner and outer series. Those of the inner series (genitals) are larger ; each is pierced by an opening, through which the products of the genital organs are extruded. One of them is riddled with minute pores, and functions as the madreporic plate.

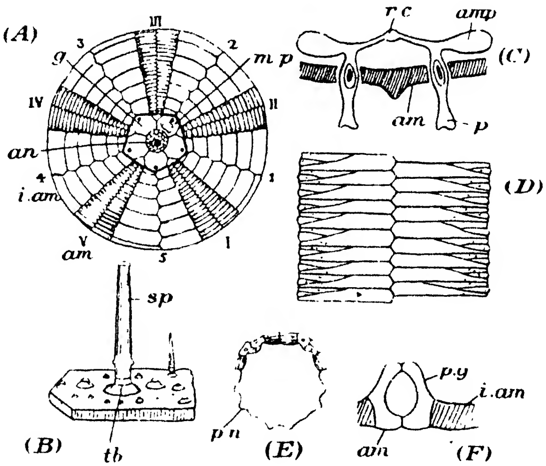


FIG. 123.—The Structural Features of an Echinoid.

(*A*) Aboral view of test. (*B*) Diagram of plate and spines. (*C*) Diagram showing relationship of podia to ambulacral plates. (*D*) Part of the ambulacral area. (*E*) Peristomial margin. (*F*) One portion of perignathic girdle.

am, ambulacral area. *amp*, ampulla. *an*, anus. *g*, genital plate. *i.am*, interambulacral area. *m.p*, madreporic plate. *sp*, spine. *p*, podium or tube foot. *p.g*, part of perignathic girdle. *p.n*, notch for peristomial gill. *r.c*, radial canal. *tb*, tubercle.

The plates of the outer series (oculars) are smaller, and alternate with the genitals.

The area occupied by the periproct and the genital and ocular plates is called the apical disc, in contradistinction to the remainder of the test, which is designated the corona. In the adult the apical disc forms but a very small portion of the whole test, but in development, after the larval stage has been passed, the proportions are almost reversed, for the apical disc area occupies not only the whole of the upper surface, but even extends on to the margin of the lower surface. At this stage the urchin bears a close resemblance to an equally young asteroid. The corona consists of a mosaic of calcareous plates, arranged in twenty vertical columns. These are associated together in alternating pairs called ambulacral and interambulacral areas. The line of separation between the areas is the adradial suture ; that between the two columns of ambulacral plates is the median or perradial suture.

The spines of a living *Echinus* are all movably articulated (Fig. 123B) by a hollow socket at the lower end to tubercles upon the test. Each tubercle consists of an upper hemispherical portion, or mamelon, and a lower smooth swelling of the surface of the test, the boss. These tubercles vary in size, the largest being called the primary and the others secondary and miliary. Granules are minute projections without distinction into boss and mamelon.

The relationship of the radial canals and tube feet to the ambulacral plates (Fig. 123C) is not the same as in the Asteroidea, inasmuch as the canals lie within the test, and are dorsal to these plates. It may be that these latter are not strictly comparable with the ambulacrals of the starfish. Each tube foot is connected by a pair of delicate tubules with its corresponding ampulla. As the latter also lies inside the test each ambulacral plate is pierced by a pair of small pores, the ambulacral pores, for the passage of the tubules.

The corona increases in size as the result of two processes, namely, the formation of new plates and the increase in size of the old ones. New plates always appear at the apical end of each column of plates (cp. Fig. 131B) at its junction with oculars. It follows, therefore, that the earliest formed or oldest plates are to be found at the base or oral end of each column. The oculars throughout development overlie the terminal point of the radial canals and might therefore be regarded as terminal unpaired constituents of the ambulacral areas. During the growth of the animal some of the first formed plates lying at the oral margin are reabsorbed and are therefore not to be seen in the adult. The plates attain their maximum development along the largest circumference (ambitus) of the corona. It has been already pointed out that the plates are all of mesodermal origin. They are therefore completely enveloped in and permeated by living tissue. This adds new calcareous material to the outer surface and along the edges of each plate. At the same time material is resorbed from the inner surface, and thus the plate is prevented from becoming excessively thick, and the test correspondingly heavy. The plates consist of crystals of calcite, each with its axis perpendicular to the surface.

The space enclosed by the oral margin (Fig. 123E) of the corona is the peristome. In *Echinus* it is occupied by a membrane bearing a few plates, and having the mouth in the centre. At the interradial portions of its outer margin this membrane grows out into delicately branched organs, the peristomial gills, the presence of which induces the formation of notches on the oral margin of the corona.

Whilst at first sight the test, as looked at from either of its poles, seems to possess a perfect radial symmetry, a close study of many individuals and species of this and allied genera reveals a tendency towards bilateral symmetry in the arrangement of the plates constituting the apical disc. This tendency is much more marked in such echinoids as the heart urchins, for in them the whole test is affected. This bilaterality is about a plane which passes through a definite ocular plate and its corresponding ambulacrum in front, and through an interambulacrum behind. It thus furnishes a useful reference plane for descriptive and comparative purposes. The fact that the madreporic plate always lies to the right of the anterior ocular renders the position of the plane readily identifiable.

In descriptions of echinoids use is made of a scheme devised by Loven of numbering the areas (Fig. 123A). In this the ambulacral areas are represented by Roman numerals, and the interambulacral by Arabic figures. Viewing the echinoid from the aboral side, the ambulacrum and interambulacrum lying to the right of the posterior interambulacrum are number 1. The remaining areas are taken in counter-clockwise sequence, and numbered accordingly. The madreporite is therefore situated in interradius 2, and the anterior ambulacrum in radius III. In each area the columns are represented by the letters *a* and *b* respectively.

The oral aperture is armed with five sharp white enamelled teeth radially arranged. These are fixed in, and worked by, a complex apparatus called " Aristotle's " lantern (Fig. 125A), consisting of numerous pieces. The largest of these are called pyramids, and are joined together in pairs with a deep notch, the foramen magnum, between their upper ends. This is arched over by a pair of ossicles called epiphyses. The whole apparatus is worked by muscles attached to a series of arched upgrowths (perignathic girdle) borne on the inside of the ambulacral plates (Fig. 123F) adjoining the peristome.

Echinoids, Ancient and Modern.—*Aulechinus* (U. Ord.) has numerous interambulacral plates arranged in irregular vertical columns. The ambulacral plates are in pairs which overlap one another at their inner ends. Near this end there is a single pore imperfectly enclosed, a condition strikingly like that seen in the early development of the podial pores of modern echinoids. *Palæodiscus* (Fig. 124B) (Lower Ludlow) is more fully known. Its test was probably subcircular or pentagonal in outline, and much flattened from above downwards. Its five ambulacral areas consisted of two columns of simple ossicles, each pierced by two podial pores. In the interambulacral areas as many as eight or nine plates occurred in the transverse rows.

In these two genera the narrow ambulacral and the numerous interambulacral plates, not yet fully systematized into regular vertical columns, are features reminiscent of the Edrioasteroids and of the more primitive cystoids.[1] *Bothriocidaris* (Fig. 124A) from the middle Ordovician of Esthonia exhibits a very different type of echinoid structure. It was almost spheroidal in form, having the corona divided into the usual number of ambulacral and interambulacral areas. The plates of the former were characterized by their height, which was so great that the plates were almost hexagonal in shape. Moreover, the pores of each pore pair instead of lying side by side were superposed the one above the other. Each interambulacral area had only one column of plates.

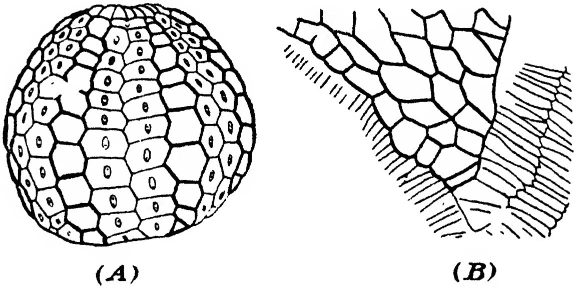


FIG. 124.—Two Ancient Echinoids (after Jackson).
(*A*) *Bothriocidaris*. (*B*) *Palæodiscus*.
Outlines of Ambulacrals thin lined, of Interambulacrals, thick lined.

These very early and primitive genera, represent two very distinct orders, the Perischoechinoida and Bothriocidaroida respectively.

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[1] For other views than those in this paragraph see Hawkins 1927 and 1929.

They not only exhibit widely different types of structure, but also illustrate quite well some of the main characteristics which distinguish the Palæozoic or Ancient Echinoids as a whole from the post-Palæozoic or Modern Echinoids. In the former, which include the majority of the ancient echinoids, increase in girth of the individual was accomplished by an increase in the number of plates from the poles towards the ambitus, but the plates themselves were of more or less uniform size throughout the test. In the latter as in modern echinoids, the same object was attained by an increase in the size of the plates towards the ambitus, whilst the number of plates remained constant for all zones. In *Bothriocidaris* the number was fifteen, there being two plates in a row in each ambulacral area and one in the interambulacral.

The echinoids were apparently only an inconspicuous section of the fauna in the Palæozoic seas. The majority of those that lived then belong to the Perischoechinoida. They existed as early as the Ordovician, and increased in numbers and variety up to the time of their acme in the Carboniferous period. As far as is known none of them survived the close of the Palæozoic, though the Jurassic *Pelanechinus* with its later allies exhibit a number of interesting features in common with them. The modern type of echinoid was represented for the first time by isolated members of the family Cidaridæ, in the Carboniferous. This family survived into the Mesozoic, and gave rise to a plastic and virile stock, from which there arose during the Jurassic and Cretaceous periods many lines of descent. These exhibited a greater range of shape and variety of detail than was exhibited by the more ancient type. The heyday of these newer races is being enjoyed at the present day.

Ancient Echinoids.

A Study in Classificatory Principles.—As already indicated, the majority of the Palæozoic echinoids may be classed together in the orders Perischoechinoida. In most of the respects in which they differ from *Echinus* they differ from modern echinoids in general. These may now be briefly considered.

The jaw apparatus, or Aristotle's lantern (Fig. 125), is known in only a few cases, and in them it exhibits a condition found only in young individuals among present-day forms. Instead of having high-angled, almost vertical sides, they were low-angled and gently inclined. The teeth were always grooved on the inner surface. The perignathic girdle was absent. The peristomial membrane was covered by interambulacral and a few accessory plates; peristomial gills appear to have been non-existent. At the apical pole the apical disc was present, but the ocular plates were usually inserted between the genitals.

As the corona is the part which has been most frequently preserved, it is better known, and consequently the study of this portion of the test has furnished the most serviceable basis for detailed classification. The ornamentation of the test ranged from such a condition as that shown by *Archæocidaris* (Fig. 128A), in which there was one large tubercle provided with a considerable spine in the centre of the plate, to that in which the plates were covered with minute granules bearing very delicate spines.

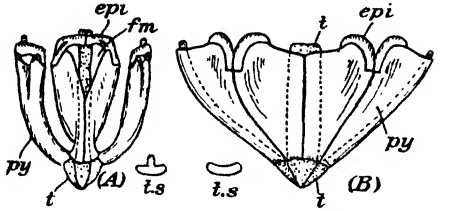


FIG. 125.—Aristotle's Lantern in Modern and Ancient types of Echinoids.

(*A*) *Strongylocentrotus*. (*B*) *Pholidechinus* (adapted from Jackson.)

epi, epiphysis. *fm*, foramen magnum. *py*, pyramid. *t*, tooth. *t.s*, section across tooth.

The most marked differences between the members of the order relate to the number and shape of the plates. These differences can be arranged in series indicative of serial change (Fig. 126). In the ambulacral areas there is a tendency towards an increase in the number of the plates in each vertical column. With this is associated a decrease in the height of individual plates. When this change has reached an advanced stage the plates of each area become rearranged so as to "form fours." Subsequently additional plates are inserted, until at the ambitus of some genera there may be as many as twenty plates in a transverse row. As each plate has a pair of pores, the number of podia was greatly increased and an added efficiency in respiration and locomotion was attained. In the interambulacral areas a similar multiplication of the plates towards the ambital region took place (cp. Fig. 128).

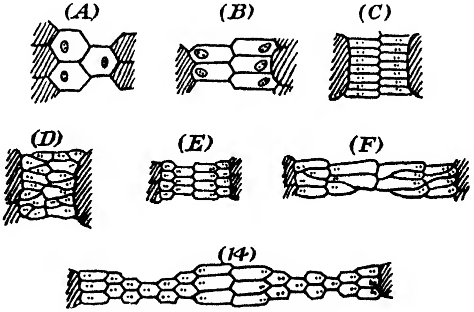


FIG. 126.—Stages in the evolution of Ambulacral Plates and areas, as illustrated by :—

(*A*) *Bothriocidaris*. (*B*) *Hyattechinus* and *Koninckocidaris*. (*C*) *Lepidocentrus*. (*D*) *Lepidocidaris*. (*E*) *Lovenechinus*. (*F*) *Oligoporus*. (14) *Lepidesthes*.

The sequence of changes in shape of the ambulacral plates, due to the decrease in height in proportion to width, and the transition from twos to fours, may be represented by the letters A, B, C, D, E, F, respectively. Similarly the number of plates in a transverse row may be represented by arabic figures from one up to twenty. These letters and figures may now be placed in two vertical columns (Fig. 127), representing the possible changes in the ambulacral and interambulacral areas respectively. In the genus *Hyattechinus* (L. Carb., Fig. 128B) the ambulacral plates have attained to stage B, and the number of interambulacrals in a transverse row at the ambitus varies from eleven to fourteen. This may be expressed in a formula, *e.g.* Amb. B–Interamb. 11/14, or more briefly B 11/14. By drawing lines joining B of one column to 11 and 14 of the other the genus *Hyattechinus* (L. Carb.) can be to some extent graphically represented. Similarly, *Meekechinus* (Perm.) (Fig. 128D) has the formula Amb. 20–Interamb. 3, or 20–3, which again may be represented graphically. A glance at the graphs shows that these are two widely divergent genera, but that they could have had a common ancestor expressed by the line B–3 or a lower line. *Lovenechinus* (L. Carb.) (Fig. 128C) (E–4/7) could not possibly be the common ancestor. On the other hand it may have originated in B–3.

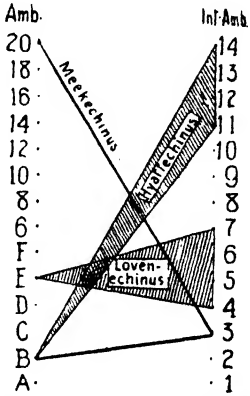


FIG. 127.—Graphic representation of the Structure and Relationships of Echinoid Genera.

The genera *Hyattechinus*, *Meekechinus* and *Lovenechinus* may be defined by formulæ, or by verbal descriptions, or by graphs; but such genera are only snapshots of grouped but flowing series of changes, called lines of descent. The difference between these lines is not in static structural detail of the ambulacral and interambulacral areas. *Lovenechinus* belongs to a line in which change took place at practically equal and uniform rates for the two areas. In the *Hyattechinus* line change took place rapidly in the interambulacral area from 1 to 20, whilst the ambulacral area advanced only from A–B. In the *Meekechinus* line the rates of change were almost the reverse. These three genera and the lineages to which they belong are differentiated from one another not by characters which are quite distinct from the outset and remain static or unchanging, but by characters which form steps in series of changes. In these cases, at any rate, the differential characters are dynamic.

In the accompanying table a classification of the Perischoechinoida is given, with formulæ for the various genera. The reader will find it a profitable exercise to plot the formulæ graphically in

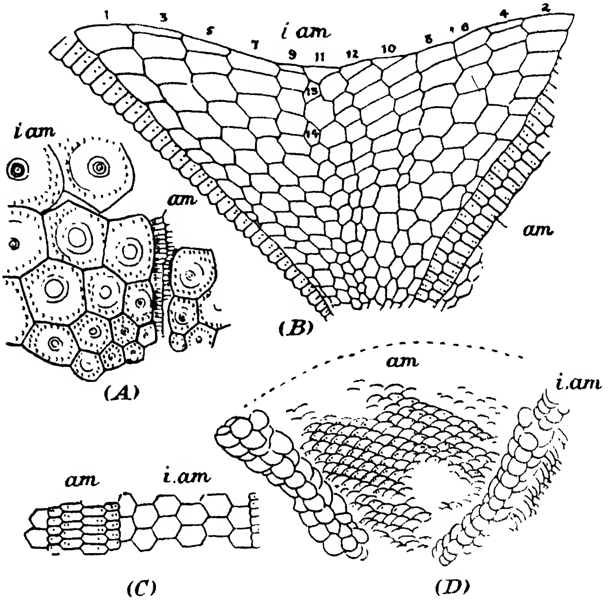


FIG. 128.—The Structure of certain Ancient Echinoids (after Jackson).

(*A*) *Archæocidaris*. (*B*) *Hyattechinus*. (*C*) *Lovenechinus*. (*D*) *Meekechinus*.
am, ambulacral area. *i.am*, interambulacral area. 1–14, number of plate columns in interambulacrum.

the manner described above, and to decide for himself whether this classificatory scheme is based upon natural or artificial principles, or upon a mixture of the two.

Order Perischoechinoida.

Family LEPIDOCENTRIDÆ—		
Aulechinus	(? B/7–9)	U. Ord.
Myriastiches	(? B/40)	Mid. Ord.
Palæodiscus	(C/8)	U. Sil.
Hyattechinus	(B–11/14)	L. Carb.
Lepidocentrus	(C–5/11)	Devonian.
Koninckocidaris	(B–7/8)	Sil.-L. Carb.
Pholidechinus	(D–9/10)	L. Carb.
Family PALÆECHINIDÆ—		
Palæechinus	(C–4/6)	L. Carb.
Maccoya	(D–4/8)	L. Carb.
Lovenechinus	(E–4/7)	L. Carb.
Oligoporus	(F–4/9)	L. Carb.
Melonechinus	(6/12–3/11)	L. Carb.

Family LEPIDESTHIDÆ—

Lepidechinus	(C–4/8)	L. Carb.
Pholidocidaris	(F/6–5/6)	Dev. and L. Carb.
Lepidesthes	(8/16–3/7)	Dev. and L. Carb.
Meekechinus	(20–3)	Permian.

Modern Echinoids.

The Establishment of the Cidaroida.—Among the numerous families of Mesozoic and later echinoids, one family alone, namely the Cidaridæ, had representatives living in Palæozoic seas. These belonged to the genus *Miocidaris* (Carb.-Perm.). Between this and the Palæozoic genera which most closely resemble them, viz. *Bothriocidaris* and *Archæocidaris*, no transitional forms are known. The development of the individual cidarid exhibits features which tend to link this type up with *Bothriocidaris* rather than with *Archæocidaris*. In the very young (Fig. 129A, B) the ambulacral plates are high and hexagonal, the pore pairs are superposed, and the lowest portion of the interambulacral area consists of only one plate. Each of these is a Bothriocidaroid characteristic.

Archæocidaris (Carb.) resembles Perischoechinoidea, and differs from other Cidaroida, in having low-angled jaws (cp. Fig. 125B) and four columns of plates in the interambulacral area (Fig. 128A). These plates overlapped one another slightly thus producing a flexible test, but this feature was less marked than in the Perischoechinoida. As in other Cidaroida, each of the interambulacral plates bore a stout tubercle, and the ambulacral areas, which consisted of low wide plates ran a sinuous course from the apex to the peristome.

During the passage from the Palæozoic to the Mesozoic the cidaroid type underwent only a slight change. This consisted mainly in the strengthening of the ornamentation; the development, for the first time, of a perignathic girdle consisting of a series of upgrowths (Fig. 132A) from the interambulacral plates adjoining the peristome; and the loss of flexibility of the test. This last feature was brought about by the gradual elimination of the bevel along the edges of the plates, so that these no longer overlapped one another, but were joined together by a sutural surface which lay at right angles to the outside of the test. This process advanced most rapidly in the peristomial margin of the corona where the development of the perignathic girdle for the attachment of the muscles which worked the jaws necessitated a more rigid foundation.

In common with all other Mesozoic and Modern echinoids the cidaroid test (Fig. 129C) consisted of two columns of plates in each ambulacral and interambulacral area. As compared with them, however, it was characterized by several features. The ornamentation was coarser and consisted of fewer tubercles, there being as a rule only one large tubercle, with correspondingly large spine, on each interambulacral plate. The ambulacral areas were narrow and sinuous (Fig. 130A), and consisted of one pattern of plate throughout. The ambulacral plates were like those labelled C (Fig 126) for the Perischoechinoida. This type of ambulacral plate will be described as Primary to distinguish it from the numerous modifications exhibited in other echinoids.

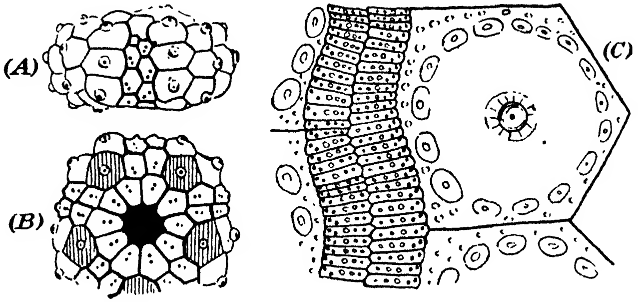


FIG. 129.—Development and Structure of a Cidarid.

(*A*, *B*) Young of *Goniocidaris* (after Jackson). (*A*) Side view. (*B*) Oral aspect. Ambulacral plates with thick outline. Note the single plate (cross-lined) at base of Interambulacra.

(*C*) Portion of test of *Paracidaris* (after Hawkins).

The cidaroids have proved to be a conservative, very slowly evolving race, ranging from the Palæozoic to the present day. At the opening of the Mesozoic they appear to have given origin to the Centreechinoida, which entered upon a more rapidly changing career, and gave rise ultimately to all the other modern types of echinoids.

Changes in Symmetry.—In all the echinoids discussed hitherto the test has had a predominantly radial symmetry. Many of those belonging to the modern type still retain this characteristic, and are therefore spoken of collectively as the Regular Echinoids (Regularia) to distinguish them from an equally imposing assemblage, the Irregular Echinoids (Irregularia, Exocycloida), which exhibit a strong tendency towards the resumption of a bilateral symmetry. Even among the regular echinoids indications of a tendency towards bilateral symmetry are exhibited, but these are confined to the apical disc. Thus the ocular plates, which in *Echinus* form a circle outside that formed by the genitals, may in some genera be pushed in between the latter. They do not, however, pass inwards simultaneously, but alternately on opposite sides of the plane which bisects Ambulacrum III and Interambulacrum 5. In other genera the anus lies to one side of the periproct, but in all these cases the corona is unaffected.

In the irregular echinoids the corona also comes under the influence of this tendency. The first distinct step towards the disturbance of the radial symmetry is the backward movement of the periproct along the plane (Fig. 130B) mentioned above. It elongates posteriorly, breaks through the oculogenital ring, and eventually escapes into the posterior interambulacrum (Fig. 130C, D). There it may move to various positions above, on, or below the ambitus. Meanwhile, the apical disc resumes once more its original radial symmetry. When the periproct rests on, or near, the ambitus there may be a slight bulging of the test posteriorly; otherwise a circular, or almost regular pentagonal outline of ambitus is maintained. All these changes may take place without there being any disturbance of the symmetry of the corona, beyond the slight change of outline just mentioned. Those echinoids which exhibit any phase of the changes just described are classed as the Holectypoida. These originated from a diademoid stock through *Pygaster*-like forms (*Plesiechinus*), as early as Liassic times. The Holectypoida were the dominant irregular echinoids during the Jurassic and early Cretaceous periods. They were still prominent during the Upper Cretaceous, but disappeared at its close.

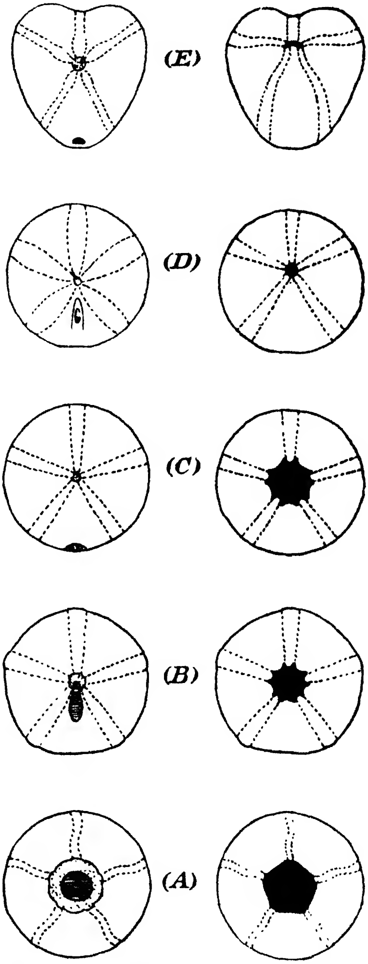


FIG. 130.—Diagrams illustrating the Change from Radial to Bilateral Symmetry in Modern Echinoids.

Left, apical view. Right, oral view.

(*A*) A Cidarid. (*B*) *Pygaster*. (*C*) *Holectypus*. (*D*) *Clypeus*. (*E*) *Micraster*.
Black = mouth. Lined = anus. Dotted = oculogenital ring. Broken lines enclose ambulacra.

From the standpoint of symmetry the holectypoid grade was exhibited during the Tertiary and subsequent periods by the Clypeastroida. In these the apical disc and peristome were still central in position, but the periproct was on, or near, the ambitus. Sooner or later, after the periproct had escaped from the oculo-genital ring, the mouth and peristome began to move towards that point of the ambitus occupied by Ambulacrum III. In some cases this was accompanied by a slight movement of the apical disc. Inasmuch as these two points carried along with them the polar extremities of the ambulacral and interambulacral areas, the symmetry of the corona and of the test as a whole became profoundly disturbed. In the more advanced stages of these movements the ambital outline tended to become ovoid or heart-shaped.

Already in the Upper Lias a slightly eccentric position of the peristome, as well as of the periproct, was exhibited by the genus *Galeropygus*, which appears to have originated either directly from a diademoid stock or from a primitive *Pygaster*. This was the earliest representative of the Nucleolitoida, a long-ranged group which is still existent. In these the peristome never moved far from the centre, the apical disc was sometimes elongated antero-posteriorly, the anus was usually in a sunken groove, and the ambitus was either almost circular or ovoid in outline. In the Spatangoida (Fig. 130E) bilateral symmetry attains its acme for the echinoids. The peristome is situated quite far forward and may lie under the ambitus. This order arose from the Holectypoida during Lower Cretaceous times, and during the Upper Cretaceous became the most prominent of the echinoids.

Among the irregular echinoids there was a tendency towards the degeneration and ultimate suppression of the peristomial gills, of the jaws, and of the associated perignathic girdle. In such forms as the Holectypoida (Fig. 130B, C) and Clypeastroida, which had a central peristome, these structures, though reduced, were still present. These two orders are therefore described as being gnathostomatous, to distinguish them from the remaining orders in which, in association with the eccentric position of the peristome, these structures had disappeared, and which are therefore described as being ateleostomatous.

Structural Changes in Regular Echinoids.—The changes now to be described relate more particularly to ornamentation and to the ambulacral areas and plates. The ornamentation among echinoids consists of tubercles of various sizes which bear movable spines. Among the regular echinoids these latter vary considerably in size for any one individual, there being usually a number of large primary spines, and more smaller secondary and tertiary spines.

Among the irregular echinoids the spines are of more uniform size, much smaller, and much more numerous, so that the creature appears to be covered by a coarse fur. Usually, however, those of the oral surface are larger, and are used as organs for locomotion. Those of the apical surface are often covered during life with cilia which set up currents of water. These flow over gill-like podia and thus aid respiration, or pass the periproct and carry away the refuse which has been extruded.

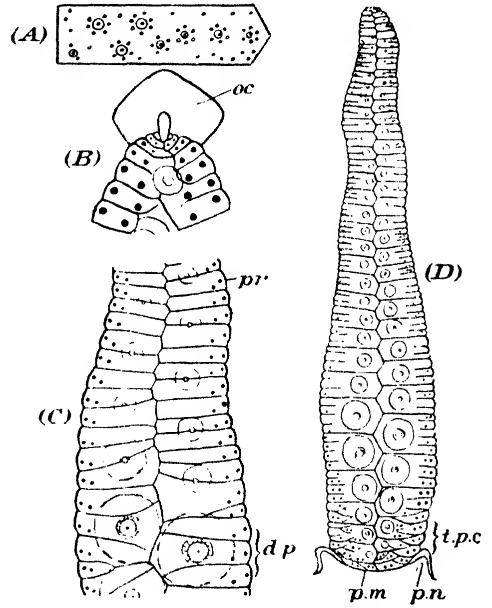


FIG. 131.—Structural Features in Modern Echinoids.

(*A*) Interambulacral plate of *Holectypus* (from Hawkins). (*B*) Apical portion of ambulacral area in *Cœlopleurus* (after Duncan and Sladen), showing mode of formation of new plates. (*C*) Portion of ambulacral area of *Hemicidaris*, showing transition from ungrouped primaries above to Diademoid grouping below with corresponding enlargement of tubercles (thin circles) (after Hawkins). (*D*) Complete ambulacral area of *Hemicidaris*.

d.p, diademoid plate. *oc*, ocular. *p.m*, margin of peristome. *p.n*, notch for peristomial gill. *pr*, primary plate. *t.p.c*, region of plate crushing.

Corresponding with these general differences in the spines the tubercular ornamentation of these two main divisions of echinoids present their own general characteristics (Fig. 123B). In the regular echinoids the ornamentation is on the whole widely spaced and coarse, having tubercles quite large enough to be examined without a lens. In the irregular echinoids the ornamentation is very fine grained (Fig. 131A), closely packed, and uniform. The chief advance shown by the regular echinoids upon their cidaroid ancestors is in the appearance and growth of tubercles upon the ambulacral areas. These ultimately rival those of the interambulacral areas in size and number. The simplest and most primitive form of ambulacrum among post-Palæozoic echinoids is that seen in the Cidaridæ (Fig. 129C). In these the ambulacral area is very narrow, and pursues a sinuous course (Fig. 130A) from the apical disc downwards. The plates are low and wide (Fig. 129C) with one pair of pores to each. Their height, as compared with that of the interambulacral plates, is so small, that as many as twenty may abut against one of these at the adradial suture.

The changes undergone by the ambulacral plates are more complicated and significant among the regular, than among the irregular echinoids, and may therefore be considered first, and in greater detail. They fall naturally under two headings, namely, those which are due to plate crushing and those which are due to plate grouping and combination.

In the Cidaridæ, as in most Palæozoic echinoids, the production of new ambulacral plates at the apical end is so prolific that there is a glacier-like flow of the whole ambulacrum towards the peristome, and even on to the peristomial membrane. In the diademoid, and all other types of regular echinoids, a structural feature developed which tended to dam this flow at the peristomial margin. This was the perignathic girdle (Fig. 132, 123F) which did not consist merely of upgrowths from the lowermost interambulacral plates, as it did in the Cidaridæ, but included upgrowths from the lowermost ambulacral plates also. These two sets of plates thus become associated together to form a rigid peristomial basis of attachment for the muscles which worked the jaw. The hereditary tendency to the production of an excessive number of plates still held sway, with the result that growth pressure developed at the oral ends of the ambulacral areas. This led to a reduction in the size of the individual plates and a consequent crowding together of the pore pairs in these regions (Fig. 131D).

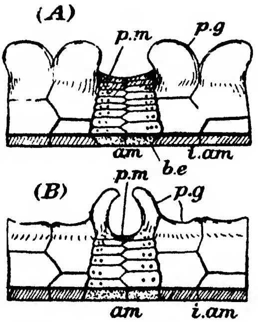


FIG. 132.—Portions of Perignathic Girdles of (*A*) Cidaroid, (*B*) Diademoid, viewed from within the test.

am, ambulacrum. *b.e*, bevelled edge. *i.am*, interambulacrum. *p.g*, perignathic girdle. *p.m*, margin of peristome.

The grouping together, and combination, of the ambulacral plates appears to be associated with the fact that in the regular echinoids the tube feet still functioned largely as prehensile and ambulatory organs. It presumably became an advantage, therefore, to develop a stronger system of plating with fewer lines of weakness, such as sutural connections. Even among Triassic diademoids there was a tendency for the primary plates to be grouped together, first in twos or dyads (Figs. 131, 133), or then in threes or triads. By Liassic times this tendency had become well established, and had even advanced beyond mere grouping to actual combination, in which the members of the group united with one another to form a single plate having its own shape and boundary, and three pairs of pores. Usually the three elements extended quite across the compound plate, which is then described as diademoid (Fig. 133B). Sometimes, however, the upper and lower elements withdrew from the perradial border, so that the plate now consisted of a large central element and upper and lower half-sized elements, or demiplates. Such a type is described as arbacioid (Fig. 133C). In yet a third type, the echinoid, it was the central element alone which became reduced (Fig. 133D). During later Jurassic and Cretaceous times yet more complex compound plates were produced, especially from the diademoid and echinoid types, either by the addition of new primaries to the upper border of the plates in the former, or by the intercalation of additional demiplates between the upper and middle elements of both types. In this way large plates were formed, having sometimes as many as fifteen pore pairs each, and having the same size as the interambulacral plates.

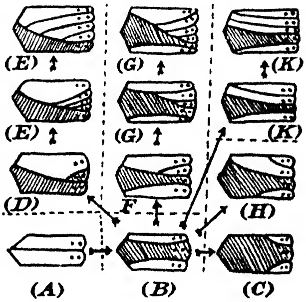


FIG. 133.—Types of Ambulacral Plate grouping among regular Echinoids.

(*A*) Dyad. (*B*) Diademoid triad. (*C*) Arbacioid triad. (*D*) Echinoid triad. (*E*) *Strongylocentrotus.* (*F*) *Pseudodiadema.* (*G*) *Cyphosoma.* (*H*) *Hemicidaris.* (*K*) *Placodiadema.*

Throughout this series of changes the tubercles played a prominent part (Fig. 131C, D). At first the tubercles on the primaries were minute and uniform in size. Then those on every third primary became enlarged. As grouping and combination took place these tubercles extended beyond the bounds of their own primaries on to those which were associated with it. Thus the compound plates were greatly strengthened. Various phases in the formation of compound plates are frequently shown in a single ambulacral area, thus furnishing another illustration of the principle " localized stages in development."

These changes, within the ambulacral areas, were accompanied by a progressive change in the areas as a whole (cp. Figs. 123, 130, 131). At first these were narrow and sinuous, as in the Cidaridæ. Gradually, however, they became straight and increased in width, until eventually they were as wide as the interambulacral regions. The fixation of the peristomial margin of the corona made possible the development of the peristomial gills. The presence of these led to the development of a notch in the edge of the lowest interambulacral plates (Fig. 131D, *p.n.*). The absence of these in the Cidaroida, and their presence in other regular echinoids has suggested the subdivision of the Regularia into Endobranchiata (Cidaroida) and Ectobranchiata (Centrechinoida).

Minor Changes in the Irregular Echinoids.—Among the irregular echinoids the same tendencies towards the grouping of the plates into dyads and triads of the diademoid and echinoid patterns were manifested, but in them there appears to have been no advance towards actual combination with the formation of the compound plates. On the contrary that series of forms leading up to, and including the Spatangoida, manifested a retrogressive tendency; for the ambulacral plates reverted to the condition of simple primaries, and in the ambital region became even bothriocidaroid in their proportions.

In many irregular echinoids, especially those not belonging to the Holectypoida, the apical podia became specially modified for respiratory purposes. In association with this the space between the individual pores of a pair widened, and the pores became united by a groove, or the outer pore became more or less elongated and slit-like. These features gave to the apical portions of the ambulacra a peculiar shape and appearance, which is described as petaloid. On the oral surface the podia tended to degenerate, and became replaced as organs of locomotion by the spines. In the spatangoids this function was performed more especially by the spines that lay between the posterior ambulacra. The plates of this interambulacral region therefore became more rigidly united with one another, and formed what is called the plastron.

Of necessity the changes undergone by the echinoids during their evolution, from the opening of the Mesozoic down to the present day, have had to be described only in broad outline; but it must not be overlooked that these changes were very slow, very gradual, and affected many minute features of the organism which have not even been mentioned. This may be illustrated by a consideration of some of the changes undergone by the genus *Micraster* during the Upper Cretaceous. Comparing specimens of this genus found in the uppermost zone of the Middle Chalk (*Terebratulina gracilis*) with those found near the top of the Upper Chalk (upper two-thirds of the zone of *Micraster coranguinum*), two types characterized by certain easily recognizable differences can be distinguished. These may be referred to as the Low Zonal or *M. cor-bovis* type, and the High Zonal or *coranguinum* type respectively. A few of these differences are displayed in tabular form below and in Figs. 134 and 135.

Though the characters of these two types may be so clearly distinguished when the specimens are collected only from the lowest and highest portions of the *Micraster*-bearing chalk, specimens

	Low Zonal Type.	Fig.	High Zonal Type.
Length and breadth	Distinctly longer than broad.	134B	Length varies from slightly longer to slightly shorter than the breadth.
Position of apical disc	Well in front of centre.	134A	Central or only slightly in front of centre.
Depth of anterior notch	Almost absent or at most only shallow.	134B	Generally deep.
Position of mouth	More distant from anterior border.	134A	Close to anterior border.
Character of the inner ends of ambulacral plates	Flat or slightly inflated, smooth surface.	135	Much inflated, granular surface.

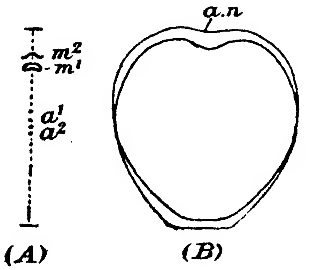


FIG. 134.—Changes in *Micraster*.

(*A*) Position of (*m*) mouth and (*a*) anus in relation to length along median line.

m^1, a^1, Low zonal (*M. cor-bovis*). m^2, a^2, High zonal (*M. coranguinum*). (*B*) General outline of low zonal (outer line) and of high zonal (inner line) *Micraster*. *a.n*, anterior notch.

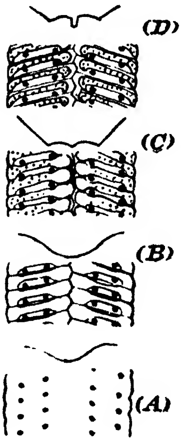


FIG. 135.—Changes in character of Ambulacral Plates (based on Rowe).

Surface view and cross-section of types of ambulacrum in various species of *Micraster*. (*A*) Smooth type. (*B*) Sutured. (*C*) Inflated—subdivided. (*D*) Divided and granular.

collected at intervening levels exhibit every grade of transition from one extreme to the other, not only in the characters mentioned and figured, but in many others. A certain range of this gradation, shorter or longer for different characters, may be exhibited by a number of specimens collected from one horizon. Thus the evolutionary principles illustrated by the Carboniferous coral, *Zaphrentis delanouei*, are confirmed by a similar detailed study of the Cretaceous echinoid, *Micraster*.

SECTION X

MOLLUSCA

Mussels, Cockles, Whelks, Cuttlefish are familiar representatives of a great phylum of invertebrates called the Mollusca. This group is of supreme importance to the Geologist, because molluscan shells are easily preserved and occur abundantly as fossils, both in numbers of species and of individuals. To the Palæontologist this group is of equal interest because of the problems it suggests and of others it solves.

At the present day the Mollusca exhibit a remarkable variety of forms corresponding to equally varied habits and habitats. " Whilst adapted, some to life on dry land, others to rushing streams ; whilst capable, some of swimming, others of burrowing, crawling or jumping, some on the other hand fixed and immovable ; some amongst the most formidable carnivores, others feeding on vegetable mud or on the minutest microscopic organisms—yet all agree in possessing in common a very considerable number of structural details which are not possessed in common by any other animals." It is possible therefore to reconstruct a general plan of which the main types of Mollusca are but modifications. This hypothetical archetypal mollusc (Fig. 136) is bilaterally symmetrical and has a well-defined head, bearing sense-organs. Its under surface is flat and forms a creeping foot whilst the dorsal surface rises into a low dome, the visceral hump, the skin of which is called the mantle and secretes a cap-shaped shell. A groove running round the entire margin of the body is called the mantle cavity and is roofed over by a freely projecting fold of the mantle. This cavity is most extensive posteriorly where it contains a pair of feather-like gills with their apices pointing backwards. The alimentary canal passes from the mouth, along the median line of the body, and opens backwards by the anus between the attachments of the gills.

The Mollusca are divided into four great divisions, the Pelecypoda, the Cephalopoda, the Gastropoda and the Scaphopoda.

The Pelecypoda include such well-known creatures as the cockle and clam. They are as a rule bilaterally symmetrical (Fig. 136E), and the anus opens backwards. They have, however, lost all trace of head and well-developed sense-organs, and may be conceived of as being derived from the hypothetical type by lateral compression. The foot thus assumes that plough-share shape so well adapted for enabling the animal to plough its way along or burrow into the muddy or sandy floor of the sea. The mantle folds hang down so far on either side that they meet below the foot. The cap-like shell is represented by a pair of valves united along the middle dorsal line by an elastic ligament, and covering the whole outer surface of the hump and mantle. The gills have become long and plate-like, and have extended nearly as far forwards as the mouth, hence the alternative name Lamellibranchiata for the group.

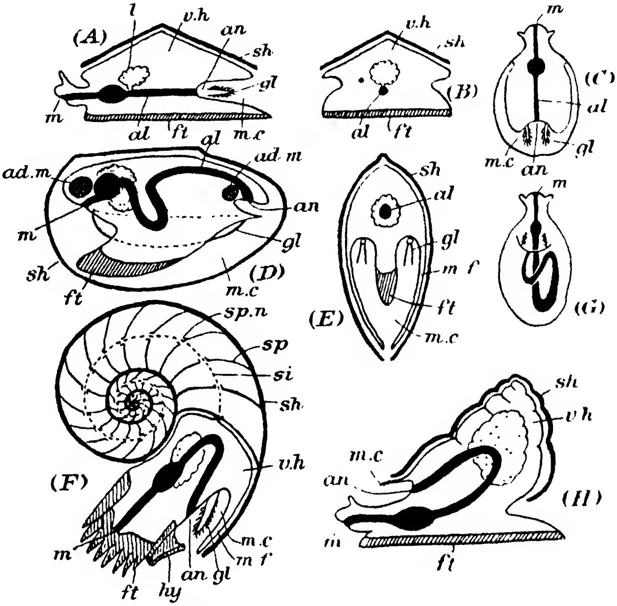


FIG. 136.—Diagrams illustrating the General Structure of the main types of Mollusca.

(*A*, *B*, *C*) Hypothetical reconstruction of archetypal mollusc (after Lankester). (*D*, *E*) Median and transverse sections of a Pelecypod. (*F*) Median section of Cephalopod. (*G*, *H*) Basal plan and median section of a Gastropod (*see* Fig. 170).

ad.m, adductor muscle. *al*, alimentary canal. *an*, anus. *ft*, foot. *gl*, gill. *hy*, hyponome. *l*, liver. *m*, mouth. *m.c*, mantle cavity. *m.f*, mantle fold. *sh*, shell. *si*, siphuncle. *sp*, septum. *sp.n*, septal neck. *v.h*, visceral hump.

The Cephalopoda to which the Pearly Nautilus, *Sepia*, and *Octopus* belong have likewise retained the bilateral symmetry, but the head and its accompanying sense-organs are highly developed. The foot (Fig. 136F) may be conceived of as having been shortened from back to front and extended laterally round the head where it bears tentacles. Meanwhile the hinder portion of the body has been rotated downwards in a vertical plane through 180°, and thus the anus, and the main part of the mantle cavity, open ventrally to the head. The gills likewise have their apices pointing forwards.

In the majority of living cephalopods the shell is either insignificant and covered by skin, or has disappeared entirely. In Nautilus, however, it develops greatly and may be pictured as a series of deep cup-shaped shells fitting into one another like a pile of tea-cups diminishing in size. This pile is coiled like a watch-spring with its median plane vertical.

At first sight the Gastropoda (Fig. 136G, H), of which the snails and whelks are representatives, bear a close resemblance to the hypothetical mollusc. This is due to the presence of a head and flat foot, and to the fact that though the primary bilateral symmetry has been lost, a secondary bilateral symmetry has been almost attained. The visceral hump with its closely fitting shell has risen into a tall cone coiled on itself sometimes like a watch-spring, usually like a corkscrew. In contrast with the Cephalopoda the plane of coiling tends to lie horizontally. The hinder portion of the body with the mantle cavity and associated parts, has shifted horizontally forward along the right side and opens dorsally to the head.

The Scaphopoda are the most insignificant group of Mollusca. Their history opens in the Ordovician, and lasts until the present day. The shell of the chief genus—*Dentalium*—is long, tubular and tapering.

CEPHALOPODA

The Pearly Nautilus and its Shell.—Reference has already been made to the Pearly Nautilus and to *Sepia*. Both breathe by means of gills of which Nautilus has four; *Sepia*, together with many other forms such as *Octopus*, *Argonaut* and *Loligo*, has only two. Along with this difference goes a sufficient number of others to indicate that living cephalopods may be grouped under two headings: Dibranchiata, having two gills; and Tetrabranchiata, having four gills. As the gills are not preserved in fossils, and as a great number of fossil cephalopods cannot be classified with either *Nautilus* or *Sepia*, it will be convenient to use the three divisions Nautiloidea (Tetrabranchiata), Coleoidea (Dibranchiata) and Ammonoidea, which more nearly fulfil the requirements of the palæontologist.

The Nautiloidea are represented at the present day by one genus *Nautilus*, having three species, of which *Nautilus pompilius* is the commonest. These are confined to the Eastern Archipelago between the Strait of Malacca and the Fiji Islands. *Nautilus* lives in water a few fathoms deep, and either creeps along the sea-floor by means of its numerous tentacles or swims rapidly by means of a strong current of water ejected from the mantle cavity through a funnel-like organ, the hyponome (Fig. 136). Its head is somewhat larger than the trunk and bears at its apex a mouth armed with horny parrot-like jaws. Dorsally it is protected by a thick shield-shaped muscular organ, the hood which, when the creature retracts into its shell, completely closes the aperture. On either side of the head are two series of tentacles, and below is the ambulatory funnel. These three structures represent the foot which thus girdles the head. The muscles which work the various parts of the foot pass backwards into a stout muscle which traverses the trunk from side to side, and abuts at its ends against the inside of the shell, making an impression there. This muscle helps to hold the shell and the body together. Posteriorly the hump gives off a long thin cord (siphuncle) (Fig. 136F), which contains only blood-vessels, and traverses the centre of all the coils of the shell as far as the apex. Where the cord enters the hump it thickens very slightly. This part is the visceral cone and contains portions of other organs besides vessels.

The fully formed shell as seen in section (Fig. 136F) consists of a spiral series of thirty-three to thirty-six small chambers and one large living chamber. In cross section the coils or whorls of the shell are horseshoe shaped (Fig. 137), or like an oval with one end pushed inwards so that it may embrace the outer portions of the inner coils. This pushed-in portion is the impressed area, and is situated on the dorsal side of the whorl. The opposite end of the oval is the ventral area, and the sides may be called the lateral areas. Taking the whorl as a whole it will be convenient to distinguish between the main body of the whorl and the limb or portion which lies against the flanks of the inner whorl. The junction between the inner and outer surfaces of the limb is the limb margin. On either side of the shell this limb margin encircles a depression (umbilicus), within which the inner whorls are just visible. In immature shells the mouth margin of the living chamber is thin and fragile, but in fully grown individuals it is thick and strong. This margin is undulating and has a faint ventral sinus. This sinus is associated with the presence of a functional hyponome. The shell grows by the addition to the mouth margin of an outer pigmented porcellanous layer and an inner thinner pearly or nacreous layer. Both layers are marked with lines of growth. The wall thus formed is further strengthened by the deposition, on its inner surface, of additional nacreous material.

The growth of the shell necessarily leads to an elongation of the living chamber. As this takes place the animal slips forward, and from time to time shuts off the excess of room behind by forming septa. This it does by first producing a horny membrane (conchiolin) over the apical portion of the hump and round the visceral cone. The membrane is then separated off from the body and becomes the foundation upon which the nacreous matter of the septum is laid.

The process of deposition commences at the margin and proceeds inwards. That portion formed round the visceral cone and proximal portion of the siphuncle projects backwards from the septum as a short tube, the septal or siphonal neck. The presence of this in the middle of each septum allows the free passage of the siphuncle to the apex of the shell. The undulating line of insertion of the septal margin into the shell is called the suture line. The forwardly directed undulations are the saddles, the backwardly directed are the lobes.

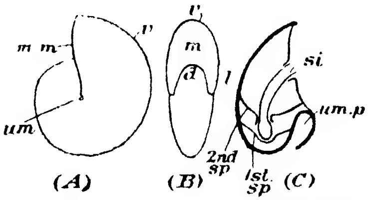


FIG. 137.—Shell of Pearly *Nautilus*.

(*A*) Side view. (*B*) Apertural view. (*C*) Median section of apex (modified from Branco). *d*, dorsum. *l*, limb. *m*, aperture or mouth. *m.m*, mouth margin. *um*, umbilicus. *um.p*, umbilical perforation. *si*, siphuncle. *1st sp*, *2nd sp*, first and second septa. *v*, venter.

The first half of the innermost whorl (Fig. 137), *i.e.* the apical portion of the shell, is the protoconch. It exhibits several peculiarities, and corresponds to the embryonic stage in development. In the first place it is not so strongly curved as the later portions. Owing to this fact, a minute passage (umbilical perforation) connects the umbilical depression of one side with that of the other. The two septa of the larval shell also differ from one another and from all the other septa. In the second septum the septal neck has relatively much greater calibre than the later ones, and it reaches back almost to the first septum. The latter has no septal neck, but only a conical depression (septal cæcum).

Fossil Nautiloids.—With *Nautilus*, the latest representative of the nautiloid race, one of the earlier representatives, *e.g.* *Orthoceras* (Fig. 139), may be instructively compared. The shell in this genus may be either straight or slightly curved and its surface may be ornamented with longitudinal and transverse markings. In cross section it is circular, and the septal suture is quite straight, *i.e.* it has no undulations. The septal neck in the centre of the septum is fusiform and, like that in the second septum of the larval *Nautilus*, is relatively large and reaches back to the preceding septum. These two genera appear to represent two long-lived races which existed side by side throughout palæozoic times.

The nautiloid stock was already represented in late Cambrian times by *Tarphyceras* which had slender whorls, closely coiled and in contact with one another. *Vestinautilus* (Carb.) showed a similar degree of coiling, but the whorls were ornamented with longitudinal fluting. In *Pleuronautilus* (Trias.) the outer coils, unlike the inner, had a slightly impressed dorsal area. The umbilicus, though still wide, was correspondingly restricted.

Forms with such a wide open umbilicus are described as being *evolute*. *Temnocheilus* (Muschelkalk) exhibits a more advanced stage, since the outer whorls embrace the inner to a greater extent. The last three nautiloids are so closely related to *Nautilus* as to be regarded as merely subgenera. In all of them the shell is more or less angulated, a condition which is indicated in the quadragonal outline of the Liassic species, *N. intermedius*, and in the young of the living *Nautilus*. In the series of species *N. intermedius*, *N. striatus*, and *N. ornatus* (Jur.), *N. elegans* (Cret.), the deepening of the impressed zone consequent upon the more complete embracing of the inner by the outer whorls is seen in various stages of progress leading up to the almost closed umbilicus of the modern *Nautilus*. Shells showing this last-mentioned condition are described as being *involute*. The climax of specialization among nautilids is attained by the Tertiary genus *Aturia*, which is quite involute and its suture line deeply folded.

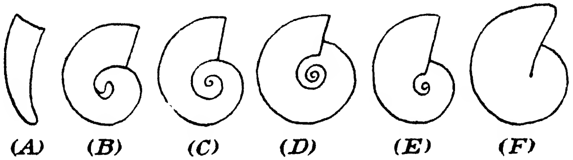


FIG. 138.—Degrees of Coiling exhibited by different Nautilids.

From left to right they become more involute. From right to left they become more evolute. (*A*) *Cyrtoceras*. (*B*) *Vestinautilus*. (*C*) *Pleuronautilus*. (*D*) *Temnocheilus*. (*E*) *Nautilus intermedius*. (*F*) *Nautilus pompilius*.

In middle and late palæozoic times the nautiloid stock produced a number of offshoots, some of which differed mainly in degree of coiling. Thus in *Gyroceras* the coiling was often open, that is to say the whorls were not in contact with one another. In *Cyrtoceras* the shell was merely curved.

The Ordovician genera *Endoceras* and *Piloceras* (Fig. 139) point back to a more primitive stock which gave rise to straight *Orthoceratids* on the one hand, and coiled nautiloids on the other. *Endoceras* and its immediate allies ranged from upper Cambrian to Ordovician. In it the septal necks occupy as much as one-third of the diameter of the septum and fit into one another cone in cone fashion. Within the canal thus formed are numerous conical conchiolin sheaths which at their apices run together to form a small canal, the endosiphon. In *Piloceras* (U. Cam.) these features are even more exaggerated; thus the septal neck is so wide that the septum itself is little more than a rim. If these genera have really retained a primitive condition it is evident that in the ancestral nautiloid the visceral hump and cone together formed a conical mass which is comparable with the whole of the visceral mass of the hypothetical molluscan archetype. Starting from this position it is possible with the aid of fossils to reconstruct the sequence of events leading up to the condition in the modern *Nautilus*. At first the visceral mass was enclosed in a closely fitting and rapidly widening conical shell. As the shell became longer the rate of widening diminished, but the visceral mass still retained its original form. In consequence of this a space appeared between the mass and the upper portions of the shell. That portion of the mass (the visceral cone) no longer in contact with the shell now secreted a conchiolin sheath as a covering for itself. With the increasing length of the shell the body slipped forward and the deposition of the conchiolin membrane took place repeatedly. For some reason, possibly in association with the need for providing an apparatus for controlling the gas pressure in the vacated portions of the shell, the apex of the visceral mass did not share in this movement, but became elongated into a cord, the siphuncle. At a later stage the visceral cone began to deposit calcareous material on the margins of occasional conchiolin

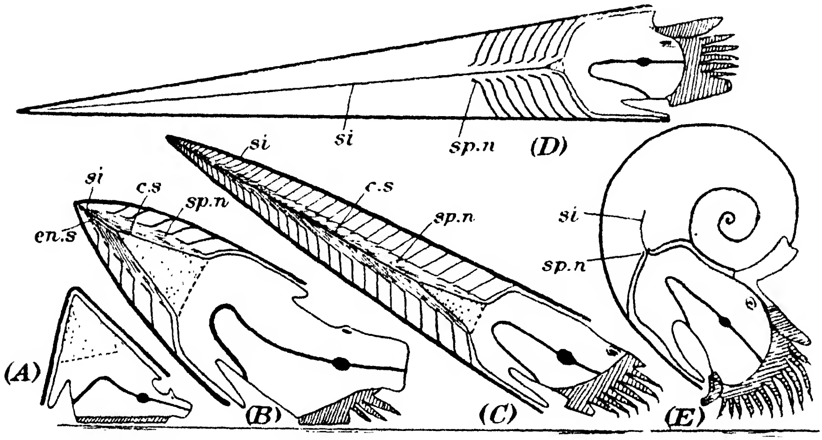


FIG. 139.—Hypothetical diagrams illustrating the probable relationships of the Animal to its Shell and especially to the Septal Neck in certain fossil Nautiloids.

(*A*) Archetypal mollusc. (*B*) *Piloceras*. (*C*) *Endoceras*. (*D*) *Orthoceras*. (*E*) *Nautilus*.

Lined area = foot. Dotted area = visceral cone. *c.s*, conchiolin sheath. *en.s*, endosiphon. *si*, siphuncle. *sp.n*, septal neck.

sheaths. The base of the visceral cone now diminished steadily, and the calcareous rim widened and became the septum. The inner margin of the septum formed an upturned edge (septal neck) around the lower part of the cone. With the continued reduction of the cone, the neck decreased in calibre, until it became the small feature seen in the living *Nautilus*.

While the series *Piloceras* to *Nautilus* and to *Orthoceras* may be regarded as approximating to the two main trunk lines of nautiloid evolution, many other special modifications arose and disappeared before the close of Carboniferous times. Since then no really new type has appeared. Thus the nautiloids illustrate a principle, so often exemplified already, that in the history of a great race there is first a period of obscurity about which little is known. This is followed by one of maximum vigour, during which there is produced a great number of new genera and species. These for the most part had only a short history. A few attain just that combination of characters required for a successful survival during a long period.

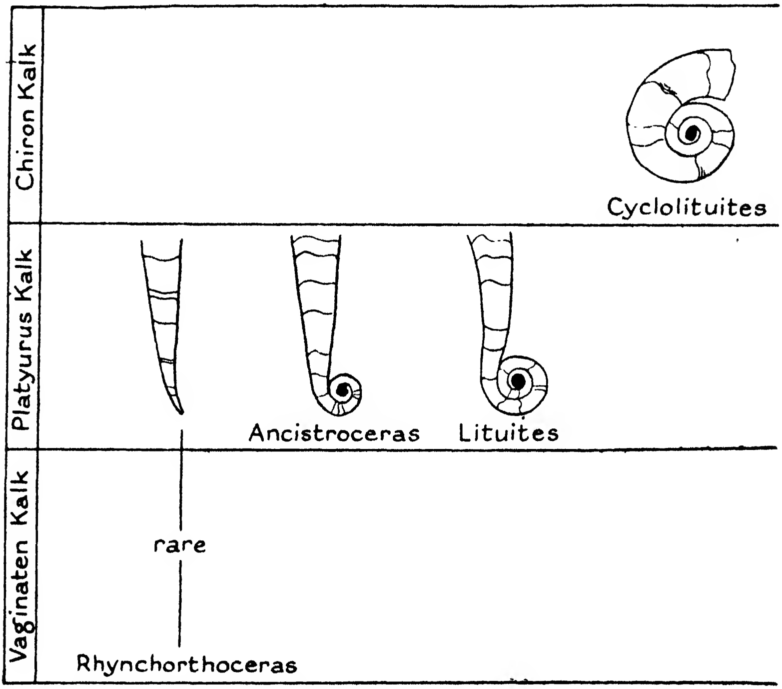


FIG. 140.—The Distribution in Time of some Members of the Nautiloid Family Lituitidæ (Modified from Schindewolf).

In *Lituites* (Ord.) the adult portion of the shell was straight, with its aperture slightly constricted, but in youth it was closely coiled as in *Gyroceras*. Careful collection from successive zones has shown that this genus arose from *Rhynchorthoceras* which was straight or slightly curved (Fig. 140). This gave rise to *Lituites* whose varieties showed differing degrees of coiling in youth, which ultimately merged into *Cyclolituites* in which the whole shell was coiled. It should be observed that the condition which characterized the final members of the series was first manifested in the youth of early members. This is a complete reversal of the sequence of events implied by the term palingenesis or the principle of recapitulation, for here the ancestral condition is reproduced in late development and the descendent condition is anticipated in youth. The Lituitidæ thus provide a clearly established example of the principle of anticipation or *Proterogenesis*.

Constriction of the aperture of the shell was carried to excess in forms like *Gomphoceras* and *Phragmoceras*, in which, however, the shell was never more coiled than in *Cyrtoceras*. In *Trochoceras* the coiling departed from the usual cephalopod type and instead of taking place in one plane it formed a spire like a snail's shell.

Ascoceras was very much like *Orthoceras* during the greater part of its development except that its septa were more widely spaced, but in adult life the living chamber became inflated. Apparently as the animal aged it diminished in size. *Actinoceras* attained the extraordinary length of 10 ft. The great width of its septal neck indicates that it arose as a very early modification. The endosiphon exhibits a special peculiarity in that it gives off a series of radiating tubes which communicate with the chambers through minute openings in the septal necks.

Belemnites and their Allies.—Of the Coleoidea the representative best known to the palæontologist is the genus *Belemnites* (Fig. 141) (Lias.-Cret.), which included 250 species. Though the commonest of fossils it is very rarely found in a perfect state. Most frequently it is found as a solid brown rod, the guard, which tapers to a point at one end and contains a deep conical cavity (alveolus) at the other. This latter may contain a chambered shell, the phragmocone. The structure of the phragmocone bears a striking resemblance to *Orthoceras*. It consists of a thin shell enveloping a series of chambers separated from one another by concave septa. The latter are perforated by the siphonal canal made up of septal necks which extend from one septum to the next. The cone is straight on its ventral side and curved on its dorsal. It differs from *Orthoceras* in several important respects ; the septa lie closer together, the septal necks lie near the ventral surface, and the shell (conotheca) is extended anteriorly on its dorsal margin into a thin shoe-horn-shaped plate (pro-ostracum). Finally the phragmocone tapers very rapidly, and bears at its apex a small spherical calcareous chamber, the embryonic shell or protoconch.

In the most perfect specimens which have been found, an ink sac, like that of the cuttle-fish (*Sepia*, Fig. 141A), occurs underlying the pro-ostracum. Some distance in front of this, impressions of arms, like those of the same animal, also occur, but instead of bearing suckers they bore two rows of hooks (Fig. 141G). These facts indicate affinity between the fossil and this living form. In the cuttle-fish the shell is not external as in the *Nautilus*, but is completely enclosed in a cavity formed by a reflected fold of the mantle on the dorsal side. No doubt that of *Belemnites* was enclosed in a similar cavity, for this is the only way to account for the absence of a living chamber, and for the secretion round the phragmocone of a guard made up of radiating calcareous fibres. Especial interest attaches to the upper Triassic forerunner (*Aulacoceras*, Fig. 141H) of belemnites. In it the guard is very small and encloses only the apex of the phragmocone. This, on the other hand, is large, being twice as long as the guard. Moreover, the phragmocone resembles that of *Orthoceras* still more closely, in that it increases only gradually in

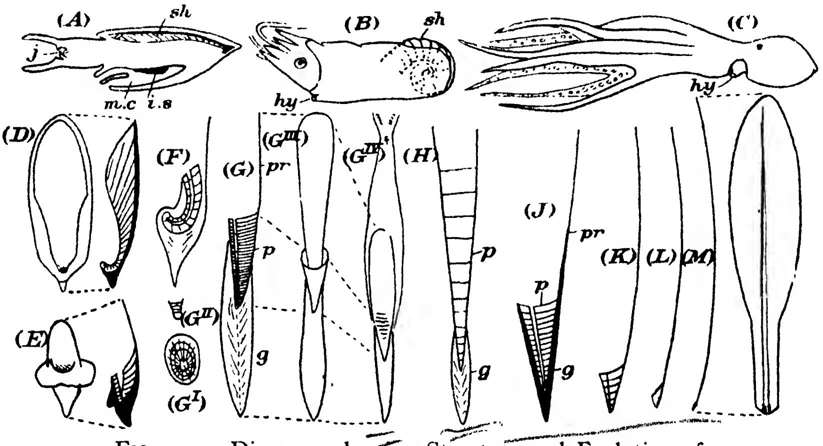


FIG. 141.—Diagrams showing Structure and Evolution of various Coleoid Shells.

(*A*) Median section of *Sepia* (cuttle-fish). *i.s*, ink sac. *j*, jaws. *m.c*, mantle cavity. *sh*, shell. (*B*) *Spirula* showing coiled shell largely enclosed by fold of body wall. *sh*, shell. *hy*, hyponome. (*C*) *Octopus*. (*D*) Shell of *Sepia*—ventral view and median section. (*E*) Shell of *Belosepia*—ventral view and median section. (*F*) Shell of *Spirulirostra*, median section. (*G*) Shell of *Belemnites*—median section. *g*, guard. *p*, phragmocone. *pr*, pro-ostracum. G^{I}, transverse section of guard. G^{II}, Protoconch and first three chambers. G^{III}, reconstruction of complete belemnite shell, ventral view. G^{IV}, fossil showing outline of body, tentacles and hooks, as well as a shell of a belemnite. (*H*) Section of *Aulacoceras*. (*J*) Section of *Belemnoteuthis*. (*K*) Shell of *Conoteuthis*. (*L*) Shell of *Ommastrephes*. (*M*) Section and ventral view of shell of *Loligo*.
(Section *D–K* from Brit. Mus. Cat.)

width, has an external ornamentation of longitudinal and transverse markings, and has its septa more widely spaced.

At the opening of the Tertiary the belemnite organization seems to have undergone a great change along two or possibly three divergent directions, each having one thing in common, viz. the conversion of the shell into a structure of little weight. This was effected chiefly by the reduction of the guard to insignificance or by its total disappearance. *Belosepia* (Eoc.) indicates the mode of transition from belemnites to modern *Sepia*. The guard (Fig. 141E) is reduced to a point like that at the posterior end of the *Sepia* bone and has lateral wing-like expansions. The septa of the phragmocone are very oblique and the siphon has become wide open. This suggests that the mass of tissue under the pro-ostracum of *Sepia* (Fig. 141D) was produced by the further extension forwards of the septa, accompanied by a great increase in their numbers. It also suggests that the conical depression at the posterior end represents the highly modified siphon. *Spirulirostra* (Oligo.-Mio.) opens out a second line of modification. In this genus the phragmocone (Fig. 141F) has become less conical in shape and the septa more widely spaced. It has, moreover, curved to an arcuate shape. The guard is so small that it has evidently become moulded to the phragmocone. In *Spirulirostrina* (Plio.) the guard is further reduced. In the living *Spirula* (Fig. 141B) it has disappeared, and the phragmocone has become coiled into a loose spiral.

It is interesting to notice that whilst the tendency to coiling of the shell possessed by cephalopod organization was expressed almost at the outset, it advanced rapidly to an extreme degree and receded repeatedly in ammonoids, it appeared late and was less strongly manifested in the nautiloids many of which were straight. In coleoids it appeared in only one minor branch and then only at the close of the evolution of the race. This difference in the degree of expression of a modification in different stocks may be further illustrated from coleoids by the repeated tendency to convert the shell into something lighter. In the belemnites this tendency was not expressed at first owing to the apparent necessity for protecting the apex of the phragmocone by the formation of a guard, but later with the opening of the Tertiary period, the guard underwent the rapid degeneration described above. Along other lines, in which the guard never attained importance, this change took place much earlier and went further. In *Phragmoteuthis* (Trias.) the guard was represented by only a thin calcareous coating, the phragmocone was conical and bore a pro-ostracum twice its own length. *Belemnoteuthis* (Oxf. Clay-Cret.) was very similar (Fig. 141J). In *Conoteuthis* (Fig. 141K) the phragmocone was smaller, and the pro-ostracum considerably extended anteriorly. In *Ommastrephes* (Indian Ocean) the phragmocone is represented by a small hollow structureless cone (Fig. 141L) at the hinder end of an extraordinarily long pro-ostracum. In *Loligo* the latter alone remains as a long thin plate of conchiolin shaped like a lance (Fig. 141M).

Already, however, as early as the Upper Lias, *Beloteuthis* exhibited a condition closely resembling that seen in *Loligo*. Other genera there were also which differed chiefly in the fact that the plate was stiffened by calcareous layers. Of the stages leading up to these nothing is directly known. As to subsequent changes it is conceivable that this tendency went further in this branch than in any of the others, and resulted in the total loss of the shell, thus giving origin to the numerous forms, such as *Octopus*, which have no shell.

The Structure and Development of a Mesozoic Ammonoid.—The Ammonoidea form the largest and most important section of the Cephalopoda. They range from the Upper Silurian to the close of the Cretaceous, and exhibit such rapid and varied changes in form and detailed structure that they furnish a more suitable basis for a time scale for that period than do any other Invertebrata. For an introduction to the study of this order *Dactylioceras commune* (U. Lias) may be taken as the type (Fig. 142).

This genus presents a striking contrast to *Nautilus* in general appearance mainly because its whorls are only a little higher than wide, and embrace one another but slightly. In consequence of these differences the umbilicus is wide and shallow, and all the inner whorls are visible. Moreover the shell is ornamented with ribs or costæ which run across the sides of the whorls in a slightly oblique direction. On the ventral area the ribs bifurcate and the ribbing becomes finer and closer. When the outer whorls are peeled off one by one, it is found that their shape in cross-section and their ornamentation undergo a series of changes and that stages in the development of the shell can be recognized. The first, or embryonic, stage in development is represented by the protoconch. This is an oval calcareous chamber with its long axis at right angles to the plane of coiling of the shell. The first three or four whorls are formed during infancy, and belong to the *nepionic* (*brephic*) stage. They are all quite smooth and much depressed ; that is to say they are low and wide in cross-section. They also increase rapidly in width from coil to coil. In consequence of this shape and rapid increase, the umbilicus is deep and crater-like.

The next few whorls are characterized by a series of changes leading from the nepionic to the adult condition, and are therefore said to represent the adolescent, or *neanic* stage. The whorls increase in height, but the rate at which they widen diminishes, until they are oval in general outline with the long axis of the oval in the plane of coiling. In consequence of this change in shape the umbilicus widens and becomes shallower. Meanwhile the ornamentation develops. Starting as a series of elongate tubercles on the flanks of the whorl (Fig. 142), they become still more elongated and form ribs as the whorls increase in height. The ventral surface next begins to show faint crenulations which grow more prominent and eventually appear as bifurcations of the ribs. The shell has now attained the adult or *ephebic* stage. In aged or senile specimens there is a tendency for the ribbing to become less clearly defined, especially upon the ventral area, and thus a final or *gerontic* stage may be recognized. Internally the shell is divided by septa into as many as 125–130 chambers. The living chamber is the largest, and occupies from two-thirds to the whole of a whorl; the creature's body must therefore have had vermiform proportions. From the ventral margin of its posterior surface a long thin siphuncle arose, and extended back through all the coils, still keeping to the same margin of the successive septa until it reached the nepionic whorls. Here it shifted nearer and nearer to the centre of each septum (Fig. 142D), and eventually ended with a slight swelling in the cavity of the protoconch. The majority of septal necks project forwards, but in the nepionic stage they project backwards as in the nautiloids. The first septum, which closes the protoconch, carries a backwardly projecting bulb instead of an open neck.

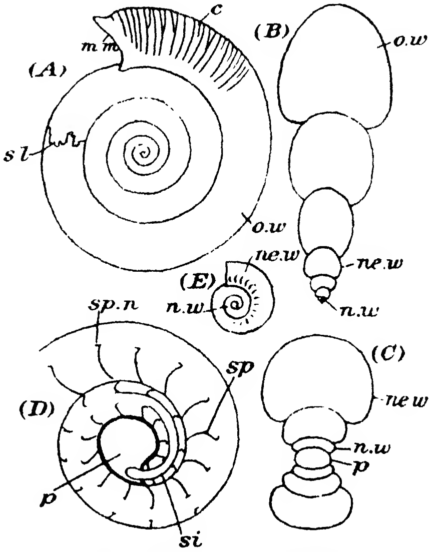


FIG. 142.—Structure of *Dactylioceras commune*.

(*A*) Side view. (*B*) Transverse section. (*C*) Transverse section of innermost whorls (greatly enlarged). (*D*) Median section of innermost whorls (greatly enlarged). (*E*) Side view of first few coils (enlarged). *c*, costa or rib. *m.m*, mouth margin. *n.w*, nepionic whorl. *ne.w*, neanic whorl. *o.w*, outer whorl. *p*, protoconch. *si*, siphon. *s.l*, suture-line. *sp.n*, septal neck. *sp*, septum.

The edges of the septa are crimped and frilled (Fig. 144), so that the suture-line or junction of the septum with the shell wall is very complex in pattern. As the sutures are followed backwards to the earlier stages in their development their complexity diminishes. In the early neanic stage the crimpings are reduced in number, and are nearly smoothed out. In the late nepionic stage the suture line is a flowing curve showing only the underlying plan of the adult suture. The forward folds are called saddles; the backward ones, lobes. There is one small saddle on the mid-ventral line, and three larger ones on either side which decrease in size to the limb margin. For each saddle and lobe on the outer rim of a septum there is a corresponding feature on the inner or impressed rim. This latter dorsal portion of the suture line can be seen only by breaking the specimens, and therefore plays a much less important part in systematic study. The total number of these elements is smaller in the earlier than in the later and adult stages; new elements are added chiefly at the limb margin, but one small one is added at the mid-ventral line also. The first suture-line, formed by the septum which separates the protoconch from the first chamber, differs greatly from the second suture, for it has a very large ventral saddle.

Just as the nepionic shell of *Nautilus* recalled the condition in the Palæozoic nautiloids, so likewise does the same stage in *Dactylioceras* recall that of the Palæozoic ammonoids. A typical example of the latter will be studied next.

The Structure and Development of a Palæozoic Ammonoid.—As an introduction to the study of Palæozoic ammonoids *Goniatites* (L. Carb.) may be taken for the type. In general appearance (Fig. 143) it resembles the nepionic whorls of *Dactylioceras* greatly enlarged, but its outer whorls embrace the inner ones to such an extent that the umbilicus is nearly as completely obliterated as in *Nautilus*. The suture of the adult *Goniatites* is very much like the late nepionic suture of *Dactylioceras*, for its lobes and saddles are entire and free from crimping, and there is a ventral saddle. This simple type of suture is very common among Palæozoic ammonoids and is described as *Goniatitic*, to distinguish it from the more complex type seen in *Dactylioceras*, which is characteristic of practically all Mesozoic ammonoids and is described as *Ammonitic*. Here again, when the development of the suture (Fig. 144C) is traced back to its earlier stages, the line becomes yet more simplified by a smoothing of the folds down to lower curves, and by a loss of the ventral saddle. In this case, however, the difference between the second and the first sutures is not so great, and it is easy to

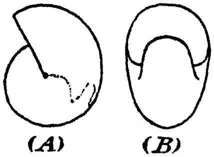


Fig. 143.—*Goniatites*. (*A*) Side view. (*B*) Apertural view.

imagine that the two large saddles of the former were produced from the median saddle of the latter by the development of a median lobe.

The study and comparison of the development of these two genera illustrate several important principles, which govern the growth of individuals.

The early stages of development exhibit a simpler, presumably more primitive, state of affairs than the later. This is well exemplified by the development of ornamentation and of the suture in *Dactylioceras*. In *Goniatites* this is not so fully illustrated, for it is a much earlier type and even in its adult stage exhibits a more primitive condition than does *Dactylioceras*. The many points of resemblance between the early stages in the latter and the majority of stages in the former are so striking as to justify the statement that the early development of the Mesozoic genus repeats many features that are manifested during the major part of the development of the Palæozoic genus. Such repetition, during development of later forms of features seen in the earlier, illustrates the principle of recapitulation or palingenesis. In ordinary usage the word recapitulate implies, not the reproduction of every detail, but the summarizing in greater or less detail, of more salient points. That is the significance which must also be attached to the term recapitulation in the study of fossils. It is therefore important to enquire what are the principles which govern the process of summarizing, that is the shortening of the story.

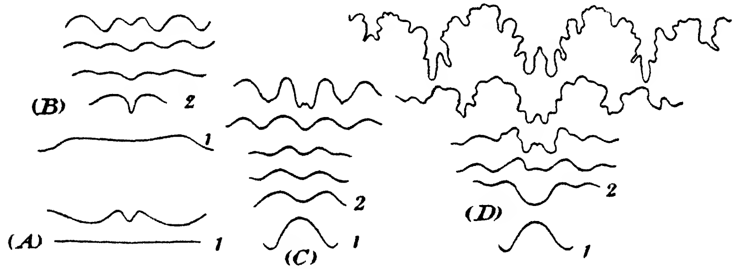


FIG. 144.—Development of Suture Line in various Ammonoids.
(*A*) *Anarcestes*. (*B*) *Tornoceras*. (*C*) *Goniatites*. (*D*) *Dactylioceras*.
1, 2. First and second septa.

The first of these is the principle of Tachygenesis, or of Acceleration in development. Thus all the changes which it took a lifetime to accomplish in the Palæozoic type were passed through by the Mesozoic individual whilst it was yet in its infancy.

The second is corollary to the first. It is the principle of Lipopalingenesis, or of omission in the development of the later type of stages passed through in evolution. Acceleration leads not merely to the shortening of certain stages of phylogenetic significance, but also to the skipping of some stages that are not essential to the establishment of adult characters. Thus, as seen above, between sutures one and two of *Dactylioceras* there is a greater difference than between the first and second sutures of *Goniatites.*

A third, the principle of Bradygenesis or Retardation of development, will be illustrated later from other types.

A fourth principle is illustrated by a comparison of the first suture of *Goniatites* with that of yet earlier ammonoids (Fig. 144). In *Tornoceras* (M. Dev.) the saddle of the first septum is low and broad, and in *Anarcestes* (L. Dev.) it is absent. The differences in the first septum of these genera may possibly be associated with increasing closeness in coiling. In *Anarcestes* the inner whorls are loosely coiled, and no pressure was brought to bear upon the soft parts which secreted the protoconch and its aperture. In later genera closeness of coiling comes on (tachygenetically) earlier and earlier in the development of the individual, and even appears in the embryonic stages during the formation of the protoconch. This pressure naturally affected the ventral area most, and bent the corresponding part of the septum forward in the process. This large saddle in the first suture line of the more advanced ammonoids is therefore a feature which never had a counterpart in the adult of any remote ancestor, but has been gradually introduced into the development of the individual in response to other than hereditary influences. It has therefore no phylogenetic significance. The introduction of such features is described as Cœnogenesis (Fig. 145), and the possibility of the presence of cœnogenetic characters must always be borne in mind when interpreting the developmental or ontogenetic record.

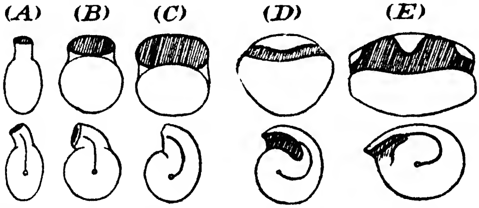


FIG. 145.—Diagrams to illustrate the Cœnogenetic Changes which have taken place in the Protoconch.

Upper row—apertural view. Lower row—side view, with axial line to indicate the degree of urvature of the axis of the protoconch.

(*A*) *Gyroceratites.* (*B*) Hypothetical. (*C*) *Gephyroceras.* (*D*) *Trachyceras.* (*E*) *Phylloceras.*

Recurrent Morphological Changes.—Ammonoids are of such value to stratigraphy and to theoretical palæontology that they have received much attention, and the mass of detailed information that has been accumulated about them is already almost overwhelming. From this it becomes evident that certain changes of form recur frequently and may be adaptations to constantly recurring modes of life (Fig. 146).

If it be imagined that an ammonite shell could be uncoiled and straightened out it would be seen to have the form of an elongated cone, the form of which varied according as its calibre increased slowly or with varying degrees of rapidity from apex to base. Coiled shells with slowly increasing calibre have a wide umbilicus within which the inner whorls are fully exposed to view. Such a form of shell is described as a *serpenticone*. Shells with rapidly increasing calibre either along all diameters or only the transverse diameter respectively have a narrow deep umbilicus within which the inner coils are almost or quite hidden from view. Some of these approximate to a spherical form, hence the name *sphærocone* for such. Shells in which the umbilicus is more or less reduced are thought of as being more closely or tightly coiled, and are said to be more or less *involute*. On the other hand, shells like the serpenticone may be regarded as more loosely coiled or *evolute*. The degree of uncoiling may be such that the whorls are no longer in contact with one another. For these the term *criocone* may be used. The condition in which the shell is straight for the whole or the greatest portion of its length may be described as *baculicone*. In some the shell straightens out in later life and then bends back upon itself for a short distance. This is well seen in the genus *Scaphites*, hence the descriptive term *scaphiticone*. A few ammonoids break away from the normal planospiral and coil up like a corkscrew, that is to say in a helicoid spiral. For these the term *helicicone* is suggested.

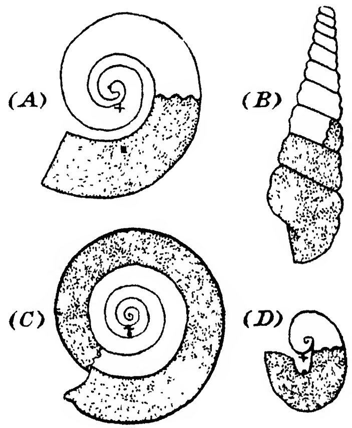


FIG. 146.—The Forms and Natural Attitudes of some Ammonites.

(*A*) *Crioceras*. (*B*) *Turrilites*. (*C*) *Dactylioceras*. (*D*) *Scaphites*. Shaded areas show the extent of the living chambers. The cross shows the centre of buoyancy of the shell and the black dot the centre of gravity. (After Trueman.)

The form of the whorl in cross-section also exerts a considerable influence upon the shape of the shell. The central form is one in which the whorl has about the same diameter dorso-ventrally as from side to side. When the former diameter is increased the whorl becomes elevated and compressed and is often triangular in section. The venter is sharp and the shell is then described as an *oxycone*. On the other hand, the transverse diameter may be greater than the vertical. The whorl is then said to be depressed. If, in this case, the venter is only gently arched and is sharply separated from the sides which are flat and converge dorsally, the shell is then called a *cadicone*.

Though it seems safe to assume that this rich variety of shapes was associated with different modes of life there is no direct evidence in support of the assumption. Presumably, as in the existing Pearly Nautilus, the chambers were filled with gas, the low specific gravity of which counterbalanced that of the heavier shell and body so that the average for the whole was about the same as that of the water. The creature was therefore not anchored to the bottom by its weight but could move without difficulty through the water. It has long been assumed that the oxycone was an adaptation to rapid movement. Probably, as with the Nautilus, the animal had some degree of control over the gas that was present and was able to change the average specific gravity sufficiently to enable it to rise and sink slowly, or even to come to rest on the bottom. The shells of more aberrant shapes, however, exhibit features which preclude the likelihood that they ever rested on the sea-floor. On the contrary very interesting work upon the relative positions of the centres of gravity of the body, the shell and the gas chambers indicates that these types spent life floating at or near the surface.

The septa, unlike shell shape, seem to have undergone a progressive change comparable with that seen in the development of *Dactylioceras*, across the whole range of ammonoid history. At first they were simply folded but towards the close of the Palæozoic they became frilled. This feature appeared first upon the lobes but rapidly extended on to the saddles. Increasing complexity of frilling was, however, a recurrent change which was repeated frequently within the history of small groups. The major pattern of frilling was often sufficiently constant to provide evidence of specific or even of generic affinity ; but the finer details exhibit such a wide range of variation, even within the same individual, as to detract greatly from their value for classificatory purposes.

The Earliest Ammonoids.—The earliest ammonoid known was *Agoniatites* (U. Sil.-U. Dev.). Its inner whorls are wide and depressed, but the outer are moderately elevated and compressed. The siphuncle is ventral and the suture line is a smooth-flowing curve like that of *Nautilus*. Its resemblance to certain silurian nautilids, *e.g. Barrandeoceras*, is so striking that it has been described as " merely a slightly modified nautilus."

During the Devonian ammonoids increased in importance. In *Anarcestes* (Fig. 147) the shell, as it grew, became more and more closely coiled. At the same time the whorls became much depressed and semi-lunar in cross-section. The outer embraced the inner to such an extent that the umbilicus became narrow and deep. The suture line (Fig. 144) had a simplicity comparable with that of *Agoniatites*.

In *Gyroceratites*. (*Mimoceras*. L. & M. Dev.) the protoconch is ovoid and has its axis in line with the rest of the shell. The whorls are circular in section and are merely in contact with one another. The suture line is like that of *Anarcestes* but less strongly folded.

Lobobactrites (*Bactrites*. M. & U. Dev.) is a straight form with a raised band along its dorsal side. The septa and sutures are the same as in *Gyroceratites*. The order of succession in time of these two genera in relation to *Anarcestes* and *Agoniatites* suggests the loose coiling of the one and the straight form of the other are secondary. In this respect they are analogous to *Gyroceras* and *Cyrtoceras* among the nautiloids.

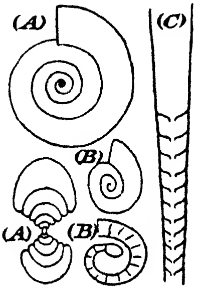


FIG. 147.—The earliest Ammonoids.

(*A*) *Anarcestes*, side view and section. (*B*) *Gyroceratites*, side view of adult and of innermost whorls. (*C*) *Lobobactrites*, ventral view.

Thus, in the Upper Silurian and the Lower and Middle Devonian the ammonoid organization is seen in its simplest expression. During the Upper Devonian the fertility of that organization began to express itself in the production of new genera some of which represent the root stocks of later strains.

In *Gephyroceras* (Fig. 148) the first septum had no saddle and the inner whorls were round in section and loosely coiled. In its neanic stages they were broad and depressed, but later they became compressed and elevated. This change is carried a stage further in the allied *Timanites*, and reaches its extreme expression in *Beloceras* (Dev., Fig. 148). In association with this progressive elevation the suture line exhibits a multiplication of parts. Already in the first genus a large ventral saddle is present. In the second this has broadened, and a notch has appeared on its apex, and new saddles and lobes have developed on the limb of the whorl. In *Beloceras* many new elements have been added to the suture line both at the mid-ventral line and on the limb.

The way in which the suture line in this rapidly evolving series increases in complexity is of especial interest. In practically all other ammonoids, as in *Dactylioceras* and *Goniatites*, the addition of new lobes and saddles takes place only at the umbilical margin. In this series, however, they are added also at the mid-ventral and probably at the mid-dorsal lines also. In consequence of this the largest elements are far removed from the ventral line, whereas in the majority of other forms they adjoin the ventral area.

The genus *Tornoceras*, though it stands alone among Devonian ammonoids, appears to be closely related to the line of descent which led from *Agoniatites* to the dominant Carboniferous forms related to *Goniatites*. Its outer whorls are slightly compressed, and embrace the inner so completely that the umbilicus is practically non-existent. The genus *Prolecanites*, though it existed in upper Devonian times, attained its main development during the Carboniferous and will be considered later. Another group, the Clymenidæ, springs into prominence in the upper Devonian, but disappears as suddenly as it comes. It differs from all other ammonoids in the position of the siphuncle, which is placed near to the dorsal, instead of the ventral, surface and thus serves as a reminder that no one structural feature should be regarded as an infallible test of taxonomic relationship. The suture line, unlike that in contemporary types, has a large median ventral saddle. As with the *Gephyroceras-Beloceras* series the shape of the whorl (Fig. 148) varies within the limits of the family from a wide depressed whorl in youth to a highly compressed and lofty one in the adults of the more specialized species.

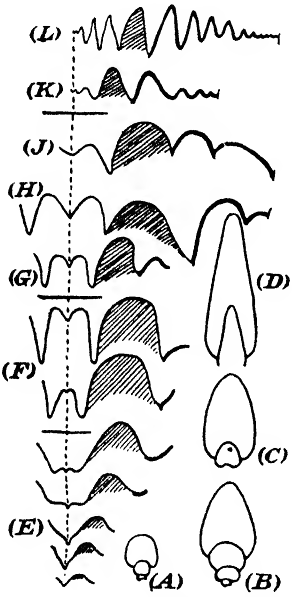


FIG. 148. — *Gephyroceras-Beloceras* series, sections of whorls and development of Suture line (after Haug).

Sections of whorls of :—(*A*) Primitive species of *Gephyroceras calculifer*. (*B*) Advanced species of *Gephyroceras wildungense*. (*C*) *Timanites hœninghausi*. (*D*) *Beloceras*. Sutural development in :—(*E*) *Gephyroceras*. (*F*) *Gephyroceras intumescens*. Sutures of :—(*G*) *Timanites hœninghausi*. (*H*) *Timanites archiaci*. (*J*) *T. acutus*. Development of suture in *Beloceras multilobata*. (*K*) Young. (*L*) Adult.

Every degree of involution, every change in shape of whorl, from extreme depression to extreme compression, every variation in the venter from flat to sharp described above for Devonian forms is repeated frequently among later ammonoids. On the other hand the patterns of suture line produced in these early types are never repeated in the adult individuals of later ages. Thus at the outset this fact may be emphasized, that for the systematic study of larger groups the suture line has greater value than the shape of either whorl or shell.

The Later Goniatitic Ammonoids.—It has been already noticed that Palæozoic ammonoids as a whole were characterized by a simple type of suture, in which the lobes and saddles were entire, that is to say they were not crimped. This goniatitic type of ammonoid attained a considerable development during the Carboniferous period. Towards the end of this period, and during the Permian, there was a tendency for crimping to appear on some of the lobes, a condition which is described as ceratitic. In the majority of cases, however, the saddles remained entire until the close of the Palæozoic.

The majority of Carboniferous ammonoids centre around *Goniatites* and were derived from *Agoniatites* through a Devonian stock similar to, if not identical with, *Tornoceras*. They tended to exhibit a depressed form of whorl which showed a tendency to widen and embrace the inner whorls. The suture line was a simple flowing curve with a small median saddle rising from the bottom of a large ventral lobe, one external saddle, one lateral saddle, and one lateral lobe.

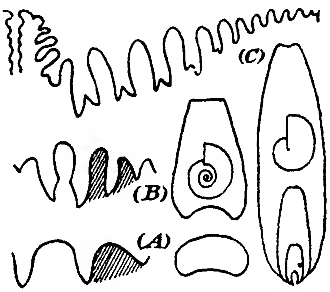


FIG. 149.—Diagrams of *Prolecanites* and *Medlicottia*.

(*A*) *Prolecanites louisiana*, whorl shape and suture (after Haug). (*B*) *Prolecanites compressa*, side view, whorl section and suture (after Haug). (*C*) *Medlicottia*, ditto (after Waagen).

In the genus *Reticuloceras* (U. Carb.) the whorls are elevated and compressed, and the umbilicus is narrow. The surface of the shell is ornamented with fine transverse striæ which at first swing forward as they pass from the umbilical to the ventral margins. On the outer whorls of the early varieties these striæ develop a forward bend upon the shoulder. During evolution this becomes progressively more marked until it forms a long tongue-shaped loop in later varieties. On the inner coils of these last, as in the earlier varieties, the striæ do not exhibit an appreciable bend upon the shoulder, but during development the bend appears gradually and becomes increasingly more marked towards the outer coils. Thus, as the shell develops, its ornamentation passes through that sequence of changes exhibited by adults in successive ancestral generations. All this has been established upon a sound stratigraphical basis and thus provides a good example of the principle of recapitulation.

In *Gastrioceras* (U. Carb., Fig. 150), the whorls are only moderately wide and slightly embracing. Consequently the umbilicus is wider and more open. It is exceptional among Palæozoic ammonoids in that it has a quite distinct ornamentation. This takes the form of long tubercles or short ribs on the flanks of the whorls.

The genus *Prolecanites* (Fig. 149), which survived from the Upper Devonian, in its most primitive species resembles *Anarcestes* in having depressed whorls even in adult life, but in the more advanced species the whorls became moderately elevated and compressed and developed a flat ventral area. In typical species the lobes of the suture line become pointed and the saddles spatulate in outline.

While it may be assumed that later ammonoids descended from these carboniferous stocks opinions differ with regard to the part played by the goniatitic and prolecanitic branches respectively.

Ammonoids in their Hey-day.—The student, situated in the British Isles, where the Permo-triassic rocks, barren of fossil ammonoids, are followed by the Jurassic rocks, in which they abound and are very varied, naturally concludes that it was during the period represented by these later rocks that the race was in the hey-day of its evolutionary development. When, however, the ammonoid faunas of the marine Permo-trias of other lands are studied, it is soon realized that it was during this earlier period that this race attained its acme as judged by the variety of stocks represented, by the variability in shape of shell and by the complexity of ornamentation and of suture line.

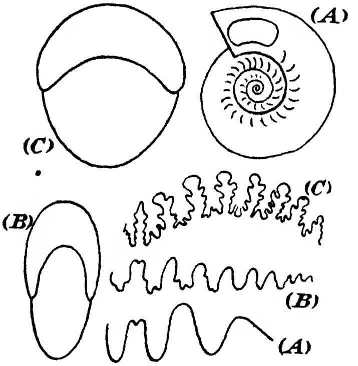


FIG. 150.—Diagrams of *Gastrioceras*, *Popanoceras*, and *Cyclolobus*.

(*A*) *Gastrioceras*, side view, whorl section and suture line (after Hyatt and Smith). (*B*) *Popanoceras*, apertural view and suture (after Hyatt and Smith). (*C*) *Cyclolobus*, ditto (after Gemmellaro).

From the Goniatitic side of the Carboniferous ammonoids arose *Popanoceras* and *Cyclolobus* (Perm.-Trias., Fig. 150). Both these were smooth, almost globose, forms; the whorls were wide and deeply embracing. As with increased elevation so with increased widening of the whorls there always comes a great addition to the number of elements in the suture line. These appear solely at the umbilical margin. It is as though the septum were flexible and the extremity at this margin were held by some invisible hand which, as the limb extended, shook it to and fro, thus throwing it into folds. In both these genera the lobes become distinctly frilled, but in *Cyclolobus* the frilling extends up the sides of the saddles nearly to the apex, which is left unaltered like a round leaflet or foliole.

This is a characteristic feature of all members of the two families which these genera represent.

The *Prolecanites* type of goniatite finds its most modified expression in the Permian genus *Medlicottia* (Fig. 149). In this, elevation and compression of the whorls were carried to an extreme; the flattened venter had become grooved, and the outer whorls almost completely embraced the inner so that the umbilicus was quite small. In association with the greatly increased height of the whorls the number of sutural elements was considerable. The suture line, however, showed two other features of especial interest. Firstly, the lobes lying near the venter were bifid, and thus exhibited incipient crimping. Secondly, the external saddle was greatly elevated and complexly frilled.

The Permian genus *Paralecanites* (Fig. 151) may have been derived from primitive species of the Carboniferous *Prolecanites*. It is planulate in form; its whorls slightly compressed; its umbilicus widely open, so that the inner whorls are exposed to view. In its suture line the saddles are still goniatitic in appearance, but the lateral lobes are finely toothed or denticulate. This combination of sutural features attains its most typical development in the genus *Ceratites* (Mid.-Trias.). This type of suture is therefore described as ceratitic. It occurs so frequently among triassic ammonoids that this period has been called the "Age of Ceratites." This name is not so apt as the name Age of Goniatites for the preceding periods, since the ceratitic type of suture was but a transitory phase in the history of the various series of ammonoids which ran their course during the Trias. In some cases, however, this history started with a goniatitic suture, and passed on to an ammonitic type before its close. Nevertheless, the ceratitic type is a characteristic feature of the Triassic period.

The majority of ammonoids hitherto considered have had smooth unornamented shells. Among the triassic ammonoids ornamentation became a prominent characteristic in some branches, though it was absent in others.

In those which retained the smooth evolute condition seen in *Paralecanites* the suture line underwent a marked change. Thus in *Gymnites* (M. Trias) the saddles (Fig. 151C), as well as the lobes, were frilled and almost truly ammonitic. In no ammonoid known is the suture line so complex as in the Upper Triassic genus *Pinacoceras*. It has numerous lobes and saddles, for the whorls are greatly elevated and compressed, and the shell deeply involute. Moreover, every element in it is divided, crimped and frilled to an extraordinary degree. The largest elements are situated away from the midventral line and well up on the flanks of the whorl.

The basal plan of the suture therefore bears a superficial resemblance to that exhibited by *Beloceras*.

The ornamented ceratitoids arose from the smooth through a second radicle (Fig. 151B) like *Tirolites* (L. Trias). This is indicated by the fact that many of them exhibit a *Tirolites* stage in their development. In this genus the whorls are slightly depressed, the umbilicus is wide, its suture line is typically ceratitic and the whorls are decorated upon the flanks with widely spaced simple ribs, and a single longitudinal ridge. At the points of intersection of the ridge with the ribs stout spines or tubercles are developed. The same simple form of shell and condition of suture line are exhibited also by *Californites* and *Shastites* (U. Trias). But in the series which these two genera (Fig. 151G, H) represent the ornamentation becomes very rapidly elaborated. In the former the ribs are still widely spaced, but there are two longitudinal ridges and correspondingly two rows of tubercles or spines. In the latter the ribbing is finer and more closely arranged, and there are as many as six ridges and rows of tubercles.

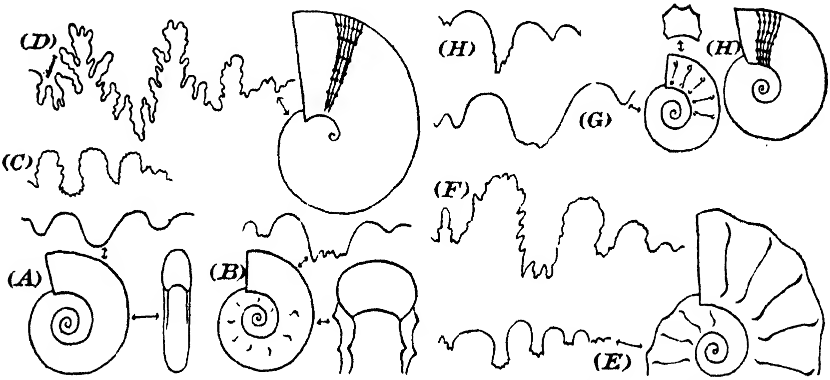


FIG. 151.—Diagrams of Ceratitoid Ammonoids (based on Smith).

(*A*) *Paralecanites*, side view, apertural view, suture. (*B*) *Tirolites*, ditto. (*C*) *Gymnites*, suture. (*D*) *Protrachyceras*, side view and suture. (*E*) *Ceratites nodosus*, side view and suture. (*F*) *Ceratites humboltensis*, suture. (*G*) *Californites*, side view, whorl section and suture. (*H*) *Shastites*, side view and suture.

The two types of Ceratitoids just considered illustrate the principle of the independence of series of changes; for in both cases, whilst the ammonoid remained in a primitive condition in most of its characters, specialization affected at least one. This one, however, was not the same for the two types: in the one it was the suture line, in the other it was the ornamentation, which progressed with the greatest rapidity. In a third type (Fig. 151D), represented by *Trachyceras* (Trias.) specialization affected a number of characters simultaneously; the whorls became stout, the shell involute, the ornamentation attained the acme of complexity for ammonoids, and the suture line passed on to a truly ammonitic stage. In the foregoing ornamented types the ornamentation was on the whole finely textured. In the remaining ceratitoids it retained the coarse character seen in the radicle *Tirolites*. This coarsely ornamented branch included the genus *Ceratites* itself (Fig. 151E). It was rich in numbers and species, but did not experience any excessive specialization in any of its members. The whorls were only moderately elevated and compressed. The shell was only moderately involute and the suture line was ceratitic, though occasionally the saddles became faintly frilled.

Thus the ceratitoids were a very varied and widely differentiated group. Yet for all branches the potentialities or possible lines of progress were the same, and few in number because they were all from the same stock, and they were presumably endowed with the same capabilities for shaping the whorls, for coiling the shell, and for elaborating the ornamentation and the suture-line. But whilst one branch progressed in the suture line, another in the ornamentation, both remained stationary, or almost so, in other respects; a third progressed in several respects and with great rapidity; and a fourth, as it were, ambled along slowly in as many ways. Such was the manner in which not only the ceratitoids, but also many other groups of animals, produced from only few structural features that wonderful variety of form and figure which both fascinates and bewilders.

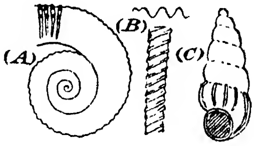


FIG. 152.—Diagrams of retrogressive Ceratitoids (after Hauer).

(*A*) *Choristoceras*, side view showing tendency towards uncoiling of outer whorl. (*B*) *Rhabdoceras*, straight shell and suture. (*C*) *Cochloceras*—with helicoid spiral shell.

Up to this point only progressive changes have been considered. The ceratitoids were, however, also subjected to retrogressive changes (Fig. 152). Thus in *Polycyclus* (U. Trias) the whorls became rounded and only slightly embracing. *Choristoceras* (Rhætic) in its adult and senile stages went further, for its outer whorls began to separate, that is to say they commenced to uncoil. In *Rhabdoceras* (U. Trias) this tendency set in at a much earlier stage in development, and practically the whole shell had assumed a straight condition as did some of the primeval ammonoids. At the same time the suture line reverted to a simple goniatitic condition. Retrogression does not always manifest itself merely in a return to conditions resembling early progressive stages; it is sometimes expressed by the assumption of new and anomalous forms. Such was the case in *Cochloceras* (Trias.), in which the shell is coiled in a turreted spire like that of a snail.

During the Triassic period three other groups of ammonoids occupied an important place in the fauna. These centred around the genera *Ptychites*, *Tropites*, and *Arcestes* respectively. The Ptychitoids characterized the Lower Trias, the Tropitoids and Arcestoids the Upper Trias. All three had their origin in the Goniatitid race of late Palæozoic ammonoids. Both ptychitoids and tropitoids include genera—the former *Nannites* (Fig. 153A), the latter *Leconteia* (Fig. 153C)—which are remarkably like the Goniatitids in shape and suture line. The history of these two groups taken together is comparable with that of the ceratitoids as a whole. The ptychitoids correspond with the smooth unornamented, and the tropitoids with the ornamented divisions, respectively. The members of the ptychitoid group pass through a *Nannites* stage in their individual development. *Parananites* has a ceratitic suture. *Ptychites* (M. Trias), the latest member of the group, has an ammonitic suture.

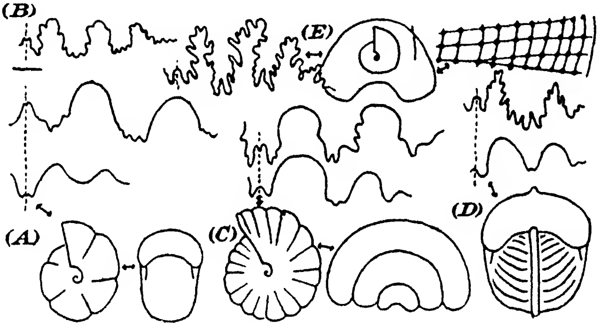


FIG. 153.—Diagrams of Ptychitoids and Tropitoids (after Hyatt and Smith). (*A*) *Nannites*, side and apertural views, young and adult sutures. (*B*) *Ptychites*. (*C*) *Leconteia*. Side view, section of whorls, young and adult sutures. (*D*) *Tropites*, apertural view, young and adult sutures. (*E*) *Sagenites*, side view, section of whorl, plan of ornamentation, and adult suture line.

Among the tropitoids the primitive *Leconteia* (Fig. 153C) already has ribs. The series of forms *Halorites*, *Juvavites*, *Sagenites*, which descended from that generic type, evolve rapidly along lines parallel to those followed by the ceratitoids leading up to *Shastites* and *Trachyceras*. Between *Sagenites* (Fig. 153E) and *Trachyceras* the superficial resemblance is very striking, and furnishes a good illustration of homœomorphy. In the series of which *Tropites* itself (Fig. 153D) is the terminal member the ornamentation is coarser than in the one just considered. Retrogressive tendencies are exhibited in the group by the genera *Tornquistites* and *Sybillites* in both of which the suture has returned to the goniatitic condition. Uncoiling of the shell has not, however, gone beyond producing an evolute shell with round whorls just in contact with one another.

The Arcestoids appear to have affinities with the Popanoceratid and Cycloloboid branches of the Goniatitidæ. They exhibit the acme in involution among ammonoids. Their suture line is ammonitic, and in the genus *Cladiscites* (U. Trias) attains a gossamer-like delicacy of subdivision.

The Age of Ammonites.—During Liassic and Inferior Oolite times the ammonoids entered upon a new lease of life, which lasted with only slowly diminishing vigour until the close of the Cretaceous period. Throughout this vast stretch of time they were characterized by the possession of typically ammonitic suture lines, and therefore it may not inaptly be spoken of as the Age of Ammonites. It should not, however, be forgotten that outside the British area many true ammonites existed during the Triassic period. With the exception of the Monophyllitidæ all these became extinct before the opening of the Liassic period. From this family two others arose :—the Phylloceratidæ and the Lytoceratidæ—which persisted with but little change until the Cretaceous. These had their European headquarters in the Mediterranean area, where time after time they appear to have given origin to new but short-lived and rapidly changing races. Such long-ranged families, which thus give rise to successive new types are called *radicle stocks.*

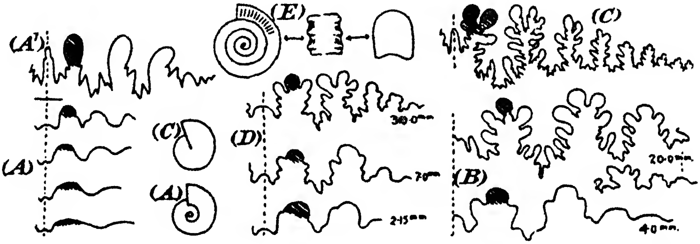


FIG. 154.—Diagrams illustrating Ammonites of Monophyllitic Origin.

(*A*) *Monophyllites*, side view and development of suture (after Spath). A¹, Suture of *Monophyllites billingsiana* (after Zittel). (*B*) *Tragophylloceras*, development of suture (after Spath). (*C*) *Phylloceras*, side view and suture (after Zittel). (*D*) *Psiloceras erugata*, development of suture (after Spath). (*E*) *Caloceras*, side view, venter and whorl section.

The genus *Monophyllites* (Trias) had a smooth almost unornamented coiled shell. The whorls were slightly elevated and compressed, and embraced one another only to a moderate degree. The suture line (Fig. 154A), after passing through a goniatitic phase in development, reaches a stage in which the larger lobes are subdivided into three parts and frilled. Much of the saddle remains entire, and assumes a distinctive oval form. Inasmuch as there is only one such oval foliole forming the apex of each saddle the latter is described as monophyllic.

The genus *Phylloceras* represents a family which was derived from the Monophyllitidæ by such close coiling of the shell that the outer whorls completely embraced and hid the inner from view, and by a further complication of the suture line (Fig. 154C). Whilst the lobes retained the same general character, the saddles became deeply divided, and each division ended in an oval foliole. At the apex there were two folioles of equal size, the saddle being on that account described as diphyllic. Corresponding with the increased height of the whorls the number of saddles and lobes also increased. Having attained this stage in specialization this branch of ammonites became practically stationary in its evolution, and persisted almost unchanged from the opening of the Lias to the close of the Cretaceous.

In *Lytoceras* on the other hand the whorls are nearly round in cross-section, and do not embrace one another. The number of elements in the suture line (Fig. 162A) has remained at the primitive number seen in the goniatites, and at the same relative proportions, but the complexity of crimping is more advanced than that seen in any other derivatives of the *Monophyllites* stock. This genus also persisted from Liassic to Cretaceous times practically unchanged. During the early Cretaceous a tendency to uncoiling suddenly became very marked. It will be seen later that the same tendency became manifest in other groups of ammonites, and thus several forms were produced which were closely similar in appearance, but very different in origin. These will be more fully dealt with later.

The history of the ammonites, as culled from the rocks of the British area, is not a continuous one, type after type rises to predominance, declines and vanishes in rapid succession. Had these evolved from one in lineal sequence, and within the area, it would have been easy to have formed a concise and clear idea of the fauna as a whole, and to have had an ideal time scale of genetically related forms. But this is not the case, for as the successive new types arose in the Mediterranean area many of their representatives streamed into the British seas, and in the course of their adaptation to new surroundings underwent considerable change. The ammonites belonging to each stream, or to each cluster of closely related streams, had features in common which imparted a family resemblance to successive faunas over an appreciable stretch of time and thus provided a basis for the creation of palæontological as well as stratigraphical divisions for Middle and Late Mesozoic times.

The Early Jurassic Ammonites.—As seen above there was a continual influx into the British area of new ammonite types, and a dying out of old ones throughout the Jurassic period. Consequently the period may be divided into a number of smaller divisions, or ages, defined more or less clearly by breaks in the succession of forms at the beginning and the ending of each, and characterized by the dominance of one or more families. There is, however, one break of greater importance which occurred shortly after the close of the Liassic period, at the close of the Aalenian stage. It will be a convenience to refer to that part of the Jurassic which preceded this break as the Early Jurassic, and that which follows as the Later Jurassic.

THE AGE OF PSILOCERATIDS.

The earliest Jurassic invasion is typified by the genus *Psiloceras* (Fig. 154D) which appears to have originated directly from a more primitive section of the Monophyllitidæ. Its sutures retained marked traces of the phylloid character seen in that family.

Its whorls are not quite so stout as those of *Monophyllites*, nor do they embrace one another to the same degree. Though the outer whorls are smooth, the inner often show ornamentation similar to that of the closely allied *Caloceras*. The species of *Caloceras* (Fig. 154E) exhibit many degrees of ornamentation and variation in shape of whorl, but all are characterized by a slow increase in the calibre of the whorl, so that the shell shows an unusual number of coils. In *Schlotheimia* the whorls tend to become more elevated, compressed and embracing. It is ornamented with ribs which pass on to, but not across, the venter. Along the median line of the latter there is consequently a smooth, or even a grooved, area which gives the genus a characteristic appearance. This little group of ammonites developed all these features almost within the limits of time represented by the lowest layers in the Lias. They do not seem to have given rise to any later forms. The period of their existence therefore is comparatively well defined, and is called the Age of the Psiloceratids.

THE AGE OF ARIETIDS.—Soon after the opening of the Liassic period and succeeding immediately upon the age of the Psiloceratids, the seas became dominated for a period by several families of ammonites which may be conveniently grouped together in one super-family the Arietida. The genus *Coroniceras* is typical of this super-family. Its whorls increase slowly in calibre (Fig. 155A–D) and only slightly embrace one another so that the umbilicus is widely open. The sides of the whorls are ornamented with stout ribs which have a forward bend as they approach the venter. On the latter surface there is a clearly marked keel with a groove on either side. The suture line had a simple plan and the lobes and saddles were not deeply subdivided. In the early stages of its development *Coroniceras* had depressed whorls with rounded venter. This stage passed directly into one in which the whorls had diverging sides and distinct keel. Later the remainder of the whorl swelled out and the whole assumed the inflated quadragonal form, which characterizes the adult. This series of form changes is regarded as progressive and is described as anagenetic.

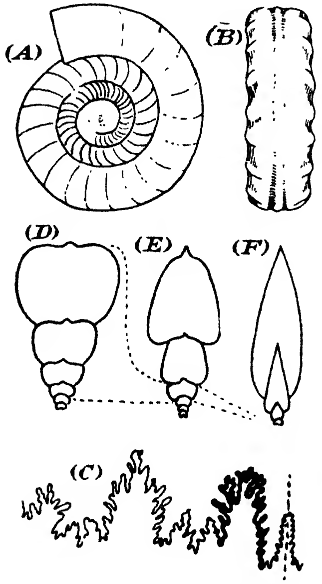


FIG. 155.—Structure and Evolution of the Arietidæ.

(*A* – *D*) *Coroniceras bucklandi.* (*A*) Side view. (*B*) View of venter. (*C*) Suture line. (*D*) Section showing development. (Based on Buckman.) (*E*) *Paracoroniceras gmuendense.* Section showing development. (*F*) *Oxynoticeras oxynotum.* Section showing development.

Paracoroniceras in its development (Fig. 155E) passed through the same stages as did this genus, but they were completed as early as the opening of the neanic stage. After this the keel increased in height, whilst the whorls became elevated and compressed ventrally, thus assuming a trigonal outline. Simultaneously the ribs became feeble and towards the venter they disappeared entirely. In *Oxynoticeras* the whorl became still more elevated (Fig. 155F) and its sides converged so much that they merged imperceptibly into the keel. At the same time the ribs disappeared entirely and the shell became quite smooth. In the development of this genus the *Coroniceras* stage was omitted (lipopalingenesis), that is to say the whorls, which at first were depressed, passed directly to a stage in which they were of trigonal form. A similar sequence of form changes was repeated for other lines of Arietid descent, and gave rise to many sharp ventered forms or oxycones of varied origin. This series of form changes is regarded as retrogressive and is described as catagenetic.

Among the many other arietids the following may be mentioned :—*Arnioceras* whose inner whorls were smooth and the outer ornamented with straight radial ribs : *Arietites*, with its whorls slightly elevated and compressed ; and *Asteroceras* in which they tended to become trigonal in cross-section.

The age of Arietids is subdivided into three parts ; a first, during which the majority of individuals and species were undergoing anagenesis; a second, during which catagenetic forms were dominant; and a third or final one when oxycones exceeded all other forms.

THE AGE OF ECHIOCERATIDS AND DEROCERATIDS.—With the passing away of the Arietidæ there came in these two families. In the Echioceratidæ (Fig. 156) the whorls increased very slowly in calibre, and embraced one another only slightly. The changes in whorl shape were similar to those just seen in the Arietidæ. The suture line, however, excludes them from being classified with this family, as it has advanced to a stage in which the external saddle is divided by an accessory lobe into two secondary saddles.

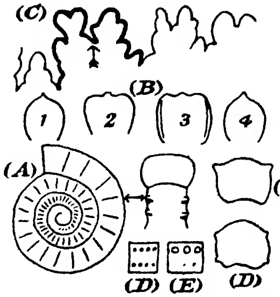


FIG. 156.—Structural Features of Echioceratidæ and Deroceratidæ.

(*A–C*) *Echioceras*. (*A*) Side and apertural view (after Buckman). (*B*) Whorl sections of various species. 1-3, anagenetic. 4, catagenetic. (*C*) Suture (after Buckman). (*D*) *Microderoceras*, whorl section and side view showing two rows of spines. (*E*) *Eoderoceras*, ditto, one row of enlarged spines.

The Deroceratidæ represent a fresh invasion of lytoceratan derivatives. In them the whorls remained round in section throughout life, and embraced one another to only a slight degree. *Microderoceras* was an early form which had complicated suture lines and was feebly ornamented with ribs and two rows of spines (Fig. 156D) of equal size. In *Eoderoceras* the row nearest the umbilicus became reduced (Fig. 156E) and even disappeared, but the outer row became greatly enlarged, thus giving to the shell the appearance suggested by the prefix Dero-.

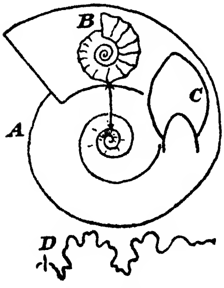


FIG. 157.—Structural Features of a degenerate *Polymorphites* (after Trueman).

A, Side view of complete shell. *B*, Side view of innermost whorls. *C*, Section of whorl. *D*, Suture line.

Microceras represents a divergent development in which the spines disappeared and strong simple ribs arose on the flanks and across the venter. This type of modification is described as *capricorn*. Not infrequently the ribs became flattened as they crossed the venter.

THE AGE OF POLYMORPHITIDS AND LIPAROCERATIDS.—The Polymorphitidæ and Liparoceratidæ belonged to a fresh invasion of forms derived from a lytoceratid stock through primitive eoderoceratids similar to the genus *Tetraspidoceras*, which in many respects resembled the earlier *Microderoceras*.

In *Polymorphites* (Fig. 157) the whorls are slightly elevated and are often ornamented with ribs which cross the rounded and feebly keeled venter. *Uptonia* is an important member of the family, representatives of which reappear later in the lower levels of the Inferior Oolite, *e.g.* *Dumortieria.*

Along with the Polymorphitidæ lived early members of the Liparoceratidæ (Fig. 158), including the wide genus *Liparoceras.* These exhibit varying degrees of inflation of the whorls so that fully grown shells range from being typical serpenticones of the capricorn type to true sphærocones. Out of this assemblage of very closely related, if not actually interbreeding forms, arose all later liparoceratids. Dimorphous forms, which have capricorn inner, and inflated outer whorls, are assigned to the genus *Androgynoceras.* On the inflated whorls the ribs tend to bifurcate on the flanks and to break up into a number of fine costæ on the venter. Tubercles also occur at the points of branching.

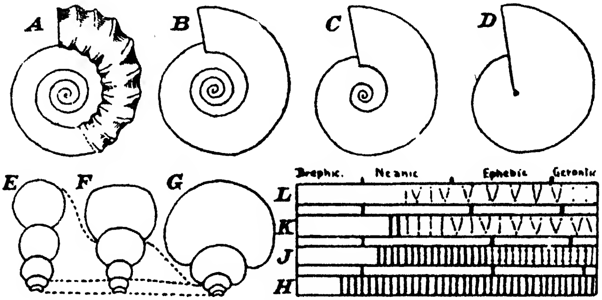


FIG. 158.—Structural Features in the Liparoceratidæ (based on Trueman).

A–D, Diagrams showing in side view the morphological series from the capricorn (*A*) ranging to the sphærocone (*D*) through the dimorphs (B.C.). *E–G,* Diagrams of sections illustrating the same series (from Trueman). *H–L,* Diagram illustrating the variations in character of ornament during the development of the individual (left-right) within the series. *H* = the capri
K, J = the dimorphs. *L* = the sphærocone.

A succession of such assemblages followed one another for a long time. Eventually the dimorphous element in this plexus of descent declined in numbers and seems to have disappeared before the close of the Lower Lias. The typical *Liparoceras* element, devoid of capricorn inner whorls, persisted into the Middle Lias. Meanwhile the serpenticone capricorn type became more evident and developed a marked forward bend of the ribs upon the venter. The importance of this feature is emphasized by the creation of the genus *Oistoceras* which was the dominant liparoceratid during the last stages of the Lower Lias and survived into the Middle Lias.

The production of such a picture of the gradual emergence of two quite different types out of very varied intermingling ancestral assemblages has been made possible by the careful collation of facts from collections made over a long period of years by many workers. If evolution be thought of only in terms of lines of descent, then two extreme and contradictory views may arise from the inspection of such collections. In one view the linear sequence may range from the typical sphærocone to the capricorn. In the other this order may be reversed. The significance of the inner capricorn whorls in dimorphs may accordingly become anticipatory or recapitulatory, proterogenetic or palingenetic according to which view is adopted. When, however, the picture is extended back towards the Age of Deroceratids, it seems probable that the mixed assemblages themselves represent an almost tumultuous outburst of variability on the part of a stream of forms derived from a serpenticone ancestral stock.

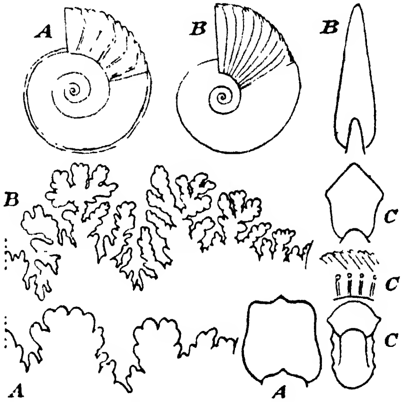


Fig. 159.—Structural Features of the Amaltheidæ.

A, *Pleuroceras*, side view, section of whorl suture line. *B*, *Amaltheus*, ditto sutures (from Buckman). (*C*) Development of *Amaltheus*. Apertural view of nepionic whorls, side view and section of neanic whorl (after Buckman).

The Age of the Amaltheids.—Whilst a few of the Liparoceratidæ lingered on after the majority of the stock had disappeared, an entirely new family, the Amaltheidæ, suddenly appears upon the British scene with all its characteristics fully developed. About their evolution little is known, though there is evidence which suggests that species of *Oistoceras* having an incipient keel and tubercles upon the ribs may have been transitional from the Liparoceratidæ to the amaltheid genus *Pleuroceras*. In this the whorl has become quadragonal in outline, and the angulation of the venter has become a definite keel. The crenulation of the keel, due to transgression by the ribbed ornamentation, distinguish it from similarly shaped and ornamented arietids. The highly involute form *Amaltheus* (Fig. 159B) represents a series which have developed into oxycones. Both these genera characterize rocks of the Middle Lias or Domerian.

The Age of Hildoceratids.—The Lower and Middle Lias were characterized by a rapid succession of different ammonite families. During the Upper Lias and immediately succeeding portion of the Inferior Oolite, on the contrary, hildoceratid ammonites held sway (Fig. 160).

The genus *Hildoceras* (U. Lias) may be taken as the type for these. The shell as a whole is not very involute, for its whorls increased in calibre slowly and the umbilicus is wide and open. The whorls are quadragonal in cross-section with keel and grooves and a tendency towards becoming elevated and compressed. The suture line, like that of *Echioceras*, has the external saddle divided by a subsidiary lobe into two secondary saddles. The ribs do not cross the venter, but exhibit a slight flexure on the lateral area, and a forward swing on the ventral which gives them a superficial resemblance to a sickle. Little is known of their early history. From the facts mentioned above it seems likely that they have affinities with the Echioceratidæ. During the Domerian a few representatives of the family existed in this country, but in the Mediterranean they were more abundant.

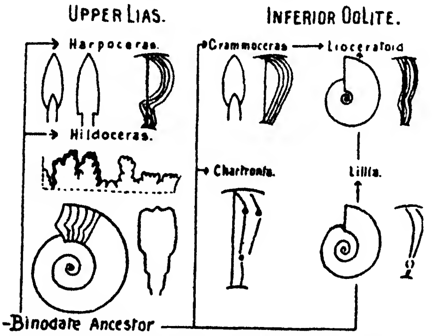


FIG. 160.—Structural Features of the Hildoceratidæ.

Lines with arrows indicate probable lines of descent.

That section of the history which can be culled from remains found in the Upper Lias and Inferior Oolite, is very detailed, but it is only half the story, and that is the catagenetic portion. The earlier stages of catagenesis are revealed by a few odd genera. *Chartronia* (Inf. Ool.) has bifurcating ribs, as is so often the case in this family, but it has in addition two rows of tubercles, an inner, situated at the angle of forking of the ribs, and another on the shoulder of the whorl. This genus points back to a bituberculated ancestor for the family. In *Lillia* (Inf. Ool:) and *Seguenziceras* (M. Lias) only one row of tubercles is present. In *Grammoceras* (M.-U. Lias) no tubercles are present, but the whorl is more primitive in form than is any more advanced type. It is a slightly compressed oval, with an angulate venter. This implies that the portion of the whorl which borders the umbilicus is convex. In all more advanced hildoceratids this portion is either flat or concave.

The remaining hildoceratids fall naturally into two divisions which arose independently out of the imperfectly known primitive stock indicated by these genera. One of these, the harpoceratan, evolved rapidly, and reached its climax in the Upper Lias (Whitbian). The other, the lioceran, arose more slowly and became dominant in the earlier Inferior Oolite times (Aalenian). In both divisions catagenesis led on to oxycone individuals in abundance. In the harpoceratan section the umbilical portion of the whorl surface was flat, and the angle it made with the lateral area increased until it was a right angle. This feature gave to the umbilicus the appearance of being surrounded by a series of steps. In the lioceran type this umbilical area became concave. With increasing involution the margins of successive whorls came closer and closer together until eventually they merged into a single curved surface, and formed a basin-like umbilicus. Maximum elevation and compression with multiplication of sutural elements is seen in *Hyperlioceras.* Among the lioceran types the tendency, on the whole, was towards a loss of ornamentation, but the angulate venter was retained by all. In the differentiation of one lineage from another, changes in the form of the ribs have played an important part.

Among the other ammonites which lived during the Hildoceratan Epoch reference may be made to the presence of *Dactylioceras* and its allies during the earlier part of this time, and to the genus *Dumortieria*, a hildoceran-like member of the family Polymorphitidæ, which, along with *Grammoceras*, characterizes the passage from the Lias to the Inferior Oolite.

The Later Jurassic Ammonites.—With the dying out of the hildoceratan ammonites there came a more important break than usual in the succession of forms. At this time there commenced a great series of invasions of new genera and families which continued throughout the remainder of the Jurassic.

THE SONNINIANS.—Among the first of these new families were the Sonnininæ. The type genus *Sonninia* exhibits a wide range of forms from one in which the whorls were round, coiled slowly, and had a keel, to one in which coiling was rapid and the shell tended to become an oxycone. In the former the ornamentation was well developed, and consisted of spines and ribs ; in the latter the ornamentation tended to disappear. The suture line is deeply divided and complex, and so closely resembles that of *Amaltheus* that near affinity has been claimed between the two families represented by these genera. Both may have arisen from a common ancestral stock, but whilst the Amaltheid branch evolved rapidly, and completed its history before the Hildoceratan Epoch, the Sonniniid branch evolved more slowly in some other region, and reappeared in this area after that epoch.

THE STEPHEOCERATIDS.—These include a large and important super-family of ammonites apparently of lytoceratan origin of which separate but successively broader streams entered the British area.

The first arrival towards the end of Lower Liassic times was the solitary genus *Prodactylioceras*, which closely resembles the later

Dactylioceras, but differs in having more slender whorls ornamented at intervals by tubercles.

The second stream appeared in Upper Liassic times and formed an abundant element in the fauna. This was so varied that one worker has divided it up into nearly thirty genera. These include *Dactylioceras* (Fig. 142) and a number of other typical serpenticones having a broad, shallow umbilicus and on that account alternatively described as planulate. Among the remainder is *Cœloceras* (Fig. 161A) which had a slowly coiling shell, in which the whorl was depressed with its ventral and dorsal areas almost flat and its sides divergent, so that the venter was broader than the dorsum. This shape gave to the umbilicus a crater-like appearance. A shell exhibiting these whorl characters is called a cadicone. The sides of the whorls were ornamented with stout ribs, the branches of which usually crossed the venter. At the point of branching tubercles were present. When the shell lies upon its side, these give to it the appearance of a crown, hence it is described as coronate. Between these two extremes lie every gradation from those which are true cadicone for the greater part of life and begin to be serpenticones in late life, to those which are cadicone for only a brief time and are serpenticone for the greater part of life. The time sequence for the appearance of this difference is still uncertain, but the indications are that the serpenticone condition preceded the cadicone, which seems therefore to have entered the evolving stock proterogenetically. In this connection it may be noted that *Prodactylioceras* is a typical serpenticone.

The third cluster of streams began to arrive during the middle of the Inferior Oolite or Bajocian times, bringing with it a similar mingling variety of form among which the following morphological genera may be taken as samples.

Stepheoceras (Fig. 161E)—a serpenticone ornamented with lateral ribs which branch towards the periphery, producing finer and more numerous ribs across the venter. Tubercles occur at the point of branching. *Teloceras* (B)—a cadicone similarly ornamented. *Sphæroceras* (H) differs from a cadicone in having a much wider whorl with its lateral margins bent over to such an extent as almost to hide the inner whorls completely from view. The sides of the whorl are not flattened but inflated and the umbilicus is deep and very narrow. The shell thus constructed is almost globose.

These three forms are linked together in a compact assemblage which includes numerous intermediate gradations.

During Upper Inferior Oolite and Great Oolite times the stepheoceratids were represented in Britain by only a few forms. *Morphoceras* (*J*) is like *Sphæroceras* in youth, but in later life its whorls swell dorsoventrally and the shell becomes planulate. *Parkinsonia* (F_2) on the other hand resembles *Stepheoceras* in youth but its whorls later become elevated and slightly compressed. Tubercles are absent and a smooth zone appears along the mid-ventral line.

During the Callovian a fourth set of forms came streaming in. These included types like *Macrocephalites* which still had much in common with the earlier sphærocones. The almost contemporaneous *Kepplerites* shows a tendency in youth for the whorl to become compressed and for the venter to flatten, but in later life it reverts to the condition seen in *Macrocephalites*. The condition seen in youth in this genus extends in such later genera as *Cosmoceras* (Oxf. Clay) to the adult in which the laterally compressed whorl with flattened venter is ornamented with branching ribs and two rows of tubercles.

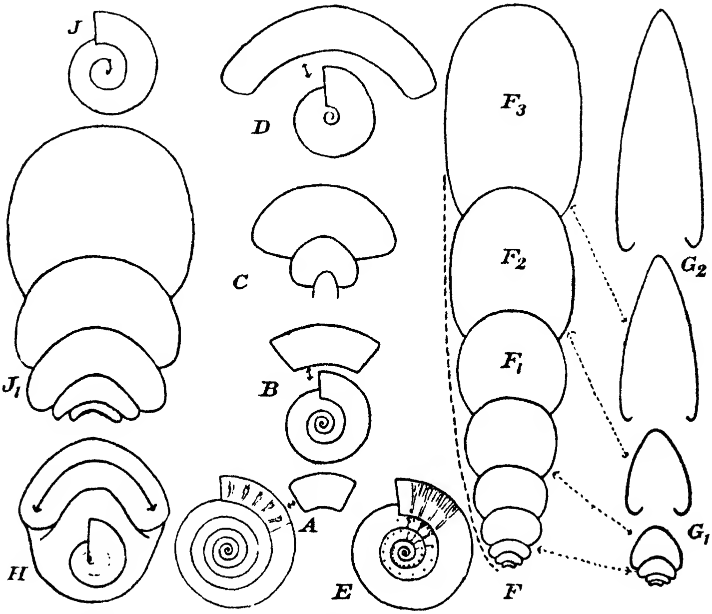


FIG. 161.—Diagrams illustrating the chief Modifications of Whorl Form, and degrees of Involution in Upper Jurassic Ammonites.

A–D, side view and whorl section in various cadicone ammonites. *A*, *Cœloceras*. *B*, *Teloceras*. *C*, *Cadoceras*. Section showing whorl shape in youth. *D*, *Cadoceras*. *E*, side view of *Stepheoceras*. *F*, hypothetical diagram showing whorl form attained by *Stepheoceras* (up to F_1) by Perisphinctoids (F_2) and Parkinsonians (F_3). Broken line shows the flattening out of umbilicus with elevation of whorl. *G*, whorl forms produced by the oncoming of oxyconic tendencies at the different stages represented by F. *G_1*, *Quenstedoceras*. *G_2*, *Cardioceras*. *H*, *Sphæroceras*, side and apertural views. *J*, *Morphoceras*, side view showing rapid change from sphæroceras-like centre to stepheoceras-like outer whorls. *J_1*, section through *Morphoceras*.

The contemporaneous genus *Cadoceras* has an angulate venter in youth but in later life reverts to the sphærocone. In the later genera *Quenstedoceras* (Oxf.) and *Cardioceras* (Cor.) that condition seen in youth extends to the adult stage. In both these genera the ribs extend across the venter and give to the keel a corded appearance. The latter genus is also ornamented with tubercles. This series of ammonites ranged upwards into the Lower Kimmeridgian.

Many of these Jurassic stocks produced perisphinctean forms, that is to say serpenticones having no other ornamentation than the ribs, and occasional constrictions. This perisphinctean type of modification was a characteristic feature of the ammonite fauna of the Upper Jurassic period. Though it was the outcome apparently of a slightly retrogressive change, some of the races affected by it were very virile, and gave rise, on the one hand, to the giant forms found in the Portlandian and on the other to forms which functioned as the radicles to new races. Thus *Peltoceras* and *Aspidoceras*, with their quadragonal whorls and advanced ornamentation, were derived from perisphinctiform ancestors.

Cryptogenes.—Brief reference should be made to the cryptogenic families of the later Jurassic whose origin is still unknown. The Oppelidæ and Lissoceratidæ appeared along with the sonninians and ranged throughout the whole of the later Jurassic.

Cretaceous Ammonites.—During the Cretaceous period the long history of the ammonoids, which started in the Devonian, came to a close. In some respects, it ended as it began, with genera ranging in shape from closely coiled to straight. In this case also these shapes were the outcome not of progression, but of retrogression. Nevertheless there were many ammonites during the Cretaceous period which were no more retrogressive than the majority of Jurassic types, and these may be considered briefly first.

The Hoplitidæ had more or less compressed whorls with flattened and often deeply grooved venters. Their ornamentation had a varied range; some shells were almost smooth, others had ribs and even tubercles, exhibiting every grade of strength. The Olcostephanidæ, on the other hand, had stout round whorls with a perisphinctean aspect. These two families were contemporaneous with one another, and were more especially characteristic of the Lower Cretaceous. They appear to have been of Southern and Northern origin respectively, and in their occupation of the British Cretaceous seas, in the Speeton area at least, they alternated the one with the other.

The Acanthoceratidæ came into prominence during the Middle Cretaceous. They were stout serpenticones with round whorls, and in such genera as *Douvilleiceras* they exhibited a high degree of ornamentation, consisting of strong straight ribs and numerous tubercles. The Prionotropidæ, of which *Schlœnbachia* is the most familiar example, were keeled ammonites and characterized the Upper Cretaceous.

Whilst the families just mentioned trespassed to a slight extent beyond the period of which they were characteristic, the Desmoceratidæ are found at all levels in the Cretaceous rocks. They were round ventered, feebly ornamented forms with a highly developed suture line. The precise relationship of these families to one another, and to their Jurassic predecessors, is still a matter for conjecture. Whilst all these were essentially peculiar to the Cretaceous system, this was not the case with the two families Phylloceratidæ and Lytoceratidæ. These, as already noted, originated in the Trias, and continued, with but little change, until the close of the Cretaceous.

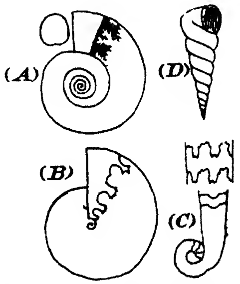


Fig. 162.—Retrogressive Cretaceous Ammonites.

(*A*) *Lytoceras*. (*B*) *Tissotia* (after Bayle). (*C*) *Baculites* (after Smith). (*D*) *Turrilites* (after D'Orbigny).

Just as the great ceratitoid group of ammonoids produced retrogressive as well as stationary and progressive forms during the Trias, so from one, or several, of the families just mentioned, there arose decadent lines of descent. This same tendency was exhibited occasionally during Jurassic times, but during Cretaceous times its influence upon the fauna became conspicuous. As manifested in any one section of the ammonites (Fig. 162) it usually affected only a portion of the organization. Thus, for example, in the series to which *Tissotia* belongs, though the suture line has most of its smaller features so smoothed out that the line closely resembles that of a ceratite, the shell itself remained closely coiled, and the whorls deeply embracing. These so-called *Pseudoceratites* were a feature of the Upper Cretaceous fauna. More frequently, however, it was the form of the shell which was affected. This is not surprising, for throughout the history of the ammonites the form of the shell was their most unstable character. In *Turrilites*, the shell still remained closely coiled, but it assumed the helicoid type of coiling which is normal for the gastropods. In most retrogressive ammonites, however, the shell tended to uncoil, and it began to do so either at the beginning of life or at the end. In the former case an open spiral resulted, *e.g. Crioceras*, *Spiroceras*, *Ancyloceras*. In certain species of *Lytoceras* the latter procedure was manifested in its inception. In these in late life the living chamber separated from the coiled earlier whorls and became straight. In scaphitoid forms the process set in earlier, and the living chamber after growing straight for a while bent back upon itself in the shape of a hook. In *Hamites* both modes of uncoiling were adopted.

This tendency exhibited by some species of *Lytoceras* attained the climax of its expression in *Baculites*. In this genus the straightening out of the living chamber had been so much accelerated that it was already begun in neanic stage, and the nepionic portions of the shell alone were still closely coiled. Whilst the plan of the suture line remained that of the Lytoceratidæ, the crimping was all smoothed out. Thus in *Baculites* the whole organization was affected by decadent influences, and it is therefore the most perfect expression of all-round retrogression among the ammonoids. Whilst some of the scaphitoid and baculitoid forms are undoubtedly offshoots of the lytoceran stock the origin of the remainder requires further investigation.

PELECYPODA

The Development of the Shell.—In early development most pelecypods exhibit a free-swimming larval stage which closely resembles a trochophore larva. Later, by a modification more especially of the swimming apparatus, it assumes a form which is peculiar to the Mollusca. The first rudiment of the shell appears on the mid-dorsal line of the larva, and corresponds in its position to the hinge portion of the fully formed shell. This rudiment extends on either side of the middle line (Fig. 163), and thus produces the two-valved condition which has given rise to the name dissoconch for the pelecypod shell. At first the hinge line is straight; the valves are equal, and almost, if not quite, symmetrical. Further growth takes place most rapidly along the ventral margin, with the result that the lines of growth are concentric about a point (the umbo) near the dorsal margin. At the same time the hinge line becomes arched. This embryonic shell is called the prodissoconch.

Eventually, the swimming apparatus disappears, and the organism adopts a benthic mode of life. This change is accompanied by an extension of the shell-secreting areas, which thus form two folds (mantle lobes) which hang down freely on either side of the body. The edges of these folds continue to secrete a horny or conchiolin film (periostracum) which forms the external covering of the valves. On the inner surface of this film the mantle deposits lime in a matrix of conchiolin. At first this takes the form of prisms, but later it is laid down in lamellæ lying parallel to the surface. When the inner layer is compact it has a pearly or nacreous lustre, but when it is loosely constituted it has a shiny white or porcellanous lustre.

Along the mid-dorsal line the deposition of lime does not take place or is reduced to a minimum, the conchiolin therefore retains its elastic character, and functions as a hinge (ligament) between the valves (Fig. 168). The springy character of this tends to make the valves gape. This tendency is counteracted by the action of two muscles (anterior and posterior adductors) which traverse the body from side to side, and are united at their ends to the inner surfaces of the shell. When these muscles contract the shell is closed and the animal is completely shut off from the outer world. Clearly marked impressions are made by the muscles on the inside of the shell (Fig. 163B); the straight line which connects them may accordingly be called the muscle axis. A very narrow impression (pallial or mantle line) marks the attachment of the mantle to the shell. This runs parallel to the shell margin and ends close to the muscle impressions. The dorsal margin of each valve is usually thickened and bears teeth and sockets (dental apparatus) which fit the corresponding features of the opposite valve. This dental apparatus is closely associated with the ligament and muscles and guides the valves in their closing movements so that their edges come to fit accurately against one another. The hinge axis lies parallel to the ligament and to the teeth series.

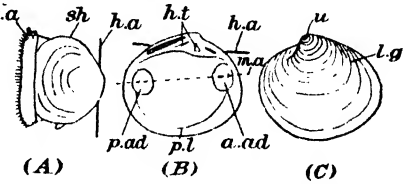


FIG. 163.—Development and Structure of the Pelecypod Shell.

(*A*) Free-swimming larva (after Meisenheimer). (*B*) Inner view of left valve. (*C*) Outer view of left valve.

a.ad, anterior adductor impression. *h.a*, hinge axis. *h.t*, hinge teeth. *l.g*, lines of growth. *m.a*, muscle axis. *p.ad*, posterior adductor impression. *p.l*, pallial line. *s.a*, swimming apparatus. *sh*, shell. *u*, umbo.

The shell of a pelecypod is not a skeleton, but a place of refuge. Unlike the test of an Echinoderm, or of an Arthropod, it is not closely associated in detailed structure with the vital organs; it is therefore much simpler, consists of fewer structural elements, and is very sensitive to adaptive influences. For these reasons the data for the study of evolutionary and phylogenetic problems among pelecypods are limited, and the solution of the problems is always accompanied with much uncertainty.

Modifications of Shell Form.—As already seen, the valves in the early development of the shell are equal in size (equivalve) and each is symmetrical (equilateral) or nearly symmetrical about its own middle line. This is likewise the approximate form of the adult shell in those pelecypods (*Nucula*, *Arca*, etc.) which creep about the sea-floor upon a foot having a flattened under-surface like that of a snail (Fig. 164). In such forms the median plane of the body is vertical; whilst the hinge and muscle axes are parallel to one another and to the substratum.

Among pelecypods more than in other molluscs there is a frequent tendency to forsake this free active mode of life, and to adopt a sedentary habit. This is manifested in one of three different ways, by burrowing into the sea floor, by secreting an anchor of horny fibres (byssus), or by cementing one of the valves to the rocks or other shells early in life. The passage from the free to any one of these sedentary conditions is accompanied by certain general adaptive modifications of shell form which may be repeated with remarkable fidelity in lineages not even closely allied to one another.

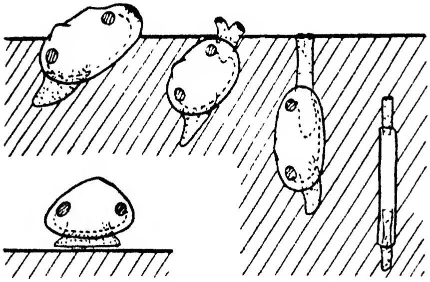


FIG. 164.—Diagrams illustrating the forms of Shell associated with the Crawling and Burrowing Habits.

Round lined areas show the positions of the muscle impressions. Broken line = pallial line. Dotted areas = foot and siphon respectively.

MODIFICATIONS ASSOCIATED WITH THE BURROWING (CAVICOLE) HABIT.—In the first step leading towards a burrowing habit (Fig. 164) the foot loses its flattened under-surface and becomes a tongue-shaped organ. This together with the antero-ventral portion of the shell and body is buried in the sand or mud. The organism still retains a large degree of freedom, and by means of its powerful protrusible foot, drags its shell from place to place through the soft deposits on the sea-floor. When stationary it rests with its posterior end protruding into the water and its valves gaping sufficiently for two openings to appear between the corresponding edges of the mantle lobes. Through the lower (inhalent opening) water streams inwards, carrying oxygen to the gills, and food to the mouth. Through the upper (exhalent) opening the exhausted water is poured forth. In many pelecypods the mantle margin which adjoins these openings is drawn out into a pair of tubes (siphons). When the valves are closed the siphons are withdrawn by means of mantle muscles which are attached along the mantle line. As the siphons enlarge these muscles become more powerful, and their attachment forms a deviation (sinus) in this line.

Where the food supply is ample the creature tends to remain in one spot and to bury itself more completely in the ground with its axis almost, if not quite, vertical. The valves now stay in contact with one another ventrally, but they begin to gape anteriorly and posteriorly where the siphon and foot are protruded. The presence of these open spaces is unaccompanied by risk to the organism for the burrow now usurps much of the protective function of the shell.

Along with these changes the shell becomes elongated antero-posteriorly (*Lutraria*, *Ensis*) and thus assumes the form which offers the least resistance to movement through a medium less fluid than water. As long as the organism burrows into soft substrata like sand and mud, through which it still drags itself by means of its foot its shell remains compressed. Those, however, which burrow into stiff clay, shale, or other rock, grind their way in by slow rolling movements of the shell, which can be accomplished only by a shell that has become more or less cylindrical (*Lithodomus*, *Pholas*).

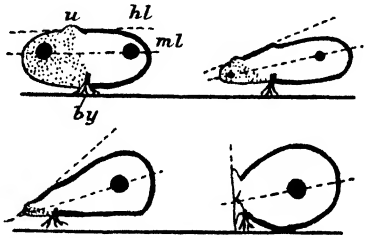


FIG. 165.—Diagrams illustrating the change in form of the Shell associated with the Byssal Mode of Attachment.

Round black areas = muscle impressions. Thick outline = posterior portion of shell. Thin outlined dotted area = anterior portion of shell.

MODIFICATIONS ASSOCIATED WITH A BYSSAL ATTACHMENT.—The byssus consists of material secreted by a gland situated on the underside of the foot. Immediately on exposure to the water this material hardens and forms root-like branching threads which are attached to the rock surface. Shells anchored thus are usually situated where currents of varying strength flow past them, and cause them, so to speak, to drag at this anchor. In association with this the byssus, and with it the foot and the byssal opening in the shell, tends to shift forwards (Fig. 165). This tendency leaves the hinder portion of the body with the highly important inhalent and exhalent openings free to function and to develop. On the other hand the organs in front of the byssus undergo reduction. The foot, which is functionally replaced by the byssus as the organ of attachment, and the anterior adductor muscle both diminish, and eventually may disappear. In correspondence with these changes the hinder portion of the shell becomes more extensive, the adductor impression enlarges and is carried further from the hinge axis. In front of the byssal opening the shell becomes greatly reduced and consequently the umbo appears to approach the anterior end. Meanwhile the anterior adductor impression decreases in size and approaches the hinge. Thus the muscle axis moves from a position in which it is parallel with the hinge axis, to one in which it lies at right angles to it. When the latter position has been attained the anterior muscle disappears, and the shell has then only one muscle impression. In this condition the shell often assumes an almost equilateral symmetry (*Modiola*, *Mytilus*, *Avicula*).

MODIFICATIONS ASSOCIATED WITH A CEMENTED ATTACHMENT.—The cementation of the shell to the rock surface usually takes place early in life, and is accomplished by means of the conchiolin and lime secreted by that portion of the mantle edge which is situated in the vicinity of the foot. This method of attachment has been adopted both by forms already attached by means of a byssus (Ostreidæ) and by others which belonged to a free stock. In both cases the preliminary to cementation was the assumption of the habit of lying upon one valve. In all subsequent modifications the free valve remained the least changed and therefore has proved to be the more useful in tracing the ancestral origin of the forms in question. On the other hand the fixed valve became modified to such an extent that all traces of the primitive condition were lost.

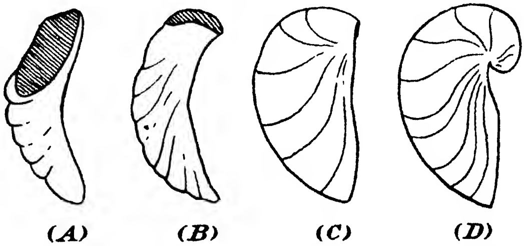


FIG. 166.—Evolution of Left Valve in *Gryphæa*, showing progressive accentuation of Curvature from the opening of the Lower Liassic to close of the time represented by the Bucklandi Zone. (After Trueman.)

One modifying tendency common to all the cemented forms is the excessive deposition of lime leading to an enormous thickening of the fixed valve. In such forms as the Chamidæ and the Rudistes, which were derived from free ancestors, the ligament was short; the addition of calcareous material took place nearly uniformly over the whole margin of the shell, and thus the fixed valve came to resemble a solitary coral in general appearance. In those, on the other hand, which arose from ancestors already fixed by means of a byssus, the excessive growth of the shell was largely confined to the ventral margin and resulted in the production of a shell which tended to become spiral in one plane or another. This coiling of the shell is well seen in the genus *Gryphæa* (Fig. 166), which descended from *Ostrea* (Oyster). *Ostrea* exhibits a very wide range of variation in shape of outline, degree of convexity, size of the area of attachment and in a number of other features. This range is maintained with great constancy throughout its history from the opening of the Lias until the present. It has, however, shown repeatedly a marked tendency to produce stocks which developed gryphæoid coiling. One of these arose in the Planorbis zone and an increasing number of its members became more and more curved, until near the top of the Bucklandi zone this valve had a spiral form with nearly one and a half complete turns.

At any one particular level the degree of coiling exhibited varied in the different individuals. Thus, for example, about one half of them exhibited approximately the same degree of coiling, whilst the remainder were coiled to either a lesser or a greater extent than this. At successive horizons (Fig. 167) the degree of coiling exhibited by the greatest number steadily increased, so that in the uppermost portions of the Bucklandi zone in some individuals the umbo of the left valve rolled over towards the outer surface of the right valve. Nevertheless, even in the most advanced assemblages the juvenile stages of growth of its various members showed variations in outline, convexity, area of attachment and other features closely resembling those seen in the adults of the ancestral ostræoid stock found in the Planorbis zone. This fact illustrates the principle of palingenesis as manifested by the recapitulation even of the multitudinous variations exhibited by the ancestral stock. The reproduction of these variations in successive populations testifies to the biological unity of the plexus of descent to which they belong.

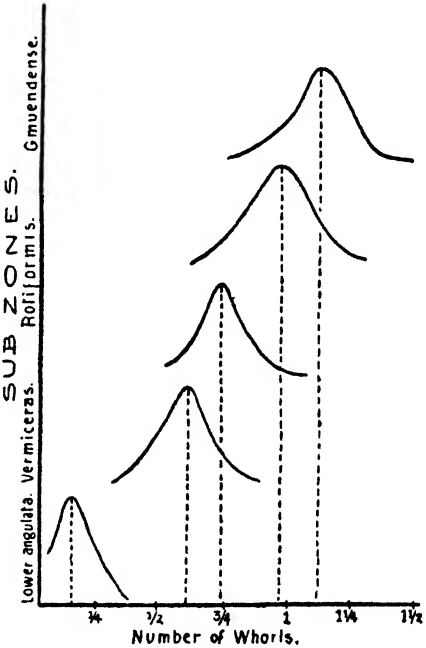


FIG. 167.—Frequency curves of variation in degree of coiling of the Left Valve in *Gryphæas* at successive levels in the Lower Lias (after Trueman).

A line joining the crests of these curves would represent a "line of descent" or a "lineage." The belt enclosed by lines joining the extremities of the curves represents the "plexus of descent."

Gryphæoid shells occur at various other levels throughout the Jurassic and Cretaceous rocks. These later forms probably arose independently from *Ostrea.* Because they inherited the same potentialities from that stock they followed the same lines of unfolding as did the Lower Liassic *Gryphæas*. *Exogyra* (U. Jur.–Cret.) likewise evolved from *Ostrea* and resembles *Gryphæa* in some characters. The disappearance of gryphæoid forms at the close of the Cretaceous suggests that these potentialities had by that time become eliminated from the Ostræa radical stock.

Changes in and about the Hinge Margin.—In the shell of a pelecypod the two valves are opened and closed with great frequency. Inasmuch as these movements are not affected to any great extent by the different modes of life described in the previous chapter, the dental apparatus does not respond appreciably to changes in habit or habitat except that in cavicole forms the need for opening and closing no longer exists and the dental apparatus accordingly tends to degenerate. Nevertheless this apparatus does experience a series of changes which may be traced in broad outlines down through geological time. On the whole these changes result in greater efficiency. The ligament also undergoes certain changes. These, however, are of a simple character and are repeated frequently on different lines of descent.

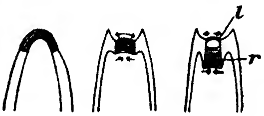
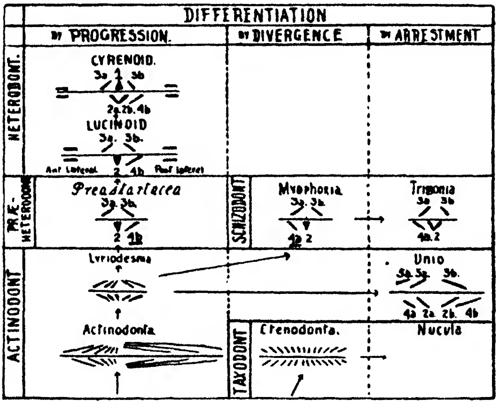


FIG. 168.—Diagrams illustrating relation of Ligament to Valves, and the chief modifications it undergoes.
l, ligament. *r*, resilium.

CHANGES IN THE LIGAMENT.—In its most primitive condition the ligament was like a long spring of semi-cylindrical form which extended in front of as well as behind the umbo (amphidetic condition). Its substance was continuous with the conchiolin matrix of the valves. Along with the general tendency for the anterior half of the shell to become reduced relatively to the posterior, the front portion of the ligament also underwent reduction until only that which lay behind the umbo remained (opisthodetic). With the thickening of the hinge margin of the shell, the ligament thickened also. When this took place the closure of the shell resulted in a stretching of the outer, and a compressing of the inner, portions of the elastic ligament (Fig. 168). This was followed by a tendency for the inner or more resilient portion (resilium) to separate from the outer. The latter remained long, and often became little more than a connecting apparatus between the two valves. The former shortened into a triangular cushion, the efficiency of which was further increased by the development of a spoon-shaped ingrowth of the shell margin upon which the cushion rested.

CHANGES IN THE DENTAL APPARATUS OF A NORMAL PELECYPOD (Table VIII).—Even as early as the Silurian a dental apparatus had been acquired by many known forms, and was then characterized by the great number of small teeth and sockets. These can be regarded as little more than slightly modified irregularities of the shell margin. In their arrangement they conformed to one or other of two patterns. In one (Ctenodont type) the teeth were arranged in a direction radiating from the centre of the valve (*Ctenodonta*, Ord.–Sil.; *Nucula*, Sil.–Rec.). In the other (Actinodont type), they radiated from the umbo (*e.g. Actinodonta*, *Lyrodesma*). The Ctenodont arrangement does not appear to have provided a suitable basis from which to produce other patterns, though it was evidently efficient enough to meet the requirements of those forms in which it occurred; for some of them are still in existence, *e.g. Nucula.* On the other hand the Actinodont type provided a condition from which a long series of modifications could be derived. In this type

Table VIII.—Showing Evolution of Dentition in normal Pelecypoda.



the teeth diverged from the umbo towards the inner border of the valve margin. The centrally situated teeth were therefore short, but the outer ones were elongated and reached the vicinity of the muscles.

In describing the various modifications of this type of apparatus it is customary to use a system of numbering starting with the lowest figure for the centrally placed teeth. The odd numbers are used for the right, and even numbers for the left valve. The letter (*a*) follows the numbers for the anterior teeth and (*b*) those for the posterior teeth. The dentition as a whole can then be represented by a formula such as this:

$$\begin{array}{ll} \text{Right valve} & \underline{5a - 3a - 1 - 3b - 5b} \\ \text{Left valve} & \quad 4a - 2a - 2b - 4b \end{array}$$

in which the sockets are represented by —. Usually this formula is shortened in this manner: $\dfrac{1,\ 3a,b.\quad 5a,b}{2a,b.\quad 4a,b.}$. It will be easier to recognize the changes which take place if, in the following pages, the fuller formula be used.

Generally speaking, the lines of modification pursued involved two processes: namely, a reduction in the number of teeth, and an increase in size and degree of projection of those which were left. Among the more common pelecypods one stage in this modification is exhibited in an arrested condition in such forms as *Carbonicola* (C.M.), *Cardinia* (Lias) and *Unio* (Inf. Ool.-Pres.). In this last there are three teeth in the right valve, and four in the left, and the formula is as follows: $\dfrac{5a - 3a - \quad - 3b}{4a - 2a - 2b - 4b}$.

The next step in the evolution of the dentition resulted in the reduction of the number to two upon each valve. At the same time the teeth shortened along with the ligament and were thus withdrawn from the neighbourhood of the muscles. This reduction in the size and number of the teeth was accompanied by a greater differentiation of the teeth and sockets themselves. This stage was already attained by some shells as early as the Devonian, and it seems to have provided a dental apparatus of great efficiency; for in later times this simple dentition, or one derived from it, was exhibited by an overwhelming majority of pelecypods. The withdrawal of the teeth from the vicinity of the muscles left the corresponding portions of the hinge margin without guiding projections. This defect was remedied in the early Mesozoic by the appearance of new teeth at these points beyond the limits of the ligament. These teeth are called the laterals, to distinguish them from the older ones which underly the ligament and which are called the cardinals. A dentition having these two types of teeth is described as heterodont, and the pelecypods which exhibit it are classed as Heterodontia. The Palæozoic forerunners of these Mesozoic Heterodontia are called the Præheterodontia.

The teeth retained for the right valve, viz. $3a$, $3b$, were the same for all the Præheterodontia and their derivatives. For the left valve the case was different, for though tooth 2 was always present and centrally placed, the other tooth in some forms lay in front of this (Trigonacea), and in the case of others it lay behind (Preastartacea). This difference may be seen on comparing the expanded formulæ for the two types.

Trigonacea $\dfrac{3a - 3b}{4a - 2}$. Preastartacea $\dfrac{3a - 3b}{2 - 4b}$.

There does not appear to be any adaptive reason for such a peculiar but distinctive difference. It marks a clear divergence of the forms from one another in evolution and is therefore a differential character of some importance.

Among the Trigonacea the dentition is shown in its least modified form by *Myophoria* (Trias.). During the Liassic period it became modified by the enlargement and splitting of tooth 2, a condition characteristic of *Trigonia* (Lias.–Pres.). This type of dentition (schizodont), like that of the more ancient and primitive condition which persists in *Unio*, does not appear to have furnished a basis for the derivation of any new types of dentition, but remains in a more or less arrested condition until the present time.

From the preastartacean type of dentition, on the other hand, was derived that of all those numerous families classed as the Heterodontia by the addition at the opening of the Jurassic of the lateral teeth. In the majority of the heterodont families development stopped at this stage (Lucinoid type). In a few families, however, further additions were made. In the right valve the innermost lateral extended to the centre of the hinge margin, and in Liassic times it became enlarged at this point. This enlargement eventually became separated and formed a new cardinal tooth between 3*a* and 3*b*. This is therefore numbered 1, and the type of dentition which exhibits it is described as Cyrenoid.

Forms having this type of dentition developed freely in the Eocene. In both these types, as in the schizodont, there is a tendency for tooth 2 to split and even to divide, thus forming 2*a* and 2*b*.

CHANGES IN THE DENTAL APPARATUS IN OTHER PELECYPODS.—As early as the Ordovician and the Silurian, and before the dentition had begun to manifest those changes which have just been described, some pelecypods had assumed the sedentary mode of existence. These gave rise to lines of descent which have remained until the present time. The byssated members of that early time and their subsequent derivatives are classed as the Dysodontia. At first they had an actinodont dentition and an amphidetic ligament. In one series leading up to the modern *Arca*, this actinodont dentition became secondarily modified into one of a taxodont pattern. In other respects, such as shell form, they did not depart greatly from the normal. In those leading up to *Mytilus* and its allies, the shell form became modified to a moderate degree and the dentition became much reduced. In *Avicula*-like forms the shell attained the extreme of adaptive modification inasmuch as the anterior portion was reduced almost to vanishing point, whilst the posterior enlarged to form nearly the whole of the shell. The muscle axis lay almost at right angles to the hinge axis and the valves showed an approximation to bilateral symmetry. In *Pecten* these changes reached their acme, but now the creature reassumed a free habit at an early time in life. When at rest it lay upon one valve. Among the Ostreidæ (Oysters), which were derived from a similar stock, the byssal attachment in early development was replaced by cementation. In all these pelecypods, from *Avicula* onwards the dentition degenerated and disappeared. The ligament remained amphidetic but developed a centrally placed resilium

The cavicole representatives (Desmodontia) among the Protozoic pelecypods appear also to have given rise to series of families which are still found in existing seas (*e.g. Mya, Solen*), leading the same mode of life. Such dental apparatus as the earliest of these possessed consisted of little more than a tooth and a notch on each valve. In many later members of the group even this disappeared.

GASTROPODA

Structural Peculiarities.—In those gastropods which retain the primitive mode of development through a free-swimming larval stage, the larva resembles that already described for the Pelecypoda, in that it is a modified trochophore with a special swimming apparatus and shell gland (Fig. 169). The cap-shaped rudimentary shell in this case, however, grows by addition to the whole of its free margin. This growth takes place most rapidly on the ventral edge, and consequently the shell becomes coiled. At first the coiling is in one plane as in most cephalopods. This stage, however, is very transitory, and is rapidly succeeded by one in which the coiling is no longer in one plane but is around a cone, like that of a corkscrew. This method of coiling is described as helicoid, and is essentially characteristic of the Gastropoda as a class.

In its development, therefore, the embryonic shell or protoconch passes through three stages, the first is characterized by a simple cap-shaped form, the second by a plano-spiral mode of coiling, and the third by a helicoid type of coiling. Whilst the shell is passing through the two first stages just described, the visceral hump region of the body increases in height so that the alimentary canal becomes bent upon itself as in the Cephalopoda. This again is but a transitory condition, as the hump presently begins to rotate around its main axis. This movement carries the mantle chamber with the gills and the renal and anal apertures, which it contains, from the primary position in which its opening faced posteriorly, round by the right on to the front side of the hump. The opening of the chamber now faces forwards. This torsion of the visceral hump during development reproduces an important change during the evolutionary history of the Gastropoda.

As development proceeds the foot, which at first is small and inconspicuous, enlarges and extends posteriorly to form a flat creeping surface. This no doubt also reflects what must have been a rapid change during evolution; for once the efficiency of such a creeping surface was felt, this would speedily attain its maximum development. It may be that by its backward extension the foot tended to push under the opening of the mantle cavity when this was posteriorly situated, and consequently to interfere with the functional activity of the gills and apertures which the cavity contained. The torsionary shifting of the cavity described above would naturally obviate this disadvantage. In a few gastropods the torsion of the visceral hump has not taken place. Though some of these forms have shells, *e.g. Chiton*, they do not form a conspicuous element in the gastropod faunas of the past.

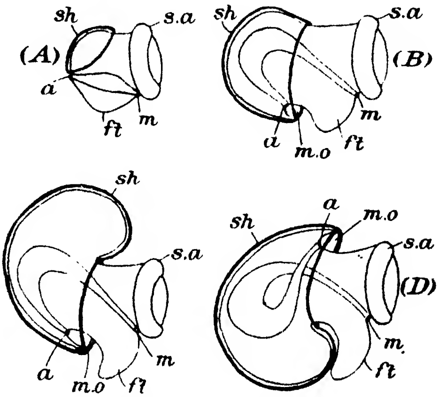


FIG. 169.—Early development of the Gastropod and its Shell (after Robert and Pelseneer).

(*A*) First appearance of the shell on the free-swimming larva. (*B*) Slightly later stage with shell still cap-shaped. (*C*) Shell beginning to coil in a plane spiral, free margin and ventrally placed. (*D*) Stage after visceral hump has undergone torsion.

a, anus. *ft*, foot. *m*, mouth. *m.o*, opening of mantle cavity. *s.a*, swimming apparatus. *sh*, shell.

In all other gastropods this torsion has taken place, and the modifications of their anatomy (Fig. 170A–C) which has resulted therefrom, have provided one of the most satisfactory bases for the classification of the class which have hitherto been found. Of especial value in this connection are the changes in form assumed by that loop of the nervous system which serves the visceral hump. This loop, which originally must have lain in one plane, had its distal portion rotated through 180° at the time when the hump underwent torsion. The outcome of this was that in plan the loop came to have the form of a figure 8. This is the condition which is found in the majority of gastropods, which are accordingly classed as the Streptoneura. In a few, grouped as the Euthyneura, a secondary untwisting has taken place which has resulted in the assumption of a primitive appearance.

In the lowliest Streptoneura, viz. the Aspidobranchia, the organs associated with the mantle cavity have, to a large extent, retained the condition found in Mollusca in which the hump has not been twisted; that is to say, the gills, the kidneys, the auricles of the heart are all paired (Fig. 170C, D). Thus apart from the torsion of the hump these forms approximate closely to the condition which must have existed in the ancestral stock of all the molluscs. After the establishment of the mantle cavity in its anterior position a gradual suppression of the right-hand member (Fig. 170E) of each pair of the above-mentioned organs took place. This course of specialization reached its full expression in the Ctenobranchia.

The naturalness of the subdivision of the Streptoneura into these two important divisions is confirmed by the study of the changes experienced by other organs, and more especially by the radula. This is a rasping organ situated just inside the mouth, and consisting of innumerable rows of minute horny tooth-like structures. In the more primitive gastropods each row contains a multitude of these "teeth," of which the central ones are the largest and most varied in form. With advancing specialization of the organism as a whole there is a tendency for the lateral teeth to become suppressed and for those near the centre to become more modified.

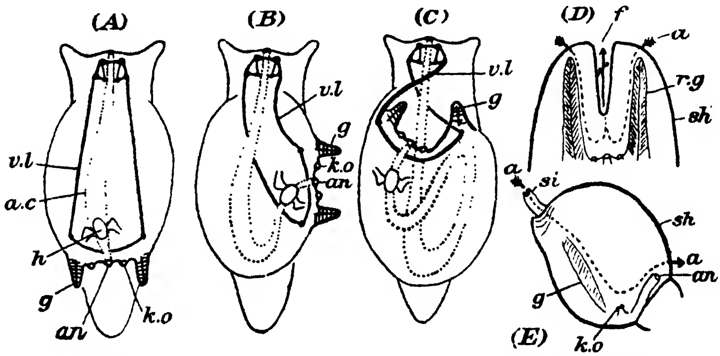


FIG. 170.—Diagrams illustrating some of the main anatomical Changes during the evolution of the Gastropods.

(*A*) Before torsion. (*B*) Torsion incomplete. (*C*) Torsion complete. (*D*, *E*) Relation of mantle complex to shell, *D* before suppression, *E* after suppression of the right gill.

a, arrow showing direction of flow of water. *an*, anus. *a.c*, alimentary canal. *f*, fissure in shell margin. *g*, gill. *h*, heart. *k.o*, kidney aperture. *r.g*, right gill. *sh*, shell. *si*, siphon. *v.l*, visceral loop.

The only portion of the gastropod organization known in the fossil state is the shell. This is moulded round the visceral hump, which, as it increased in height, coiled upon itself in a helicoid spiral. Unfortunately, the great anatomical changes described above are reflected by the shell to only a slight extent. Nevertheless, the number of characters which make up the shell is sufficiently great to provide distinctive features for a great multitude of genera and species. The palæontologist may hope, therefore, by tracing out the evolution of these step by step to discover sequences of change running parallel with those found by the zoologist in the more perishable organs.

The Gastropod Shell.

The Coiling of the Shell.—In all those gastropods in which the development of the shell has been studied the protoconch when fully formed is coiled in a helicoid spire. This, together with the fact that many of the earliest known shells (*e.g. Raphistoma*, L. Camb.) are similarly coiled, shows that this condition must have been established very early in the history of the class, and certainly before Cambrian times. There are, it is true, some nearly conical cap-shaped shells (*e.g. Scenella* and *Stenotheca*) from the Lower Cambrian. These are usually classed with the limpets (*Patella*, Sil.–Rec.) which are of like shape but have a helicoid protoconch (Fig. 173D). If this reference is incorrect then it is not unlikely that these forms are to be regarded as survivals of that still more primitive stage in evolution represented by the first stage (Fig. 169A) in the development of the protoconch.

In a few cases (*e.g. Bellerophon*, Camb.–Ord.) the shell is coiled in one plane as in the second protoconch stage, and it was probably carried, as in the Cephalopoda, with the median plane vertical. Unlike the members of that class these planospiral gastropods carried the shell with its free mouth margin placed dorso-anteriorly as in certain free-swimming forms (*e.g. Atlanta*) found in existing seas. It may be that they also were pelagic in habit. Whether the planospiral stage in the development of the protoconch represents a pelagic phase in the evolution of the gastropods is at present a matter for conjecture. As in the cephalopods, the planospiral gastropod shells which are known exhibit various degrees of coiling from one in which the outer whorls are only just in contact (*Bucania*, Ord.-Sil.) to one in which the outer completely envelope all the inner whorls (*Bellerophon*). The assumption of a helicoid type of coiling in the main gastropod stock was probably associated with a bottom crawling as opposed to a free-swimming habit. On the whole it opens out much greater possibilities in the way of variation of form than does the planospiral type.

In some gastropods (*Euomphalus*, Sil.-Trias.) the departure from the planospiral condition is only slight, and consequently the umbilicus is only a little deeper on the under than on the upper side. With more marked departure the spire begins to rise in the form of a cone above, whilst the umbilicus deepens and narrows on the under side (*Solarium*, Jur.–Rec.). Further departure is accompanied by an increasing height of the cone above (*Buccinum*, Tert.–Rec.) and narrowing of the base and umbilicus below, until ultimately the latter closes. When this stage is attained a section of the shell shows that its axis is occupied by a solid column (columella) formed by the close contact of the whorls with one another. This series of changes from a planospiral to a closed helicoid spiral is one which is repeated with great frequency within the class. It may even be exhibited almost completely within the limits of one species, viz. *Planorbis multiformis* (Mio.). The variations of this species (Fig. 171A–C) found in one piece of rock range from forms coiled as in *Euomphalus* to others which are coiled almost as closely as in *Buccinum*. A similar range may be exhibited during the development of one individual (Fig. 171D). Evidently, therefore, this series of changes does not provide characters of great systematic importance.

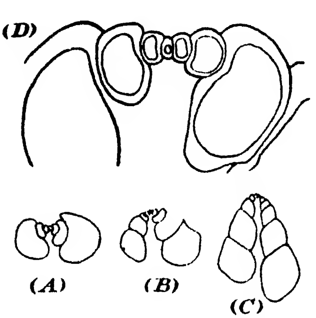


Fig. 171.—*Planorbis multiformis.*

(*A–C*) Sections showing range from planospiral to turreted form in different individuals. (*D*) Section showing similar change in form during the lifetime of one individual (after Hickling).

As among ammonoids, retrogressive uncoiling may begin in the old age of an individual or in the later history of a lineage. Here also it is expressed either by the loosening of all the coils simultaneously or by the non-coiling of the later whorls. This phenomenon affects both low- and high-turreted forms indifferently. Thus *Platyceras* (Sil.-Carb.) is a low-spiral form with its apex closely coiled, but with its outer whorl free from contact with the inner. In some species of *Eccyliomphalus* (Ord.-Sil.) all the whorls are free as in *Ancyloceras*. On the other hand, among high-spired forms, such as *Vermetus* (Tert.), the shell, which in early life is a lofty turreted form, opens out in later life like a corkscrew.

Shape and Calibre of the Whorl.—The form of the shell as a whole is largely affected by the shape of the exposed surface of the whorl. Primitively no doubt the whorl was circular in section and therefore its exposed portion was round (cp. *Straparollina*, Camb. ; *Natica*, Trias.–Pres.). It becomes modified by the appearance of a flattening of its upper zone which results in the production of an angular outline for the whorl and a terraced outline for the shell (cp. *Pleurotomaria*). By the extension of this flattening and a reduction of the rounded portions of the exposed area, these terraces merge into one another and form a continuous slope. A shell having this shape is said to be trochoid because this shape is well exemplified in the genus *Trochus* (Fig. 172B). Here again the whole range from a rounded or naticoid form to the trochoid may be exhibited within the limits of one genus, *e.g.* *Trochus* itself (Fig. 172A, B).

Another factor which exerts a considerable influence upon the shape of the shell is the rate of increase in calibre of the whorls (Fig. 172C–E). This may be gradual (*Euomphalus*) or rapid (*Natica*, Trias.–Pres.). In progressive or anagenetic stocks this increase is regular, but in retrogressive stocks it changes. Sometimes the rate diminishes until the whorl remains uniform in calibre, or even decreases slightly. The shell as a whole then tends to become cylindrical (*Pupa*, Tert.–Rec.). More frequently, however, senescence expresses itself by a rapid increase in calibre so that the outer whorls may become greatly expanded and consequently envelope the inner whorls more or less completely (*Cypræa*, Jur.–Rec.). In a number of quite unrelated lineages there is a combination of this expansion with retrogressive uncoiling. An extreme example of this is provided by *Patella* (Sil.–Rec.). In it the protoconch alone is coiled (Fig. 173D), whilst the remainder of the conch has the form of a low, broad-based cone. This particular form of shell appears to be especially well adapted for those gastropods which live attached to rocks in situations washed by breakers or swept by rapidly flowing currents (*Ancylus*, Tert.–Rec.).

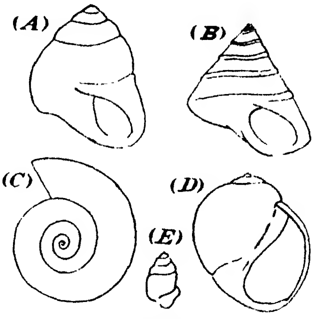


Fig. 172.—Whorl form and Shell shape.

(*A*) *Trochus umbilicatus*. (*B*) *Trochus zizyphinus* (after Randles). (*C*) *Euomphalus*. (*D*) *Natica*. (*E*) *Pupa*.

The Apertural Margin.—The changes described above may for the most part be passed through within the limits of quite small divisions, both of classification and of time. Those which affect the aperture of the shell, however, are of wider extent and longer range.

In its most primitive form the aperture of the shell is round. For the purposes of description its margin is divided into four regions, viz. inner, outer, anterior and posterior respectively. These terms are quite conventional and do not necessarily correspond to the actual position of the parts during life (cp. Fig. 170E). The form of the inner margin is largely determined by the closeness of coiling of the shell, and by the extent of contact with the adjoining whorl. The features of the remainder of the margin are intimately correlated with the functional activities of the mantle cavity. These necessitate an inflow and an outflow of water for bathing the gills and for cleansing the cavity from the refuse which is discharged into it. These movements of the water are either pulsatory or continuous. In the former case the water is taken in and expelled alternately through the general opening of the mantle chamber. There does not appear to be any special modification of the margins of either mantle or shell associated with this type of movement. With the establishment of a more continuous flow of water these margins may exhibit marked modifications.

In many primitive gastropods, which have the gills and excretory apertures paired or even unequally developed, the margin of the mantle and of the shell have a slit or excavation in the region of the median line (Fig. 170D). The water enters by the main opening of the cavity, flushes both the right and the left portions of this, and then flows out through the slit. In such forms as *Bellerophon*, *Pleurotomaria* (Sil.–Rec.), *Emarginula* (Carb.–Rec.), this slit is long, but at its posterior end it becomes closed up as growth proceeds. In *Fissurella* there is a similar slit in youth (Fig. 173A–C), but in later life the shell margin meets across its anterior end and thenceforward the slit is represented by a hole. In the adult this lies near the apex of the shell, and is said to function as an incurrent aperture. In *Haliotis* (Quat.) the slit is closed and opened repeatedly as growth proceeds, so that a series of openings exists for the outgoing current. Such forms, having a marginal slit, provide a much larger proportion of the Palæozoic than of the later faunas.

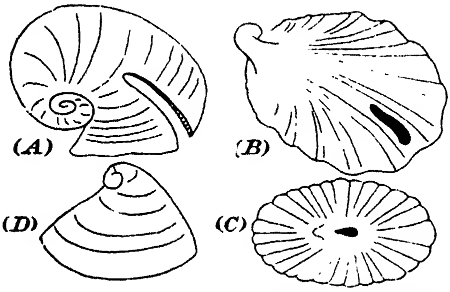


FIG. 173.—Development of Shell in *Fissurella* (*A–C*, after Boutan) and *Patella* (from Pelseneer).

In many of the more specialized gastropods which have lost the gill and excretory aperture of the right-hand side (Fig. 170E), the need for a balanced flushing of the mantle cavity does not exist, and a tendency for water to flow in on the left (anterior) over the gill, then past the renal and anal apertures and out on the right (posterior) side frequently becomes manifested. In association with this the mantle margin on the left grows out into a process with a groove on its under side. The edges of this groove may come together and thus form a tube. This structure, called the siphon, is often of considerable length. Frequently it secretes a corresponding feature on the shell margin, which ranges in degree of development from a mere notch (*Cerithium*, Jur.–Rec.) to an almost closed tube of considerable length (*Murex*, Cret.–Rec.). Among Palæozoic gastropods this type of modification of the shell margin did not exist, but during Jurassic times every degree referred to above became established. Analogous modifications of the right (posterior) margin are of much less frequent occurrence.

Ornamentations of the Shell.—The successive additions of shelly material to the margin of the shell give rise to fine striæ (lines of growth) upon the surface of the shell. These do not, however, constitute an important item in the ornamentation. This is usually made up of tubercles and spines and of ridge-like markings or costæ which may be referred to one or other of two directions. One set (spiral costæ) run parallel to the length of the whorl; the other (axial costæ) cross the whorl transversely, and run more or less parallel to the axis of the shell. These two elements in the ornamentation are independent of one another, consequently in the species of some of the genera, *e.g. Holopea* (Ord.–Sil.), only axial costæ occur, in those of other genera, *e.g. Cyclonema* (Ord.), only spiral costæ are found. In yet other species, *e.g.* of *Procerithium* (Lias.), both may be present but in varying proportions. When both elements are present and equally developed a pitted or cancellated appearance is produced. Tubercles and spines arise usually at the intersection of axial and spiral costæ or along the line of angulation of the whorl.

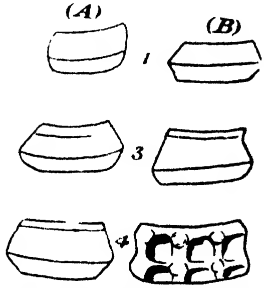


Fig. 174.—Early development of the Shell in two species of *Procerithium* from the Lower Lias. (*A*) From Birchi zone. (*B*) From Jamesoni zone. (From MacDonald and Trueman.)

Figures indicate the whorl-number.

In any given lineage the evolutionary sequence in ornamentation is from smooth to highly ornamented and back again to smooth. Here also the same principles are manifested as have been so frequently noted in other groups of organisms. Thus in any lineal series of forms the development of ornamentation in the later members of the series is accelerated (tachygenesis) so that corresponding stages put in an appearance at earlier and yet earlier whorls. Thus, in *Procerithium* there is one stage characterized by two widely spaced spirals. In certain species (Fig. 174A), from the Birchi zone (L. Lias.), this stage is exhibited as late as the fourth whorl from the apex. In other species (Fig. 174B), from the Jamesoni zone (L. Lias.), it is not seen later than the third whorl. In Tertiary species of *Cerithium* which are descended from *Procerithium* tubercles are frequently present by the time the third whorl develops and the spiralled stage is commonly omitted.

An interesting type of homœomorphy is illustrated by two unrelated species of *Procerithium* from different horizons, viz. the Lower and Middle Lias respectively. In both species (Fig. 175) the ornamentation of the adult whorls is almost identical, and consists of a reticulation formed by the equal development of both the axials and the spirals. When, however, the earlier stages of development are examined it is found that this condition has been reached from two quite different directions. In the young specimens of the Lower Liassic species the spirals are strong and the axials are weak. In those of the Middle Liassic species it is the axials that are strong, and the spirals that are weak. By a progressive strengthening (anagenesis) of the weak element in the former and a weakening (catagenesis) of the stronger element in the latter the reticulate condition of the adult is attained. A continuation of the same trends in development of these two stocks would lead to their complete divergence once more. Such a transitory resemblance between members of two stocks which are evolving along cross-lines is described as " transversal homœomorphy."

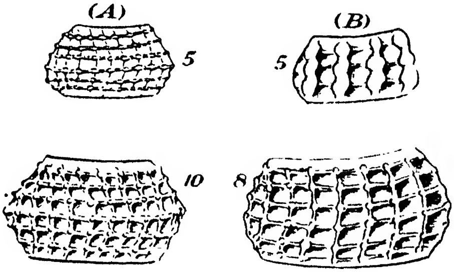


FIG. 175.—Diagram illustrating the Development of two Homœomorphic Gastropods (*Procerithium*) of different descent (from MacDonald and Trueman).

(*A*) From Lower Lias. (*B*) From Middle Lias.

The General History of the Gastropoda.—In their general history the gastropods present one feature which distinguishes them among the Invertebrata. In spite of the fact that they have been producing new families from the opening of the Cambrian down almost to the present period, very few even of the most ancient families have become extinct. Consequently examples of nearly every branch representing all the steps in evolution taken in past ages occur among living forms. Whilst, therefore, the shell does not reflect even the main anatomical changes it is sufficiently distinctive to make it possible to fix the date of appearance of each family, and therefore to determine the time sequence of those changes.

Palæozoic Gastropods.—Taken as a whole the gastropod fauna of the Palæozoic is characterized by shells having little or no ornamentation. *Pleurotomaria* and its allies provide an exception to this.

Before the close of the Palæozoic all the broad anatomical changes associated with the visceral loop and the organs which make up the mantle complex, described above and upon which the broad divisions of classification are based had become established. Nevertheless, those in which the suppression of the organs on the right side had not begun or was still incomplete, viz. aspidobranchs, dominated over all others.

Euthyneurous forms, in spite of their apparent simplicity, do not put in an appearance until the Carboniferous period. Even then they were represented not by typical forms, but by those which like Actæonidæ occupy a transitional position from the Streptoneura, in that the visceral loop is not yet completely untwisted. Thus palæontological evidence confirms the conclusion to which zoologists have gradually come that the Streptoneura are the more primitive, and that the simplicity of the nervous system of the Euthyneura has been secondarily acquired. The complete untwisting of the loop was probably accomplished before the close of the Palæozoic, as *Scaphander* which exhibits this condition occurs in the Trias.

Mesozoic Gastropods.—During this period the aspidobranchs attained their maximum development, and several new families appeared (Haliotidæ, Neritidæ). Towards the close a few families became extinct, *e.g.* Euomphalidæ, Trochonematidæ.

Forms in which the suppression of organs on the right-hand side was almost or quite complete (ctenobranchs), and which occupied a position of minor importance during the Palæozoic, now increased so greatly that during the Cretaceous the number of families had been multiplied five times, and with but few exceptions every family now living was in existence. Among Euthyneurous forms the Philinidæ (Cret.–Pres.) are of especial interest because, upon anatomical grounds it is believed that they provided the ancestral stock for the dominant freshwater (*e.g. Limnæa*) and land (*e.g. Helix*) forms of to-day.

Tertiary and Recent Gastropods.—From the opening of the Tertiary to the present day a few new families have put in an appearance, but apparently none have become extinct. The fact that so very large a proportion of the known families of gastropods still exist indicates that the inevitable period of decline which is usually heralded by the extinction of family after family has not yet set in, and that therefore the Gastropoda are at the acme of their development. As compared with previous periods specialized mouth margins are more frequently seen.

There are not wanting signs that this period of acme has now almost reached its limits, for phylogerontic tendencies are manifested in a number of families. This is suggested by the ornamentation of the shell. On the one hand some families exhibit an over-specialization in this respect in the form of an extraordinary development of spines, *e.g.* Muricidæ. Others have lost all ornamentation, or the last formed whorls have experienced excessive expansion.

SECTION XI

ARTHROPODA

The Arthropoda include such familiar creatures as lobsters and crabs (Crustacea), scorpions and spiders (Arachnida), beetles and butterflies (Insecta), centipedes and millipeds. They also include large and important groups of extinct Palæozoic forms.

With rare exceptions the Arthropoda all have every portion of the body enclosed in a hard covering consisting of chitin, sometimes impregnated with lime. This covering does not grow with the body, but at regular intervals, throughout the life of the individual, it is shed. This process is spoken of as ecdysis, and is followed by a short period of rapid growth of the body before a new covering or exoskeleton is formed. This covering serves all the purposes of a true skeleton in that it provides a foundation for the attachment of muscles, and because it lies externally to these it is called an exoskeleton. It is very intimately related to the soft parts of the organization, which it reflects more completely than do the hard parts of any other group of invertebrates. It may be reasonably expected therefore that fossil remains will eventually shed more light upon the evolutionary problems of this than of any other phylum of the Invertebrata.

In addition to the possession of such a hard covering the Arthropoda are characterized by bilateral symmetry, and metameric segmentation. That is to say the body consists of a lineal series of divisions more or less closely resembling one another. Only one other section of the invertebrates, the Annelida, exhibits this feature in the same degree of perfection. In both annelids and arthropods, at the earliest stage in the development of the individual, the body is unsegmented. In both of them that portion which immediately surrounds the anus remains throughout life the posterior end, and produces new segments from its anterior border until the full number for the adult has been attained. This ability to undergo metameric segmentation is seen to only a slight degree among the molluscs, and not at all among the other great division of the invertebrates. It is therefore regarded as a character of such importance as to justify the opinion that the Annelida and the Arthropoda are more closely allied to one another than to any other division of the animal kingdom. Indeed, in the opinion of a great many experts the Arthropoda have descended from an annelidan ancestral stock.

As the name Arthropoda implies, this division is further characterized by the presence of a pair of true limbs upon many or all of the segments (Fig. 176). The Annelida often have similar extensions of the body-wall, which are likewise used as organs of progression, but are not so highly adapted for this purpose as are the arthropodan limbs. In the majority of arthropods the limbs in the vicinity of the mouth are adapted to function as jaws. This feature has no parallel among the annelids.

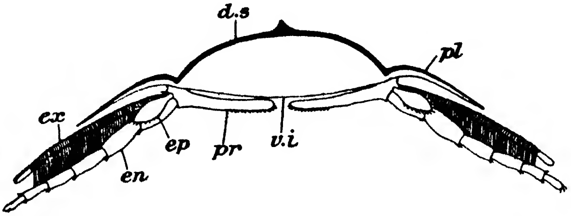


FIG. 176.—Diagrammatic transverse section of the Third Thoracic Segment of *Triarthrus* (after Walcott).

d.s, dorsal shield. *en*, endopodite. *ep*, epipodite. *ex*, exopodite. *pl*, pleuron. *pr*, protopodite. *vi.*, ventral integument.

The Trilobita are at once the simplest, the most fully known, and the most important group of fossil Arthropoda. They therefore provide a suitable starting-point for the study of the phylum.

TRILOBITES

Structure and Habits.—The genus *Triarthrus* may be taken as the type trilobite because very perfectly preserved specimens of the species *T. becki* have been found which show the anatomy of the ventral as well as the dorsal surface. As in arthropods generally the exoskeleton consists of a number of segments (Fig. 177), some fused together, others free. Each segment exhibits a body portion and a pair of limbs. The body portion is divided into middle or axial, and lateral or pleural portions. The dorsal exoskeleton is thick and marked by a pair of grooves which define the axial and pleural regions. These grooves appear as projecting ridges on the internal aspect, where they provide a place of attachment for the muscles which actuate the limbs. The ventral exoskeleton was very delicate and consequently rarely preserved.

The limbs were attached to the ventral surface beneath the axial grooves. The stout basal portion (*protopodite*) bore a long projection on its inner side, and a pair of branches on its distal surface. Of the latter anterior and upper (*exopodite*) consists of numerous joints furnishing support to a series of stiff flattened bristle-like structures, thus providing an efficient swimming apparatus. The posterior and lower branch (*endopodite*) was made up of six stout joints, and must have functioned as a walking leg. Behind the basis of attachment of these branches there may have been a leaf-like organ (*epipodite*) which functioned as a gill. The exopodite may also have served, however, this purpose. At the anterior and posterior ends of the body the segments are fused together to form the head-shield (*cephalon*) and the tail-shield (*pygidium*) respectively. In the intervening region (*thorax*) the segments are all separate or free. All three sections of the body have axial and pleural portions and consequently the body as a whole has a trilobed appearance.

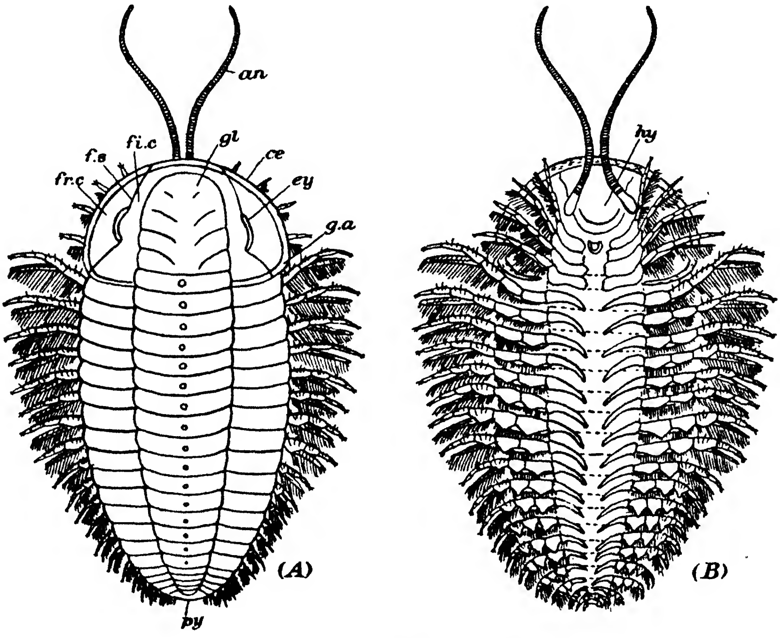


FIG. 177.—*Triarthrus becki.*

(*A*) Dorsal aspect (from Beecher). (*B*) Ventral aspect (after Beecher and Raymond). *an*, antenna. *ce*, cephalon. *ey*, eye. *f.s*, facial suture. *fi.c*, fixed cheek. *fr.c*, free cheek. *g.a*, genal angle. *gl*, glabella. *hy*, hypostome. *py*, pygidium.

On its dorsal aspect the cephalon exhibits indications of its original segmented character only upon the axis which is here described as the glabella. The hinder end of this is marked off in front by a groove, and thus closely resembles a separate segment (neck segment). Portions of similar grooves appear upon the rest of the glabella. The number of divisions thus indicated suggests that at least five segments have been united to form the cephalon. The pleural portions of the cephalon are called the cheeks and the junctions of their posterior and lateral margins are the genal angles. Each cheek is divided by a line of weakness in the chitinous shield into an outer or free cheek and an inner or fixed cheek. This line is the *facial suture*, and is the one along which the carapace splits when ecdysis takes place. In *Triarthrus* the ecdysial splitting line starts near the genal angle and passes obliquely forward across the cheek to the anterior border, along which it passes to join its fellow from the opposite side. This ecdysial line is intimately associated with the eye and is accordingly called the facial suture to distinguish it from similar lines in other arthropods which have no relationship to the eye. The visual area of the eye is borne upon the inner margin of the free cheek, and abuts against a swelling on the outer margin of the fixed cheek. When ecdysis took place the eye was the first portion of the body to be set free, a fact which had obvious advantages to the creature at this critical time of life.

The cephalon of a trilobite differs from the anterior end of an annelid in the fact that it is essentially bent down in hook fashion so that the mouth faces backwards, and the upper lip or hypostome is therefore ventrally situated. The antennæ differ from all the other appendages on the body in consisting of only one branch, and in the fact that they originate in front of the mouth on either side of the hypostome. Each antenna, like an exopodite, is made up of numerous short segments.

Behind the mouth there are four pairs of biramous limbs similar to those already described for a type segment from the thorax. In these, however, the inner process borne by the protopodite is flattened and overlaps its fellows before and behind. These processes function as jaws, and break up the food before it is passed into the mouth. The presence of these five pairs of limbs upon the cephalon confirms the inference based upon the number of glabellar grooves, that this section of the body has been formed by the fusion of at least five segments. How many additional limbless segments may be involved is a subject for speculation and inquiry. In the thoracic region there are fourteen segments. These tend on the whole to decrease in size posteriorly. In the pygidium the segmental origin is clearly indicated by the presence of transverse grooves upon the pleural and axial portions.

Triarthrus, like all other trilobites, occur only in rocks of marine origin. This together with the presence of swimming legs proves it to have been an aquatic animal living in a marine habitat. The position of the eyes well up on the dorsal surface, and the walking character of the endopodites points to a bottom living habit, within depths sufficiently shallow for the floor to be at least dimly illuminated. This, together with the varied character of the rocks in which its remains are found, indicates proximity of its habitat to the coast. It probably spent its life grubbing in the mud and sand in search of worms and other soft-bodied organisms. The structure of the exopodite and the occurrence of flattened joints on some of the endopodites enabled it sometimes to rise and swim with moderate rapidity just above the floor in search of fresh feeding grounds.

The Trend Lines of Structural Change.—Whilst other trilobites resemble *Triarthrus* in the broad features of their structure, they differ from it and from one another in many details. The individual details which characterize any one species or genus are not to be regarded as isolated phenomena, for they are really steps in various series of changes which are passed through in the serial succession of ancestors and descendants to which each trilobite belongs. The known trilobites represent merely fragmentary portions of a great many different lines of descent, all of which possess not only a common basis of structure, but also common tendencies, which to a large extent govern the changes which they may undergo. By a careful comparison of the fragments from different lines, it is possible to piece together a record of the more common changes through which the various parts of the body tend to pass, and to determine the earlier and the later, or the primitive and the specialized, stages. This is the method of comparative anatomy of the adult, as opposed to the method of embryology, which may also be invoked in the working out of the series of changes.

Though the cephalon has been formed by the fusion of segments, there is as yet no evidence to show that it has absorbed any new segments since the opening of the Cambrian period. The number of cephalic segments must have become fixed in pre-Cambrian times. Of all the parts of the cephalon the glabella retains the most easily recognized traces of original segmentation. The number of glabellar grooves is usually not more than four, but occasionally indications of one or two more grooves in front have been discovered. The most primitive condition (Fig. 178) is that in which all the grooves extend unbroken quite across the glabella. The chief tendency which affects these is towards the smoothing out of the grooves. This shows itself first of all anteriorly by the disappearance of the middle portion of the groove or grooves. As a rule the last groove remains unaffected. This stage in which there are three incomplete, or lateral, furrows and a complete neck furrow appears to be a very stable and important one. Eventually the lateral portions follow suit also, and then the most specialized state is attained in which the whole glabella is smooth and without furrows. The general outline of the glabella (Fig. 178*b*) is also subject to a definite series of changes. In the more primitive state it is shaped roughly like an isosceles triangle having its base on the posterior margin of the cephalon and the apex in front. From this there is a progressive increase in calibre anteriorly. At an early stage the glabella thus attains an approximately rectangular shape; later the width increases still further anteriorly.

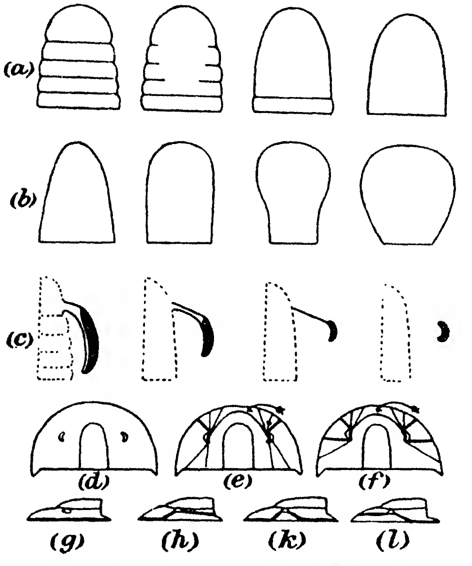


FIG. 178.—Diagrams illustrating the Morphology of the Cephalon.

Serial changes in (*a*) the glabellar furrow, (*b*) shape of glabella, (*c*) the eye lobe and eye. In each series the primitive condition is shown on the left, and the specialized on the right.

(*d*) Protoparian cephalon, ecdysial line is marginal. (*e*) Opisthoparian. (*f*) Proparian cephalon. In *e* and *f* the ecdysial line leaves the margin and passes across the cheek to the inner margin of the eye. The primitive course across the cheek is shown by thick lines. The arrows indicate the direction in which the preocular portion shifts with advancing specialization.

(*g–l*) Side views of the cephalon showing course of ecdysia line and facial suture, (*g*) Protoparian, (*h*) Opisthoparian, (*k*) Proparian, (*l*) Specialized proparian.

The eyes (Fig. 178*c*) in the most primitive condition appear only as modified portions of lobular extensions from the first glabellar segment. These eye lobes curve backwards over the cheek, and bear the visual area on the outer surfaces of their most swollen portions. At this stage the eye is long and crescentic. Advancing change takes the form of a lengthening out of the eye line or connecting ridge between the glabella and that portion of the lobe which bears the visual area. With increased length, the eye-line becomes thin and eventually disappears. The visual area in its turn becomes more concentrated and consequently the eye becomes more compact. The eye may, under special circumstances, undergo yet further reduction and even disappear entirely.

The facial suture (Fig. 178*d–l*), as already seen, was intimately associated with the eye and when, as sometimes happened, the eye declined and disappeared the suture likewise vanished from the dorsal surface. In some primitive trilobites, however, though the eye was well developed no suture was present. This condition, regarded by some as primary, may be described as protoparous. In those trilobites which have a suture the parts which lie behind or in front of the eye are spoken of as post-ocular or pre-ocular portions, respectively. The latter may cut the cephalic margin in front of the genal angle, at this angle, or behind it, and the conditions thus exhibited are described as proparous, gonatoparous or opisthoparous respectively. The development of some trilobites (see Fig. 180) suggests that the opisthoparous stage may be preceded by a proparous in evolution. Others, however, as for example the proparian *Pagetia* (Fig. 187) and the opisthoparian *Paradoxides* (Fig. 184), are so closely associated with protoparian allies in the rock succession as to preclude the existence of intervening stages.

The pre-ocular portion of the suture cuts the anterior margin of the cephalon in both types. The point of intersection, however, tends to shift towards the middle line with advancing change. When it has travelled that far the sutures of the opposite side merge into one another on the dorsal surface of the head-shield and in front of the glabella. With regard to the limbs details are known about only a few types and therefore it is not possible as yet to recognize any clearly defined lines of serial change.

One structural feature which is essentially characteristic of the trilobites as opposed to other arthropods is the presence of pleuræ on all the segments. If it be true, as the main mass of zoological evidence indicates, that all arthropods including the trilobites, were descended from annelid-like ancestors, then there must have been a stage when no pleuræ were present. The first traces of pleural structures to evolve appear to have been spines (pleural spines), such as those seen in the hindmost, and therefore the last-formed segments, of the earliest and most primitive trilobite *Nevadia* (L. Camb.) and of the more familiar *Paradoxides* (M. Camb.) (Fig. 184). Passing forwards from the youngest to the oldest segments of the latter genus, it will be seen that the pleural spines become further and further removed from the axial portion of the segment by the growth of the pleuræ, that is of outgrowths from the side of the segment which are continuous in front and behind with one another. If the principle of " Localized stages in Development " has any significance these facts reflect the course followed in the evolution of pleuræ. This gradual advance in the degree of development of the pleuræ as the anterior end is approached imparts to the body as a whole a triangular form. A general change in form from this to oval (Figs. 182–185), or elongate oval, is brought about in other trilobites by an increase in the number of segments in which the pleuræ attain full development and a limitation in the number of those in which it is arrested. On the whole also the increase in the size of the pleuræ is accompanied by a decrease in that of the spines.

The last series of changes that will be noted may be spoken of under the term caudalization. In the most primitive trilobites (Fig. 182) there is no pygidium. The segments of the body remain free as far as the last or anal segment on the underside of which the anus is situated. This anal segment is called the telson ; trilobites exhibiting this condition are described as apygous. In these respects they approach very closely to the state which is normal among annelid worms. In trilobites, as in other segmented animals, new segments are formed from tissue produced at the anterior margin of the telson. When these segments become completely separated off as quickly as the corresponding mass of tissue is formed, an apygous condition is maintained. But when the rate of complete separation is not as rapid as the formation of the rudimentary segments, then " fusion " of segments appears to take place and a pygidium results. In highly specialized trilobites the process of separation is arrested at an early stage, but inasmuch as the formation of rudiments continues, a large pygidium is formed. According to its size the pygidium is described as micropygous, when very small (Fig. 184) ; heteropygous, when not equal to the size of the cephalon (Fig. 186) ; isopygous when equal to or larger than the cephalon (Fig. 191B).

Looking at the trilobite body as a whole it may be seen to be affected by one or other of two tendencies even in closely related genera and families. On the one hand there may be a marked development of spines (cp. Figs. 181C, 195) and on the other a suppression of those which are normally present with the consequent rounding off of all angles (cp. Fig. 198).

The Development of Trilobites.—The egg of the trilobite evidently hatched out at an early stage in the development, for the youngest-known larvæ differ greatly from the adult. In *Elliptocephala* (Camb.) the earliest larvæ, the protaspis (Fig. 179), was almost circular in outline and had no free segments. The axis, which was already clearly defined, extended close to the anterior margin, where it was produced laterally into a pair of ridges. Posteriorly it was divided by transverse grooves. The fixed cheek region of this protaspis is divided into pleuræ by grooves and provides additional proof that the cephalon had a segmental origin. The presence of these pleuræ indicates that this early larva of *Elliptocephala* is a more primitive one than the corresponding larvæ of other trilobites; it is therefore a more reliable guide in the discussion of phylogenetic and classificatory problems. It is significant that in this case the eyes are placed not at the margin, but upon the upper surface of the cephalon, a position usually associated with a benthic habit.

These facts suggest that the appearance of the eye at the margin of the head-shield in the development of other trilobites is not a feature of phylogenetic significance, but that on the contrary it is more probably a larval adaptation to a planktonic mode of life. Later development proves that this larva, like the crustacean nauplius (Fig. 199), consisted mainly of the cephalon and telson.

The next stage, the meraspis, is characterized by a series of changes leading up to the establishment of the adult condition. The most striking of these is the formation of a number of free segments produced from the front margin of the telson thus bringing the thoracic and pygidial regions into being. In the cephalon the glabella withdraws from the anterior border. Eventually, the central portions of the glabellar grooves are smoothed out and visual areas or eyes develop on the outer surfaces of the ridges.

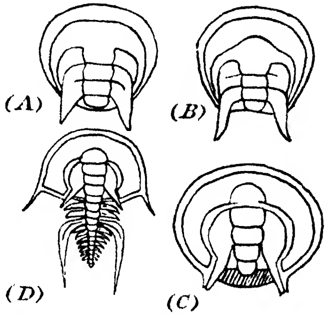


FIG. 179. — Development of *Elliptocephala* (after Walcott).

(*A*) Youngest or protaspis stage. (*B*) Slightly older stage. (*C*) Protaspis with indication of telson (shaded) and of genal and intergenal spines. Stage with two free thoracic segments. (*D*) Meraspis stage with spines separated and seven free thoracic segments.

The development of *Peltura* (U. Cam.) may be used to illustrate the growth features of trilobites which, unlike the one just described, possess a facial suture. Here once more the larva in the protaspis stage has a simple, almost oval outline broken, posteriorly, by a pair of spines. The absence at this stage of a facial suture suggests comparison with the protoparous condition. The axial portion is divided by furrows into six portions. With the entry into the meraspis stage eyes appear connected by straight ridge-like eye-lines with the anterior lobe of the glabella. Facial sutures are now present and pursue a curved course from the anterior border along the inner side of the eye to the lateral margin, thus cutting the free cheeks off from the fixed cheeks. Since the suture cuts the margin in front of the genal angle the proparous condition is exhibited. In the later meraspis stages the point of intersection of the suture with the margin shifts backwards, trespasses across the genal angle and passes on to the posterior margin, thus exhibiting the gonatoparous condition on its way to assuming the opisthoparous.

In some types of trilobites, such as *Dalmanites*, the eyes and facial sutures and free cheeks likewise appear in the same position at a correspondingly early stage but the proparous condition, thus established, persists on into adult life.

The development of trilobites does not, at first sight, appear to furnish support to the view, based upon the comparative study of adults, that they were descended from annelidiform ancestors, as the protaspis is quite unlike an annelid. Nevertheless the order of appearance of new segments in the individual trilobite is the same as that in an annelid such as *Polygordius*. In both types the segmented portion of the body at first forms only a very insignificant part of the whole; gradually, however, it increases in importance by the addition of new segments posteriorly, until it forms the preponderating portion of the whole. This close parallelism can only indicate affinity. Presumably a hastening in the development of the exoskeleton took place as the annelidiform ancestor passed on into the trilobitic type, and led to the appearance of this outer covering at early and yet earlier stages until eventually it entered even the unsegmented stage. This, together with a similar speeding up of the development of other characters may be said to have trilobitized the unsegmented trochophore out of all recognition into the almost equally unsegmented protaspis. This phenomenon has its counterpart in the larval development of other groups, cp. protœcium in Polyzoa (Fig. 79), and the prodissoconch in pelecypods (Fig. 163A) enclosing the free-swimming trochophore larvæ.

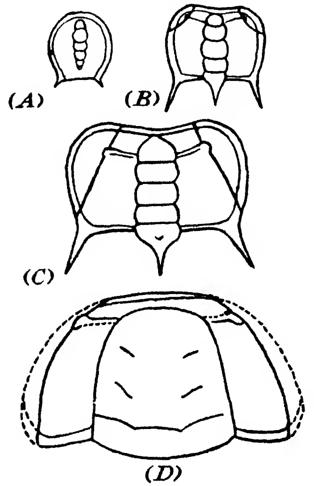


FIG. 180.—Development of *Peltura scarabæoides*.

(*A*) Protaspis stage. (*B*) Early merapsis stage. (*C*) Late merapsis stage. (*D*) Adult. (From Stubblefield after Poulsen.)

Adaptive Modifications.—Trilobites occupied the same prominent position in the fauna of the Protozoic sea as the Crustacea do in modern seas, and like these they found their way into widely different nooks and crannies in their marine surroundings, and became correspondingly adapted. Generally speaking, they are rare in coarse-grained rocks and planktonic deposits, but are more common in argillaceous and calcareous strata which yield many thin-shelled and thick-shelled forms respectively. Some of the special features in which these adaptively modified trilobites differed from such a normal type as *Triarthrus*, bear a close resemblance to features possessed by existing arthropods whose habits are more or less fully known. This furnishes a valuable clue to the life conditions of these extinct forms.

Olenellus (L. Camb., Fig. 183) resembles the living arachnid *Limulus* or King Crab (Fig. 207E), in the shape and rigidity of the head-shield, in the position of its eyes far up on the dorsal surface of the cephalon, in the triangular shape of the remainder of its body, and above all in the presence of a long tail spine. These points of resemblance may be reasonably associated with a similarity of habits. *Limulus* lives in water from ten to forty feet deep. Sometimes it burrows into the mud, but usually it merely ploughs its way through the surface deposits with only the lower portion of its carapace covered. By pushing its tail spine into the ground it secures a fixed point from which to force its body forward. In this it is also assisted by scooping movements of its flattened limbs. The tail spine is also used as an accessory to movement upon firmer ground, and with its aid the creature is able to right itself if by accident it falls upon its back.

It is probable that the pointed or spined pygidium (Fig. 196) of such trilobites as *Homalonotus* (Sil.) and *Dalmanites* (Sil.) served similar functions. In the former genus the shape of the cephalon with its scoop-like anterior margin, the much reduced eyes, the smoothing out of the glabellar grooves and of all projecting features of the body such as the glabella itself, suggest that it tunnelled like a mole more deeply below the surface. Other trilobites (Fig. 189), such as *Cryptolithus* (Ord.), which are likewise believed to be tunnellers, have become quite blind and have lost the facial suture so that the head-shield has become a more rigid piece. Some specimens of *Cryptolithus* have been found containing stone casts of the stomach and intestine, a fact which suggests that the animal gorged itself with mud and abstracted nutriment therefrom as does the earthworm to-day.

Cyclopyge (Fig. 181) introduces quite a different set of modifications. Its eyes are relatively as large as those of a dragonfly or a bee, and the visual area extends from the dorsal surface far on to the ventral, sometimes reaching even to the mid-ventral line. This fact alone suggests an open water habit with light all round both below and above, and excludes the benthic habit from consideration. The present-day crustacean *Cystisoma*, which lives in the open sea and is nocturnal in habit, also has greatly enlarged eyes. During the day it is said to sink into dimly lighted depths, but at night it rises to the surface. The fact that *Cyclopyge*, unlike other trilobites, is sometimes found in graptolitic shales tends to support the view that it led an open water mode of life. The large-eyed type of modification is shown to a more or less marked degree in other trilobites such as *Remopleurides* (Ord.) and *Nileus* (Ord.). In *Cyclopyge* (Ord.) the glabella is greatly inflated, a feature which is frequently exhibited by trilobites and which reaches its maximum development in *Staurocephalus* (Sil.) and *Sphærocoryphe* (Fig. 195). It has been suggested that in these cases the glabella has become modified into a floating apparatus.

The genus *Acidaspis* (Ord.-Dev.) resembles many planktonic organisms in the possession of numerous delicate spiny outgrowths from various parts of the body (Fig. 181). These by acting as a frictional hindrance to sinking enabled the creature to keep floating near the surface with the minimum of effort. In floating and free-swimming types the eyes usually take up a position close to the margin of the head-shield. This feature is common, though not universal, among protaspid larvæ. The larvæ, even of some benthic crustacea living in existing seas, are of planktonic habit and there is no reason for denying the same privilege to the protaspids of many trilobites. In the development of *Triarthrus* the eyes remain marginal until as many as thirteen segments have been formed (Fig. 181B). At the next ecdysis there is a reduction in size such as frequently accompanies metamorphosis in other organisms. The eyes now leave the margin. These facts point to a change from a pelagic to a benthic habit. Some trilobites, like *Ampyx* (Ord.–Sil.) are armed with long spines. These may have shifted the centre of gravity and so served as balancers, or, as in crustacean larvæ which swim on their backs they may have acted as keels. In any case the

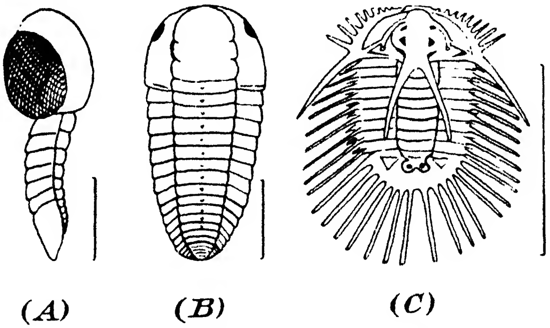


FIG. 181.—Some Adaptive Modifications among Trilobites.

(*A*) *Cyclopyge*, side view (after Barrande). (*B*) Young *Triarthrus*, before metamorphosis (after Walcott). (*C*) *Acidaspis* (after Richter).

presence of such spines must certainly have made the animal an awkward morsel of food for all except very large-mouthed enemies.

The frequency with which the pygidium develops to the size of the cephalon in widely separated lineages suggests that this is an important adaptive modification. The available evidence seems to indicate that by a rapid upward and downward movement the pygidium would function as a powerful propelling organ, and enable the trilobite to swim much more rapidly than it could by means of its legs alone. Moreover, a sharp downward and forward stroke of the tailpiece would send the animal darting rapidly backwards out of danger when this was presented. Both small- and large-tailed trilobites were accustomed to roll themselves up, with the hinder part of the body shut tightly against the fore part. This action provided shelter for the delicate limbs and ventral surface within the relatively thick dorsal shield. This study of the ethology of extinct forms is one that bristles with difficulties which can be solved only by a yet fuller enquiry into the habits of existing aquatic arthropods.

Cambrian Trilobites.

Lower Cambrian Trilobites.—The richest and most completely known Lower Cambrian trilobitic fauna is one which has been found in North America. The oldest member of it is called *Nevadia* (Fig. 182), a trilobite which exhibits a full suite of characters in a primitive state. Its glabella diminishes anteriorly, and is divided by unbroken transverse furrows into five divisions of which the first is the largest. From this stout eye ridges are given off laterally which bear elongated crescentic visual areas. The eyes are far removed from the margin of the shield, and lie close to the glabella, so that the free cheek region is very broad, and the fixed cheek region narrow. No facial suture is present. The trunk and tail consist of twenty-eight free segments terminating in a telson. There is no pygidium. The anterior segments have well-developed pleuræ ending in long pleural spines. Passing backwards the pleuræ decrease in size and disappear at about the

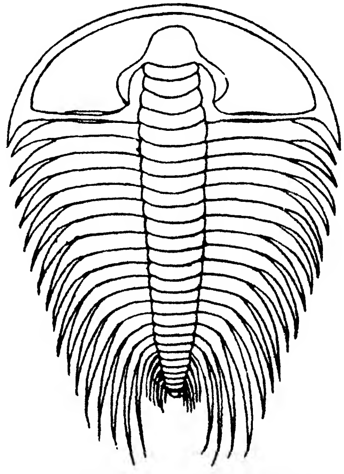


Fig. 182.—*Nevadia* (after Walcott).

seventeenth segment. In the last eleven segments the pleural spines are attached directly to the axis.

At higher levels in these American Lower Cambrian rocks other trilobites occur which have so many of the same general characteristics as *Nevadia* that they are classed together with it in the family Mesonacidæ. They exhibit the usual stages in the specialization of the glabella and eyes, and also a reduction in the number of segments without pleuræ. In *Callavia* (Fig. 183) these have been reduced to two ; in *Elliptocephala* there are about five, each of which bears a dorsal spine. In *Mesonacis* (Fig. 183B) and *Pædumias* only the first of these bears a spine. In the former the remainder are normal but in the latter they exhibit varying degrees of degeneration. In *Olenellus* (Fig. 183) all except the spine-bearing segment have gone, and the spine of that has become the large tail spine whose function has already been discussed.

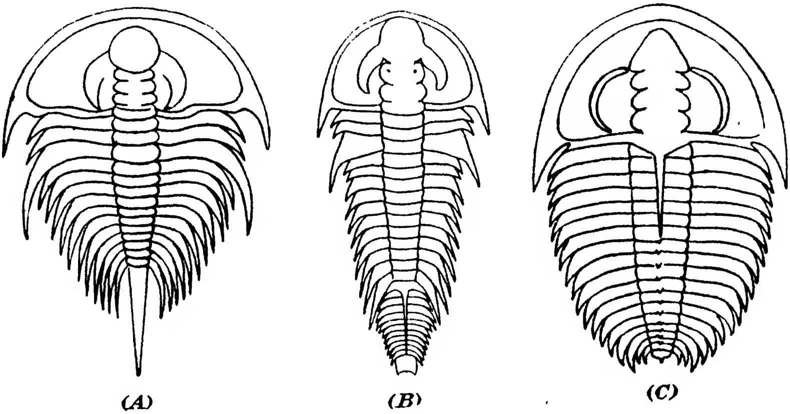


FIG. 183.—Some Lower Cambrian Trilobites.
(*A*) *Olenellus.* (*B*) *Mesonacis.* (*C*) *Callavia.*

The Mesonacidæ are confined to the Lower Cambrian rocks which are therefore also called the Olenellidian series after the most widely distributed member of the family. In America this series has been divided into five zones of which four are named, from the oldest upwards, after *Nevadia*, *Elliptocephala*, *Olenellus*, and *Callavia.* The last two have long been recognized in the British rocks.

THE MIDDLE CAMBRIAN TRILOBITES.—In the British area a quite rich trilobitic fauna, having only two genera in common with the earlier fauna has been found in the Middle Cambrian rocks. The most characteristic family is the Paradoxidæ, which has given the name Paradoxidian series for these rocks. The members of this family resemble the Mesonacidæ in so many adult and developmental features, that there can be little doubt that they have evolved from the same stock. Intermediate stages may be represented by *Redlichia* which occurs in the Lower Cambrian of the Far East. *Paradoxides* seems to have entered the British area already fully evolved and consequently a palæontological break occurs between the Lower and Middle Cambrian faunas.

Paradoxides differs (Fig. 184) from the mesonacid trilobites in the presence of a perfect facial suture, the disappearance of the eye-ridges, the greater concentration of the visual area, and the presence of a small pygidium. The following sequence of species given in order from oldest to youngest has been found valuable for zonal purposes in Scandinavia; *P. œlandicus*, *P. tessini*, *P. davidis*, *P. forchammeri*. Of these only the first and the last have not yet been recognized in the British Isles.

THE UPPER CAMBRIAN TRILOBITES. — The passage from the Middle to the Upper Cambrian is marked by an even more distinct palæontological break than the one already mentioned, for it is signalized not only by the disappearance of the Paradoxidæ, but also by the incoming of the Olenidæ which have no direct affinity with that family. Since the Olenidæ have much in common with the Ptychopariidæ (L. and M. Cam.) it seems likely that these may include the ancestral stock. The Olenidæ are sufficiently characteristic of the Upper Cambrian Rocks to justify the name Olenidian for the series.

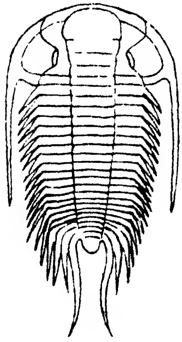


FIG. 184. — *Paradoxides*, a Middle Cambrian Trilobite.

Olenus (Fig. 185) differs from the mesonacid type in the tendency for the cephalon to assume a quadragonal outline, in the presence of a facial suture which conforms to the opisthoparian pattern, but divides the cheek region into portions of approximately equal width. It also has a well-formed pygidium which like the free thoracic segments has comparatively large pleural portions, a feature which distinguishes it from *Paradoxides*. In the uppermost levels of the Olenidian series (the Dolgelly stage) the olenid type of trilobite became modified in curious ways. In *Eurycare* (Fig. 185) and *Sphærophthalmus*, the cephalon became very wide and more definitely quadragonal in outline; the genal spines, instead of projecting backwards in a line continuous with the lateral cephalic margin as in the normal olenid, sprang abruptly outwards from it at a large angle. The eyes also became much reduced in size. Again in *Peltura* (Fig. 185) *Acerocare* and *Triarthrus* (Ord.) the olenid organization tended to become simplified by the loss of spines and the rounding of the genal angles.

OTHER CAMBRIAN TRILOBITES.—Along with these three types, which were characteristic of the successive epochs, there lived others the range of which was not confined to any one epoch. The Ptychopariidæ (L. and M. Cam.) were nearly world-wide in distribution, but were most common in the regions which now adjoin the Pacific. Apart from the form of the glabella they closely resemble *Olenus*.

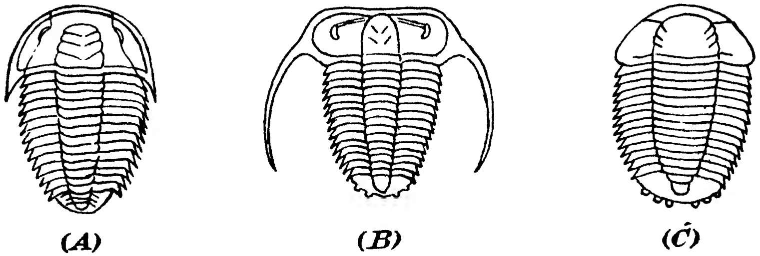


FIG. 185.—Some Upper Cambrian Trilobites.
(*A*) *Olenus*. (*B*) *Eurycare*. (*C*) *Peltura*.

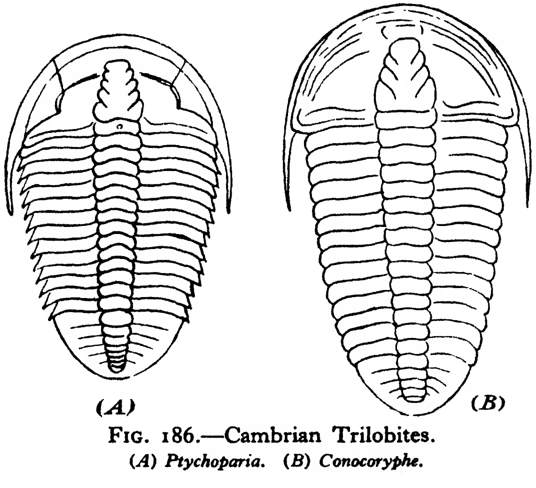


FIG. 186.—Cambrian Trilobites.
(*A*) *Ptychoparia*. (*B*) *Conocoryphe*.

The Conocoryphidæ ranged through the Cambrian in Britain, but attained their maximum development in the Paradoxidian series. The features which distinguish them from the last family are the absence of eyes and of facial sutures. In the latter they probably retain a primitive condition, but it is unlikely that this is the case also for their blindness. The Agnostidæ are also present in the

Olenellidian, but they also attain their acme during the Paradoxidian epoch; they subsequently range with diminishing vigour up into the Ordovician.

In the absence of facial sutures *Agnostus* (Fig. 187) may be primitive, but in other respects, such as its blindness and the large pygidium it seems to exhibit an advanced stage of specialization. It has only two free segments; and these are little more than a hinge upon which the enlarged cephalon and pygidium may turn and close against each other like the shell of a bivalve mollusc. Other signs of segmentation are almost if not quite absent. The closely allied genus *Eodiscus* (*Microdiscus*) ranges through the Olenellidian and Paradoxidian. It usually has three free segments (Fig. 187) and signs of many segments upon the pygidium.

The American Middle Cambrian has yielded two genera of especial interest, *Pagetia* and *Mollisonia.* The former (Fig. 187) is closely related to *Eodiscus*, but differs in having eyes and a proparian facial suture. The latter genus (Fig. 187) also shows traces of these, but whilst it is isopygous it also possesses seven free thoracic segments, and thus if correctly placed here, it carries the segmentation of the agnostid type back to an even earlier stage than is seen in *Eodiscus.* Other trilobites having interesting relationships to certain Ordovician types are also found in the American Middle Cambrian. These will be referred to again later.

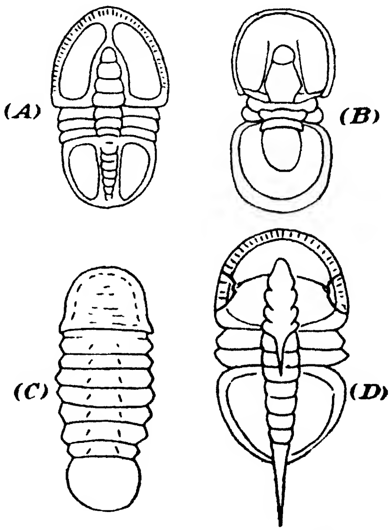


FIG. 187.—Some Agnostidæ.

(*A*) *Eodiscus.* (*B*) *Agnostus.* (Both reconstructed after Lake.) (*C*) *Mollisonia.* (*D*) *Pagetia.* (Both after Walcott.)

A TRANSITIONAL TRILOBITIC FAUNA.—Table IX shows the distribution in time of the families to which the trilobites dealt with in this chapter belong. From this it will be seen that the Tremadoc Series yield an assemblage that is of especial interest, for while it includes a few families that survived from the Cambrian it also contains a number which are characteristic of the Ordovician and later systems. The apparent suddenness of their appearance is due to the fact that having evolved in extra-European regions the removal of some barrier opened the way for them to migrate freely into the

British area. Many of the genera, *e.g. Anacheirurus*, and *Orometopus*, were primitive members of the families to which they belonged. Though *Shumardia* is regarded as characteristic of the Tremadocian its actual range is longer. The whole assemblage thus exhibits the peculiarities of a Transitional fauna.

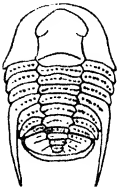


Fig. 188.—Shumardia (reconstructed after Raw).

Trilobites in Acme and Decline.—From Table IX it will be seen that the Ordovician period was characterized more by the appearance of new trilobites, than by the disappearance of old ones; consequently there never was a time when they were so numerous and varied so much in structure and mode of life. The Silurian, on the other hand, was characterized by the fact that no new families appeared and that many disappeared. The same is true of the Devonian period into which only about five families survived. The Permian period saw the complete disappearance of the trilobite race.

Cambrian Survivals.—The genus *Agnostus* lingered with but few species until almost the close of the Ordovician. Though the Olenidæ did not actually survive they were represented during the Ordovician by a closely allied genus *Aulacopleura*, which differed mainly in having a narrower and shorter glabella. This was the most primitive member of the Proëtidæ which ranged through the Ordovician, Silurian and Devonian. In the genera *Phillipsia* and *Griffithides*, this family survived into the Carboniferous and Permian, as the only remnant of the Trilobite stock. The family progressed

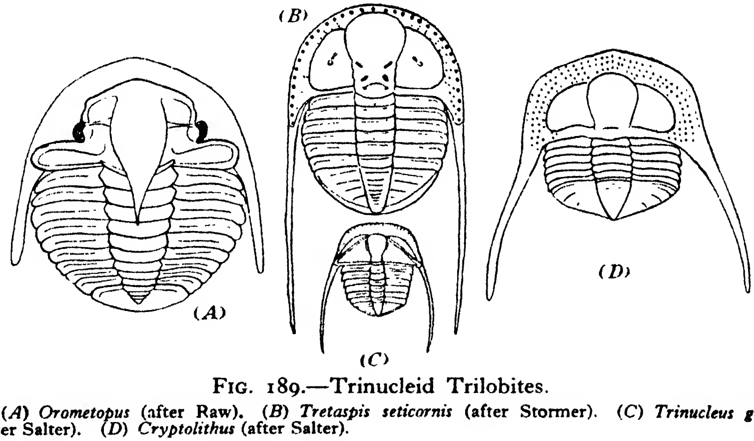


Fig. 189.—Trinucleid Trilobites.

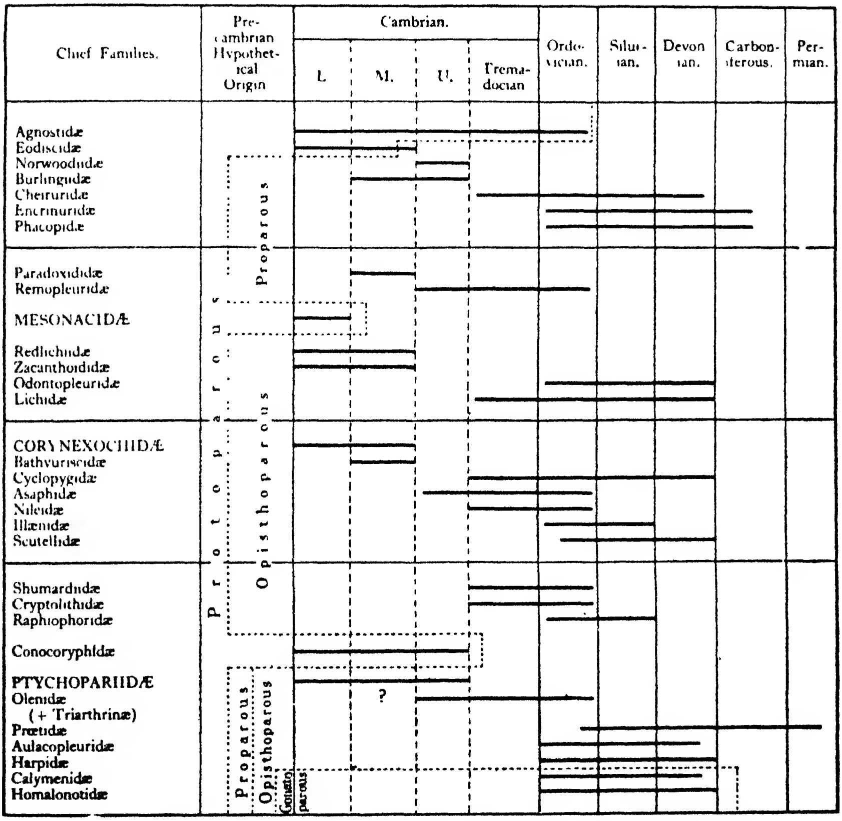
(*A*) *Orometopus* (after Raw). (*B*) *Tretaspis seticornis* (after Stormer). (*C*) *Trinucleus gibbsi* (after Salter). (*D*) *Cryptolithus* (after Salter).

structurally by a loss of the eye-lines, a backward shifting of the eyes and facial sutures, and by the enlargement of the glabella.

Ordovician Specialities.—By specialities is here meant those types which were peculiar to the Ordovician. The Cryptolithidæ (Trinucleidæ), were blind trilobites without facial sutures (Fig. 189). The head-shield is larger than the remainder of the body, and is provided with a broad flat margin variously ornamented with pits and grooves. They appear to be specialized derivatives from some form like the Tremadocian genus *Orometopus* (Fig. 108) which had

TABLE IX

The Chief Families of Trilobites and their distribution in Time.



Note.—Capitals indicate families which lie near to the ancestral stocks of the remainder.

well-developed eyes and a typically opisthoparian facial suture. In Britain *Trinucleus* ranged from the Arenig to the Caradocian; *Cryptolithus*, a southern form, from the Llandeilian to the Ashgillian; *Tretaspis*, a northern form, appeared in and was dominant during the Ashgillian.

The Asaphidæ when they first appeared in the British area during the Tremadocian had already attained their definitive characters. In North America, however, the Cambrian Rocks have yielded such forms as *Bathyuriscus* (Fig. 190B) which by their development and adult structure connect up this family with a Corynexochid stock. The Asaphidæ arose out of these by specialization of the glabella, backward and inward movement of the eyes and facial suture, and consequent widening of the free cheeks, the further enlargement of

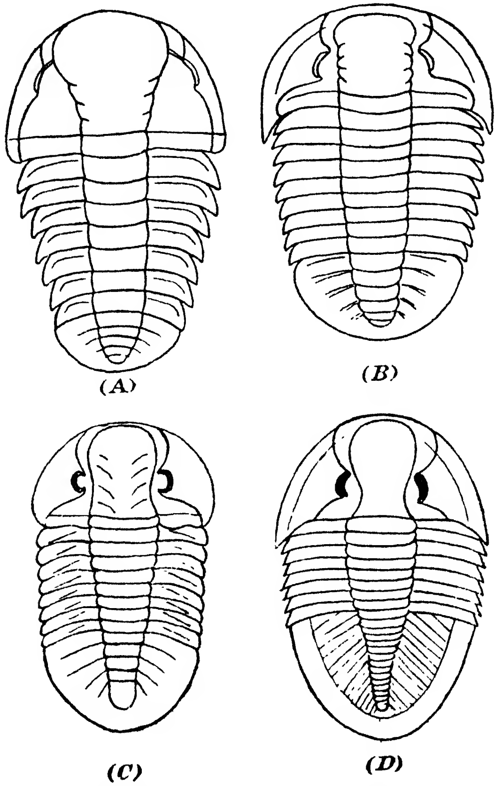


Fig. 190.—Asaphid Trilobites.

(*A*) *Corynexochus* (adapted from Walcott). (*B*) *Bathyuriscus* (after H. Woodward). (*C*) *Niobe* (after Salter). (*D*) *Asaphus*.

the pygidium, the reduction of the free segments of the thorax to a fixed number, viz. eight (Fig. 190). The Asaphidæ dominated the Ordovician waters by reason of their great plasticity of organization, which enabled them to adopt a wide range of modifications. Of the normal genera *Ogygia* characterized the Arenig, and *Asaphus* the Llandelian and Caradocian, though both genera transgressed beyond these boundaries.

Stable Stocks.—Some families, much less plastic than the one just considered, were very stable, and had a long range in time. The Illænidæ appear to be related to the Asaphidæ. They differ, however (Fig. 191), in having a marked convexity of the dorsal carapace, an excessive widening of the glabella, and in the smoothing out of its grooves and furrows. They were so stable in their organization that in spite of their long range they produced very few genera. *Illænurus* (M. Camb., N. Amer.) carries the type back to an early stage in evolution, when as yet the pygidium was small, and the number of free segments, being ten, was becoming settled.

The Calymenidæ ranged with but little change from the Ordovician to the Devonian. In them the semi-circular head-shield showed a slight tendency to assume a trigonal outline. Anteriorly the facial sutures cut the margin some distance from one another but posteriorly they cut it at the genal angle. In earlier forms the glabella was parabolic in outline (Fig. 192) and did not project beyond the margin of the cheek. In later forms it became inflated anteriorly and did project beyond this. The deepening of the furrows resulted in a marked lobulation of the sides of the glabella. In Upper Bala and Silurian times the second lobe came into contact with a projection from the cheek. The primitive genus *Synhomalonotus* (Arenig) provides a link with the family to be considered next.

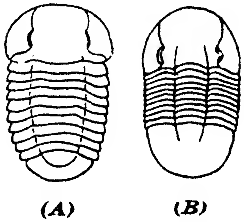


Fig. 191.—Illænid trilobites.
(*A*) *Illænurus* (after Walcott).
(*B*) *Illænus* (after Holm).

The Homalonotidæ (Ord.-Dev.) differ from the Calymenidæ in the trigonal form of the head-shield and the union of the facial sutures in front of the glabella and in the much less distinct trilobation of the body. The pygidium is usually pointed, but in the earliest and most primitive species, from the Lower Ordovician, it is rounded. These belong to the genus *Eohomalonotus* which is closely connected with *Synhomalonotus*. These two families were derived from a common stock which may have originated in the Ptychopariidæ.

Strange Modifications.—Among the multitudinous forms which characterize the race in its acme are some which strike the eye by reason of their strangeness. Of these *Remopleurides* and *Cyclopyge* are confined to the Ordovician, and have already been described. *Harpes*, which is allied to the Trinucleidæ survives into the Devonian and is characterized by the primitive simplicity of its trunk and tail, and by the enormous size of its genal spines. *Ampyx* has similar affinities, but its head-shield has the triradiate form. *Bronteus* (Fig. 193) is an isopygous form with only ten free segments. Its pygidium has a very short axis surrounded behind as well as on either side by a very broad pleural area marked by radiating grooves. *Acidaspis* (Fig. 181) belongs to the Odontopleuridæ, a family in which there is a marked tendency towards the breaking up of the glabella into separate lobes by the union of the inner ends of the furrows with one another. This same tendency is also manifested in the Lichidæ in which all the modifications of the glabella can be derived from a simple type (Fig. 194) with three pairs of lateral furrows, and a complete neck furrow, by the backward prolongation of the first pair to meet the others in succession. Two clearly defined stages cover all known genera :—

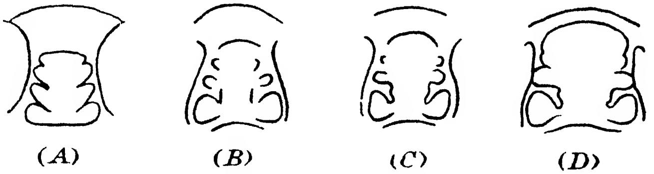


FIG. 192.—Glabellæ of Calymenids.

(*A*) *Synhomalonotus tristani* Arenig. (*B*) *Flexicalymene cambrensis* Llandeilo. (*C*) *Flexicalymene caractaci* Bala. (*D*) *Calymene blumenbachi* Wenlock (after Shirley).

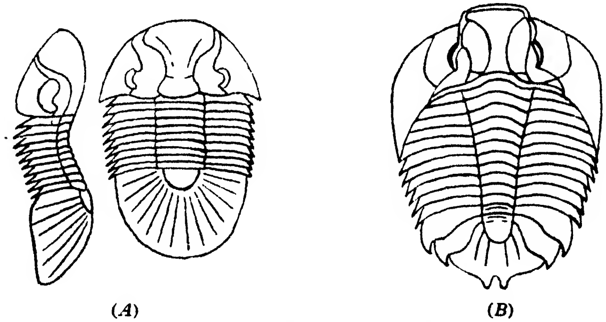


FIG. 193.—Strange Trilobites.

(*A*) *Bronteus*, side and dorsal view (after Bronn). (*B*) *Homolichas* (after Reed).

(1) The *Protolichas stage*, in which prolongation stops at the third furrow and so produces a lobe consisting of two parts. This undergoes various changes in form and marking, but its separation from the neck furrow is usually clear enough to enable the stage to be recognized.

(2) The *Deuterolichas stage* in which prolongation extends to the neck furrow and thus forms a tricomposite lobe.

In the British Isles both stages are represented in the Arenig but the *Protolichas* reaches its maximum development in the Silurian and persists into the Devonian. In other regions *Deuterolichas* has a similar range.

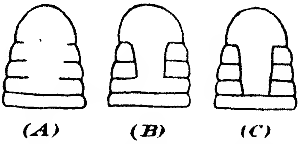


FIG. 194.—Types of Glabella in Lichidæ.

(*A*) Archetype. (*B*) Protolichas type. (*C*) Deuterolichas type. (Modified after Reed.)

PROPARIAN TRILOBITES.—Among the proparian trilobites mentioned in Table IX three families must now be described. The Cheiruridæ were represented in the Tremadocian by *Anacheirurus*. This primitive form has a small pygidium and eleven or twelve free segments. Its free cheeks, like those of the young of other proparia, were small and situated at the antero-lateral margin of the head-

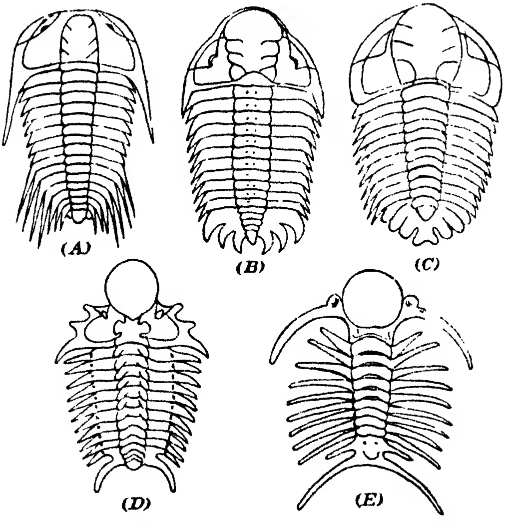


FIG. 195.—Members of the family Cheiruridæ.

(*A*) *Anacheirurus* (reconstructed after Salter). (*B*) *Cheirurus* (after Salter). (*C*) *Cyrtometopus* (after Salter). (*D*) *Sphærocoryphe* (reconstructed). (*E*) *Deiphon* (after Barrand).

shield (cp. Fig. 180B). The glabella has almost parallel sides, an unbroken neck furrow and three pairs of lateral furrows. Other genera in this family advance from this condition by a swelling out of the whole glabella and by the backward extension of the third furrow until, through meeting the neck furrow, it isolates a pair of basal lobes (Fig. 195B). The swelling up of the glabella may affect the whole of the region in front of the neck and be accompanied by a reduction of the cheek as in *Cyrtometopus* (Fig. 195C) and *Sphærexochus*; or it may be confined to the anterior part of the glabella and be accompanied by a reduction of only the free cheeks as in *Cheirurus* (Ord.-Sil., Fig. 195B), *Sphærocoryphe* (Ord.-Sil., Fig. 195D) and *Deiphon* (Sil., Fig. 195E). The Encrinuridæ are allied to the Cheiruridæ, and in the series of genera *Cybele* (Ord.), *Encrinurus* (Ord.-Sil.), *Staurocephalus* (Sil.) exhibit a sequence of changes parallel to those seen in that family.

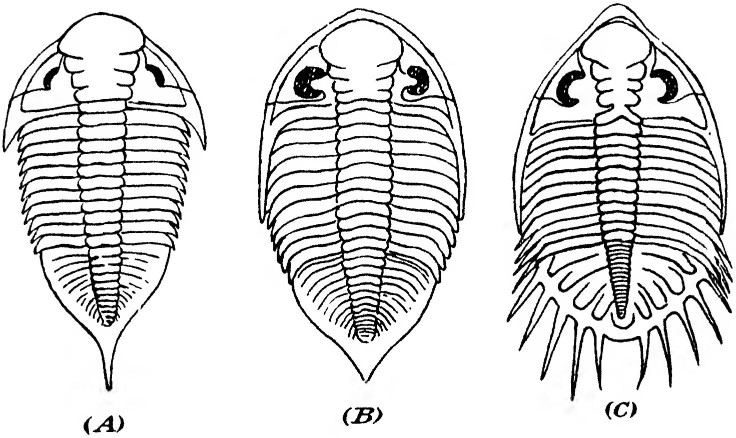


FIG. 196.—Trilobites of the Dalmanites series.
(*A*) *Dalmanitina* (after Beecher). (*B*) *Dalmanites*. (*C*) *Asteropyge* (*Cryphæus*) (after Salter).

The Phacopidæ have large free cheeks and eyes made up of separate facets. The thorax has a fixed number of segments, namely eleven. In more primitive species the lobulation of the glabella is well defined, in more specialized forms (Fig. 198B, C) it has disappeared. Three main series of forms may be mentioned.

The *Dalmanites series* has *Dalmanitina* (Ord., Fig. 196A) for its most primitive member. Its glabella, though it has three pairs of lateral and one complete neck furrow, is already swollen anteriorly. Its free cheeks are relatively small, and its pygidium has only ten segments. In *Dalmanites* itself (Sil., Fig. 196B) the furrows are deepened so that the more swollen anterior lobe tends to become detached. The head-shield has elongated and extends in front of the glabella. The free cheek has enlarged by the backward and inward shifting of the eyes and facial sutures. The genal and pleural spines are stronger. The pygidium has eleven to sixteen segments and may be prolonged into a caudal spine. *Asteropyge* (*Cryphæus*, Fig. 196C) represents this series in the Devonian. Its glabellar features are less distinct, but the development of spines is still more marked especially posteriorly. The pygidium has more than sixteen segments.

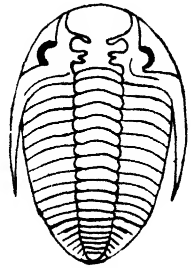


FIG. 197.—*Chasmops.*

The *Chasmops series* is confined to the Ordovician. Its earlier representative *Pterygometopus* resembles *Dalmanites*, but the first glabellar lobe has developed at the expense of the second and third; a process which reaches its maximum development in *Chasmops* (Fig. 197) from the Upper Ordovician.

The *Phacops series* appears in the Ashgillian with the primitive genus *Acaste* (Fig. 198A). Its glabella closely resembles that of *Dalmanitina*, but this genus and indeed all the members of the series differ from those of the other series in the greater convexity of the dorsal surface, in the absence of spines, in the rounding off of all angles, and in the relative shortening of the glabella or of the head-shield. The whole of the glabella in front of the neck bulges dorsally as well as laterally. In *Phacops* (Fig. 198B), which appears later and does not attain its maximum until the Devonian, the glabellar grooves have disappeared. During the Devonian this series exhibited specialization in two strongly contrasted directions; in the one represented by *Trimerocephalus* (Fig. 198C) the eyes, accompanied

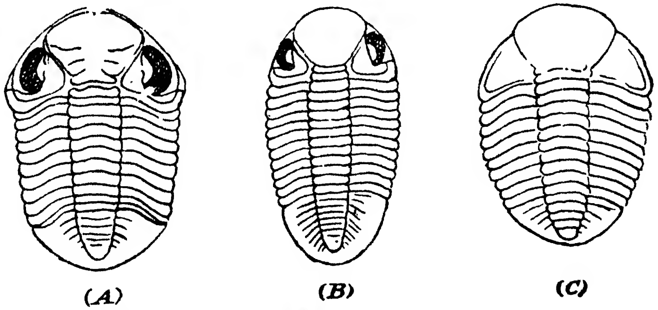


FIG. 198.—Trilobites of the Phacops series.
(*A*) *Acaste*. (*B*) *Phacops*. (*C*) *Trimerocephalus*. (*A–C* after Salter.)

by the facial suture, shifted to the margin and gradually disappeared; in the other, which comes to a climax in *Reediops*, the eyes became large, and the glabella greatly distended antero-dorsally. This genus is not present in Britain.

CRUSTACEA

Early Palæozoic Crustacea.—The Crustacea, like the trilobites, are predominantly aquatic animals and breathe by means of gills. They exhibit, however, a much greater variety and divergence of structure, and accordingly it is more difficult to form a concise idea of the group as a whole than in the case of the trilobites. Nevertheless, the earliest larval stage (Fig. 199) in development, the Nauplius, is remarkably similar for all divisions of the Crustacea. This larva has an oval body without trace of division into segments. Its mouth is situated on the under side, and is overhung by a labrum. It has three pairs of appendages all of which are provided with setæ for seizing food. The first pair, like that of the trilobite, is attached a little in front of the mouth, and consists of only one axis or branch, made up of several segments. The second and third pairs, also like those of the trilobite, are biramous, and lie on either side of or slightly behind the mouth. The basal segment of each of these is provided with inwardly projecting bristles, which are used for seizing food and passing it to the mouth.

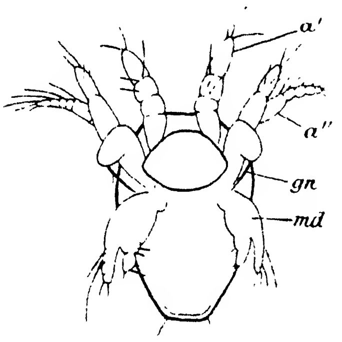


FIG. 199.—Early Nauplius Larva (after Calman).

a', antennule. *a''*, antennae. *gn*, prehensile process. *md*, mandible.

From time to time the larva sheds its chitinous covering. After every such moult the larva increases in size, and exhibits some new structural feature. As in the trilobite the formative region for new segments lies just in front of the telson. Between the first segment thus formed and the three pairs of appendages described above, two more pairs are formed, which in the adult likewise function as jaws. These five pairs evidently correspond with those borne upon the cephalon in the trilobite. In Crustacea, however, during further development the second pair of limbs shifts to a position in front of the mouth and ceases to function in the processes of catching and masticating food. This and the first pair become mainly tactile organs called antennæ and antennules respectively. Meanwhile the other cephalic limbs become still more perfectly adapted for performing a masticatory function. Thus the Crustacea as a whole advance beyond the lowly grade of organization of the Trilobita.

Behind the cephalic region each segment, as in the trilobites, bears a pair of limbs, which function in the lower crustacea only as locomotory and respiratory organs. In the higher Crustacea, as will be seen later, some of the front pairs take on a masticatory function also. The number of post-cephalic segments differs greatly in the various sections of the class, ranging from as many as forty-two in some Branchiopods, *e.g.* *Apus*, to the condition seen in Ostracods in which the thorax shows no distinct signs of segmentation. In the majority of these the trunk limbs differ markedly from those of the trilobites in not being biramous and in having flattened axes with flat attachments on either side (Fig. 200D). This latter peculiarity gives to the limb as a whole a leaf-like character. One pattern of segmentation has proved to be extraordinarily stable and effective. In this there are fourteen or fifteen post-cephalic segments, of which the first eight can invariably be distinguished from those which follow and constitute the thorax. The Crustacea having this pattern make up the Malacostraca, and include the largest forms.

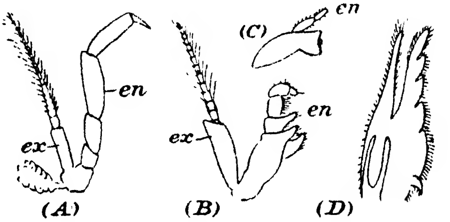


FIG. 200.—Typical Limb and Limbs modified for masticatory purposes (after Calman).

(*A*) Normal limb. (*B*) Maxilliped showing partial modification for purposes of mastication. (*C*) Mandible showing complete modification for purposes of mastication. (*D*) Leaf-like limb.

en, endopodite. *ex*, exopodite.

An exquisitely preserved suite of fossils from the Middle Cambrian of British Columbia proves that already at that early date most if not all of these differences existed (Fig. 201). Thus the genus *Opabinia* exhibits little to distinguish it from certain modern Branchiopods. As in these the pre-oral appendages are highly modified, the trunk limbs are leaf-like. It differs, however, in having its eyes at the end of stalks, a fact which suggests that the sessile eyes of the modern branchiopod have been secondarily acquired. The genus *Burgessia* in some respects recalls *Apus*. Like this it has a bivalve carapace extending from the back of the head and covering part of the trunk. The latter region has thirty-eight segments. The eyes are sessile; the antennules, small; the antennæ, large and many jointed. The other cephalic appendages are leg-like. The nine pairs of trunk limbs are not leaf-like as in *Apus*, but have endopodites with seven sections like those of trilobites.

Waptia likewise has a loose fold-like carapace. Its trunk shows distinct differentiation into eight thoracic and six abdominal segments, and thus anticipates the characteristic segmentation of the Malacostraca. The trunk limbs, however, tend to be leaf-like. *Hymenocaris* is a genus which has long been known from the Cambrian rocks. It is closely related to the living *Nebalia* which has a thorax with eight free segments covered by a loose carapace, the abdomen having seven segments in both genera. Whilst the thoracic limbs of *Nebalia* tend to be leaf-like, those of *Hymenocaris* are typical walking legs (Fig. 201A), a fact which gives support to the suggestion that the leaf-like limb, which at one time was regarded as the more primitive, has been secondarily acquired.

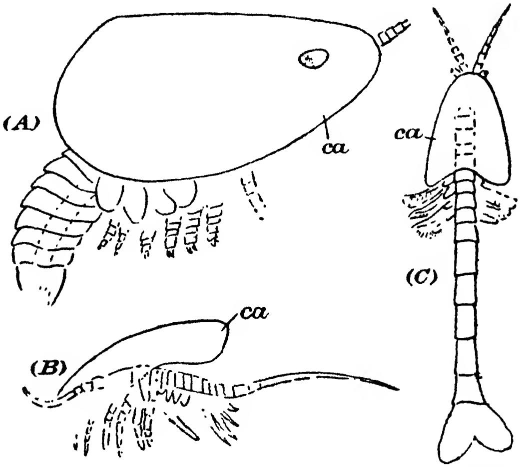


FIG. 201.—Middle Cambrian Crustacea (after Walcott).
(*A*) *Hymenocaris*. (*B*) *Burgessia*. (*C*) *Waptia*.
ca, carapace.

Concerning the other fossil Crustacea which do not belong to the Malacostraca, very little is known, and that little refers more especially to the Ostracoda, a group of very small forms having only an ill-defined segmentation of the trunk. The whole body is enclosed in a bivalve shell. Such shells occur quite commonly at numerous horizons from the early Cambrian until to-day. The Cirripedia (barnacles and sea-acorns) are an aberrant group which has adopted a sessile mode of life. Starting life as a typical nauplius the individual cirripede becomes attached by an outgrowth of the head which elongates and forms a stout stalk. In the earliest members

(*Pollicipes* and *Turrilepas*, Sil.) this stalk and the body become enclosed in a coat of mail consisting of overlapping calcareous plates. Those which enclose the body are usually larger and form the capitulum. From this central type there arose two diverging stocks. In the one the stalk persisted, but lost its mail-like covering; this culminates in the modern goose barnacle (*Lepas*). In the other the stalk tended to shorten until the capitulum was placed almost, if not quite, upon the ground. In this way arose the ordinary sea-acorn (*Balanus*).

Late Palæozoic Crustacea.—The majority of the familiar and more conspicuous Crustacea (*e.g.* crabs, lobsters, shrimps), of the present day, form a compact group of closely related forms which on that account are classed together as the Malacostraca. In early Palæozoic times these were already represented by a primitive type, such as *Hymenocaris*. As judged by known fossil remains they were only scantily represented during the Devonian, but they attained some degree of prominence during the Carboniferous period.

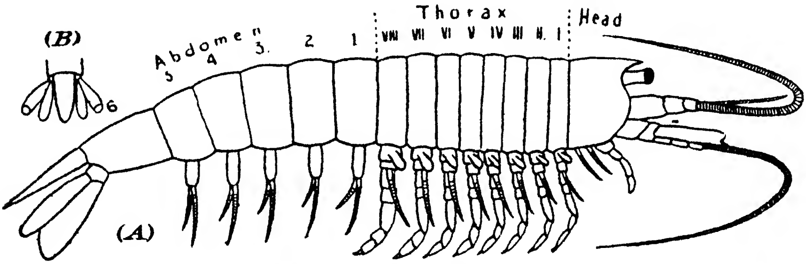


FIG. 202.—Hypothetical reconstruction of Archetypal Palæozoic Crustacean (based on description by G. Smith).

(*A*) Side view of reconstruction. (*B*) Upper view of tail region.

A careful comparison of living and extinct forms has made it possible to reconstruct, in broad outlines, the probable characteristics of the immediate ancestor of these later Palæozoic crustacea (Fig. 202). Its body was composed of nineteen segments and had three clearly recognizable regions called respectively the head, thorax and abdomen. The head, as in trilobites and all Crustacea, evidently consisted of five segments fused with one another. The eyes were carried upon movable stalks, the antennules were biramous, on the antennæ the outer branch was flattened and scale-like and all the other limbs were more or less perfectly adapted to perform a masticatory function. The thorax contained eight segments, all free from one another. Its limbs were all alike, and consisted of a basal portion with two divisions. The endopodite had six divisions, and was bent sharply downwards at the middle joint, and functioned entirely as a walking limb. The exopodite, on the other hand, was adapted for swimming. The abdomen had six free segments and a telson, the latter being usually flattened. The limbs were biramous; the last pair was much flattened, and together with the telson formed a tail fin.

The nearest approach to this archetypal malacostracan was made by a group of forms (Syncarida) represented in Carboniferous times by *Præanaspides*, *Gampsonyx*, etc., and in the freshwaters of to-day in Tasmania and Australia by *Anaspides*. This latter provides an illustration of a not uncommon phenomenon, the preservation of relics of an ancient race in the freshwaters of modern times.

Præanaspides (C.M.) has departed from the archetype described above by the union of the first thoracic segment with the head. Its first thoracic limb is unknown, but in the very closely related living genus *Anaspides* this limb differs from the other thoracic limbs only in a slight modification of the basal segments for masticatory purposes, and in the reduction of the exopodite. This last feature is exhibited also by the last two thoracic legs. In *Gampsonyx* (L. Perm.) the first thoracic segment was free and the corresponding limbs were adapted for predatory purposes.

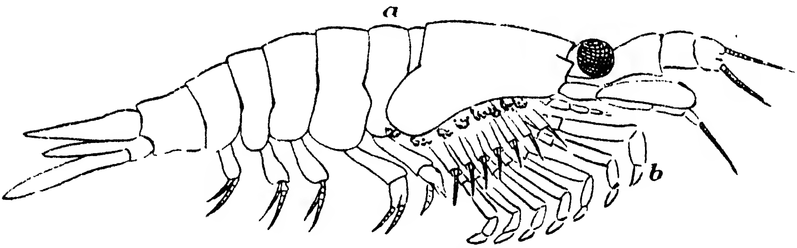


FIG. 203.—*Crangopsis* (after Peach).
a, 1st Abdominal segment. *b*, 2nd Thoracic limb.

The dominant Malacostraca of the Carboniferous were, however, the Percarida which include the extinct genera *Pygocephalus*, *Anthrapalæmon*, *Tealliocaris* and *Crangopsis* (Fig. 203). These conform to a plan and grade of structure exhibited to-day in certain deep-sea and open-ocean forms of which *Mysis* is the most familiar genus. In all these there is a carapace which nearly covers the thorax, and unites with the dorsal surface of the two or three front segments. In specimens of extinct forms the first thoracic leg is very imperfectly preserved, but it probably had the same structure as in *Mysis* in which the exopodite is retained; but the endopodite is reduced, and the basal portions of the limb have become modified to help in mastication. Such a limb is called a maxilliped. It is evident, even in the fossil forms, that the remaining seven thoracic limbs still retain the primitive condition, except that the number of divisions in the endopodite has been reduced from six to five. In the female the basal joints carry flattened structures which overlap and enclose a space, the brood chamber, on the under side of the body. Though the Percarida and their allies occupied a similar place in the economy of nature in Carboniferous times as do the lobsters and prawns in that of to-day, they do not appear to have attained any greater size than such small living forms as the shrimps. Nevertheless they exhibit various adaptational shapes; thus *Pygocephalus* is broad and depressed, and *Crangopsis* is slightly compressed.

Ostracods and branchiopods, which were dominant in earlier times, were still in existence.

Mesozoic and Later Crustacea.—The dominant Crustacea of post-Palæozoic times were modern in aspect, for already as in modern shrimps and lobsters the carapace not only covered, but had coalesced with the dorsal surface of all the thoracic segments (Fig. 204). Laterally, however, the carapace still remained free and thus covered in a space on either side of the thorax in which the gills were situated. At first sight they appear to have only five pairs of thoracic appendages. In each of these the exopodite has been lost, but the endopodite is relatively strengthened and forms an efficient walking leg. There are accordingly ten walking legs, a fact which is expressed in the name Decapoda for the order to which these crustacea belong. In reality the full complement of eight pairs of thoracic appendages, seen in the malacostracan archetype, is present; but the tendency, already noticed in late Palæozoic crustacea, for the anterior pair to exchange the locomotory for the masticatory function has now attained its maximum development in the complete modification of no less than *three* pairs of thoracic limbs into maxillipeds by the extension of their basal portions, and by the reduction of their branches.

Already in Triassic times the Decapoda, as represented by the genera *Æger* (Trias.-Jur.) and *Glyphæa* (Trias.-Cret.) had differentiated into two main stocks called the Natantia and Reptantia respectively. As these names imply the former (*e.g.* *Æger*, Fig. 204A), whilst they were essentially benthic types, were adapted for swimming freely forwards by means of well-developed abdominal appendages, or darting backwards by a rapid flapping movement of the abdomen, which greatly exceeded the rest of the body in size. As seen in *Æger* the carapace projected in front of the eyes into an elongated serrated rostrum, and no doubt served the purposes of a keel. The thoracic legs were all slender, though one or other of them might be enlarged. The shrimps and prawns (Caridea) are typical representatives of the Natantia. They appeared towards the close of the Jurassic, and are characterized by the enlargement of the second abdominal pleura. This feature was also exhibited by the Palæozoic *Crangopsis*.

The Reptantia (*e.g. Glyphæa*, Fig. 204) tended to be more typically benthic in habit. The natatory abdominal appendages were reduced, but the thoracic walking legs were correspondingly strong, and the first pair was often greatly enlarged. The abdomen was relatively much smaller than in the Natantia, and its first segment was reduced. The body as a whole tended to be depressed. *Eryon* (Trias.–Cret.) was allied to *Glyphæa*, but its body was greatly depressed. Its cephalothorax was almost crab-like in outline (Fig. 205), but its abdomen was still large and extended. Four or even all five pairs of walking legs were chelate, that is to say were armed with pincer-like organs at their tips. With *Eryma* (Lias.–U. Jur.) and *Hoploparia* (L. Cret.-Eoc.) forms more closely allied to the lobster and crayfish put in an appearance (Fig. 205). Unlike the two genera described above these have a well-developed rostrum, which, however, is not laterally compressed.

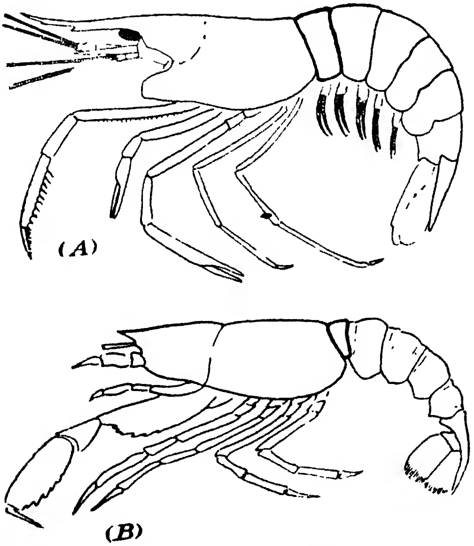


FIG. 204.—Mesozoic and later Crustacea.
(*A*) *Æger* (after Zittel). (*B*) *Glyphæa* (after Woods) The first abdominal segment has its outline thickened.

About the middle of the Jurassic period the tendency already noticed in Reptantia, especially in *Eryon*, for the cephalothorax to become relatively large in proportion to the abdomen, became much more emphasized, with the result that at that time there appeared forms in which the abdomen became reduced to a mere adjunct of the cephalothorax, and lay hidden from view along the under side of this. These are accordingly classed as a section of the Reptantia called the Brachyura, in contradistinction to all the forms described above which are described as being macrurous. The Brachyura include the Crabs, *Protocarcinus* (L. Ool.) being the earliest brachyuran known. In it the loss of the extended condition of the abdomen was not yet effected. *Prosopon* (U. Jur.) is of peculiar interest because its nearest allies at the present day live in the deep sea, another haven of refuge for displaced and ancient types. In *Dromia* (Eoc.–Pres.) vestiges of the flattened limbs on either side of the telson are still present. In typical crabs these have disappeared entirely.

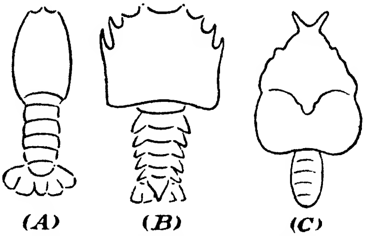


FIG. 205.—Outlines of Crustacea illustrating growing predominance of Cephalothorax over Abdomen. (*A*) *Eryma* (after Oppel). (*B*) *Eryon*. (*C*) *Palæinachus* (after H. Woodward).

ARACHNIDA

Aquatic Arachnida.—At the present day the Arachnida are predominantly air-breathing organisms and live upon the land. There is, however, a small group of forms, including the King-Crab (*Limulus*), which breathe by means of gills and live in the warm marginal seas of the Pacific and West Atlantic. These are a relic of a great race of aquatic arachnids (the Merostomata) which attained its maximum development in Silurian times.

The most completely known merostome is *Eurypterus* (Sil.–Perm.). This creature had an elongated depressed body (Fig. 206D). Its head region or prosoma was enclosed in a continuous covering, the carapace, the remainder of the body being clearly segmented. The first six free segments were wide and short and made up the mesosoma. The last six were narrow and long and constituted the metasoma. At the posterior end was a long tail spine. The metasoma bore no limbs, but the segments of the mesosoma bore, upon their ventral surfaces, large plates which carried gills hidden from view upon their upper sides.

On its under side (Fig. 206E) the prosoma bore six pairs of appendages, all consisting of one branch which resembles the endopodite of Crustacea. The bases of these came together around the mouth and functioned as jaws. The first pair were small and chelate, the next three increased in size from before backwards, and tapered towards the apex and were armed with spines. The fifth pair were slightly modified for scooping, and the last were large clumsy oar-like organs which could be used either for swimming or for digging.

The prosoma had a scoop-like margin and had large compound eyes placed upon its dorsal surface half-way between the median line and the margin. These structural features indicate a creature which usually crawled upon the sea-floor, but could occasionally swim clumsily or could bury itself in the sand.

Eurypterus appears for the first time in the Lower Silurian, it became abundant in the Upper Silurian and lasted until Permian times. Those found in the coal measures exhibit a tendency towards the development of spiny outgrowths upon the limbs and exoskeleton. This is a phylogerontic characteristic and is indicative of the onset of racial decline. Two modifications of the eurypterid stock reached their extreme development in *Stylonurus* and *Pterygotus* respectively. In the former the limbs became greatly elongated as in the modern spider crabs. In the latter, on the other hand, the first pair of appendages became enormously developed and modified for predatory purposes. In this they were assisted by the marginal position of the eyes, the less clumsy oar-like character of the last limbs, and the broad fin-shaped telson. Some species of *Pterygotus* were as much as five feet long.

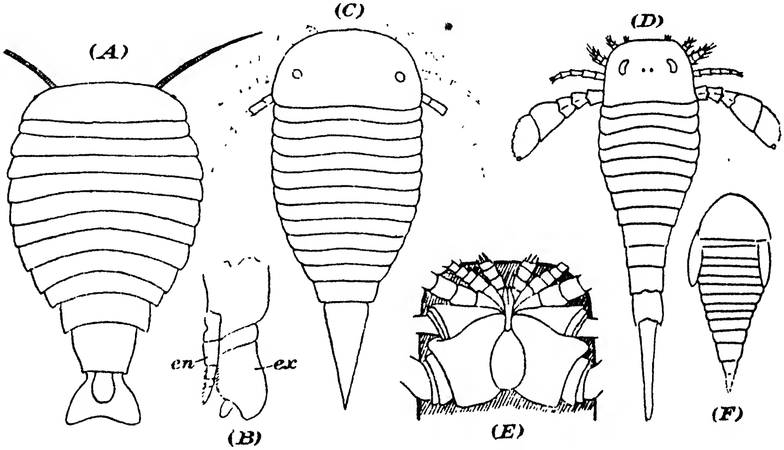


FIG. 206.—Aquatic Arachnids from Palæozoic Rocks.

(*A*) *Sidneya.* (*B*) Thoracic limb of *Sidneya.* (Both after Walcott.) (*C*) *Strabops* (after Clarke and Ruedeman). (*D*) *Eurypterus* (after Clarke and Ruedeman). (*E*) Basal portions of the appendages of *Eurypterus* (after Holm). (*F*) Very young *Eurypterus* in Strabops stage (Clarke and Ruedeman).

en, endopodite. *ex*, exopodite.

Along with the large Eurypterids there lived a smaller and less conspicuous race of merostomes (Fig. 207), which were closely allied to the living *Limulus*. Especially interesting is the genus *Neolimulus* (U. Sil.). This, like *Limulus*, had a large half-moon-shaped carapace and a spiny telson ; but, unlike it, the segments of the trunk region were nine in number and all free. Along with this genus there lived other, but aberrant, representatives of the same stock, *e.g. Hemiaspis*, and *Bunodes*. In the Carboniferous period this race was represented by the *Belinurus* and *Prestwichia* (C. M.). The former bears an even closer resemblance to *Limulus* in general form, but its trunk segments are still free. The latter exhibits a striking similarity to the newly-hatched larva of *Limulus*. *Limulus* itself is known from Triassic times onwards.

Concerning the pre-Silurian history of the Merostomata little is known, but it would seem that as early as Cambrian times the two great stocks described above were already differentiating from one another. *Strabops* (U. Camb.) with its short wide carapace (Fig. 206C), its twelve free segments undifferentiated into meso- and meta-soma, and its tail spine with quadragonal cross-section,

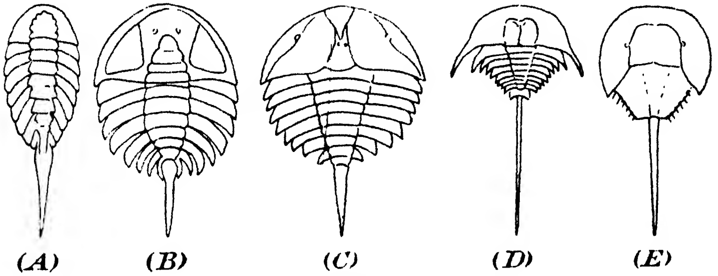


FIG. 207.—Aquatic Arachnids.

(*A*) *Molaria* (after Walcott). (*B*) *Aglaspis* (after Clark). (*C*) *Neolimulus* (after H. Woodward (*D*) *Belinurus* (after H. Woodward). (*E*) *Limulus*.

almost fulfils the requirements of a prototype for the Eurypterida. Similarly *Aglaspis* (U. Camb.) and *Molaria* (M. Camb.) carry the limulid type of organization back to a simpler and more primitive condition (Fig. 207.)

Especial interest attaches to the genus *Sidneya* (M. Camb.). In dorsal aspect (Fig. 206) it is not unlike *Strabops* in the shape of its carapace and in the shape and number of its trunk segments. Its marginal eyes and fin-like tail point to a free-swimming habit. Ventrally, however, it has a wide epistome, antenna-like first limbs, and biramous limbs upon its first nine-trunk segments. In these respects it resembles the trilobites. It would appear, therefore, that this genus occupies a position intermediate between the Arachnida and the Trilobita. With the passage of time the Palæozoic merostomes changed their habitat. Until the close of the Lower Silurian they were marine organisms. During the Upper Silurian they appear to have been equally at home in either salt or in brackish water. From the opening of the Devonian to the close of Permian times they lived under freshwater conditions. This change of habit has been ascribed to the coming of the more powerful and predacious vertebrates.

Air-Breathing Invertebrates.—The conditions of life upon the land are in several respects different from those in the water. This is largely due to the fact that, for the efficient performance of the functions of the body, water in one guise or another must pervade the tissues, and that consequently an animal is a moisture-laden organism. In an aquatic environment the maintenance of this moist condition presents no difficulty. Under terrestrial conditions, however, loss by evaporation is continuous, and unless it is counter-acted or reduced to a minimum life becomes impossible. For slow crawling movements the conditions both on the sea-floor and upon land are the same, but for rapid movements a very different mechanism is required. In the water the weight of the body is borne by the water, but on the land it must be lifted by strongly supported limbs.

Among invertebrates, other than arthropods, the adoption of a land-dwelling, air-breathing habit was very exceptional, *e.g.* earthworms among annelids, slugs and snails among the molluscs. Among the Arthropoda, on the other hand, this habit was adopted with ease by members of every large section of the order, for even under aquatic conditions they already had peculiarities of organization which fitted them for a terrestrial mode of life. Thus the body was completely enveloped in chitin, a material which because it was practically impervious to water prevented evaporation. This same chitinous covering gave to the limbs sufficient rigidity to enable them to bear the weight of the body and lift it clear of obstacles on the ground. It is not surprising, therefore, that the earliest air-breathers known were arthropods. The Crustacea have always been predominantly aquatic, nevertheless to-day there are such creatures as sand-hoppers and land-crabs which are equally at home in both habitats. Woodlice are, however, Crustacea which have advanced yet further and spend their life entirely upon the land.

Air-Breathing Arachnida.—The arachnida in Palæozoic times were likewise predominantly aquatic. It is only necessary to mention scorpions, spiders and mites to indicate that to-day they are predominantly terrestrial. Of these the scorpions are the most primitive. In their general organization they bear a striking resemblance to the Eurypterida. They have a prosoma which bears a pair of eyes dorsally and six pairs of limbs ventrally. The remainder of the body consists of twelve segments having similar proportions to those exhibited by the meso- and meta- soma in the extinct forms. The scorpions differ, however, in that the limbs of the second pair are enlarged and chelate (Fig. 208), whilst those of the hind four pairs are ordinary walking limbs, each provided distally with two small hook-like claws. Again the third to the sixth abdominal segments bear a pair of openings (stigmata) upon the ventral surface. Each of these opens into a cavity that contains a book-like structure which has been derived from gills, and which is used for breathing air. *Palæophonus* (U. Sil.) is one of the earliest and most perfectly known scorpions (Fig. 208). It closely resembles the modern form but its walking legs, like those of *Eurypterus*, consist of a series of short segments which diminish in calibre distally and end in a single claw. Up to the present no indications of stigmata have been found. This fact together with the character of the rocks and fossils with which they are found indicate that it was an aquatic marine form.

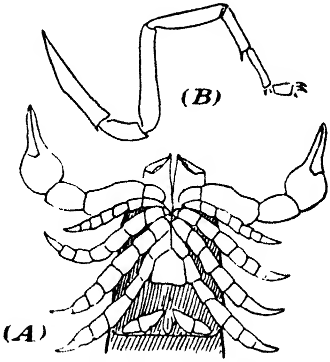


FIG. 208.—Air-breathing Arachnids.
(*A*) Ventral view of the limbs of *Palæophonus* (after Peach). (*B*) Leg of *Scorpion* (Pocock).

The transition to an air-breathing habit on the part of the arachnids was accomplished as early as Carboniferous times, for rocks of this age have yielded forms like *Eoscorpius* which have assumed the detailed characters of modern scorpions. The scorpion may be regarded as a conservative branch of the arachnid stock which under terrestrial conditions has retained the main characteristics of its aquatic ancestors in an unaltered form. In other branches, however, modifications of those characters have taken place and given rise to a wide variety of forms. The main lines of these modifications had already been established as early as the Carboniferous period, which was the period of maximum development of the Arachnida.

The most striking of these modifications are those which affect the abdomen (Fig. 209). Here the distinction into pre- and post-abdominal portions does not usually exist, but on the whole an oval form is assumed. In many, *e.g.* *Eophrynus* (C. M.), as in the Arachnida hitherto considered, the attachment of the abdomen to the head region is broad so that in the body outline there is no distinction between these two regions. It is probably from the family represented by this genus that the modern whip-scorpions (Carb.–Pres.), harvest men (Tert.–Pres), and mites (Tert.–Pres.) have been derived. In other forms, *e.g.* *Anthrolvcosa* (Carb.) and

Protolycosa (Carb.), the body was sharply constricted at the junction of the head and abdomen. It was in such forms that the modern spiders took their origin. The mites and ticks on the one hand, and the spiders on the other appear to have specialized in some respects along parallel lines, for in both the abdomen lost all trace of segmentation by fusion of the segments.

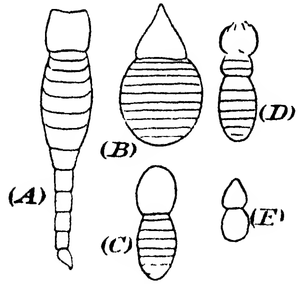


FIG. 209.—Diagrams showing modifications of Body Shape in Air-breathing Arachnids.

(*A*) *Palæophonus.* (*B*) *Eophrynus.* (*C*) *Anthrolycosa.* (*D*) *Protosolfuga.* (*E*) *Spider.*

A third group of forms, *e.g. Protosolfuga* (C. M.), contained a second constriction of the body between the third and the fourth pairs of limbs, thus producing a superficial resemblance to the insects. This condition is still maintained among tropical arachnids by the genus *Galeodes.*

Protacarus, a mite found in the Rhynie chert (M.O.R.S.) of Aberdeen, is the earliest-known air-breathing animal.

INSECTA

Flying Arthropods.—Of all air-breathing Arthropods, the Insecta are the most highly modified for in addition to being adapted for life upon the land they have acquired the art of flying.

An insect's body is typically divided into three parts, head, thorax and abdomen. The head bears four pairs of appendages, the antennæ, which are regarded as the equivalent of the antennules in Crustacea, and three pairs of jaws structurally comparable with the mandibles and maxillæ of the same class. The thorax consists of three segments which in more specialized forms are fused with one another. Each segment bears a pair of walking legs, and there are usually two pairs of limbs upon the two hind segments. The abdomen has as many as ten free segments, usually without limbs, though rudiments of these may be present in some lowly types. The breathing apparatus in insects is tracheal, that is to say it consists of delicate branching tubules. Air enters these through small paired openings on the sides of the body and is carried directly to all the tissues. They also impart to the body a lightness in proportion to the bulk which is a great advantage to a flying organism.

The course taken by development is exceedingly varied in the different types of insects. In some, *e.g.* grasshoppers and cockroaches, the young on hatching out closely resembles the parent;

and though it may not at first have wings, these appear as externally visible structures at an early stage, and increase in size with every ecdysis until the full stature is attained. In others, *e.g.* butterflies, bees and beetles, the young hatch out in the form of a caterpillar or grub presenting but little resemblance to the parent. The developing organism remains in this form until it is fully grown, and though in reality the rudiments of wings are present these are buried or hidden in the substance of the body. With remarkable suddenness the organism passes into a resting stage called the chrysalis. After a more or less prolonged period of time the fully-developed insect with wings and all other organs complete emerges from this with great rapidity.

Between these two extreme types of development of the whole organism there are many grades shown by different insects; but between the two types of wing development, the visible and the hidden respectively, no such gradation is evident, and they may be considered as diagnostic of two great groups of insects called the Exopterygota and the Endopterygota.

The earliest-known insects come from the Carboniferous rocks. They already possessed highly-developed wings, and were capable of sustained flight. Their advanced grade of structure implies a long previous history, extending back to early Devonian or possibly even Silurian times. The ancestral stock of the Insecta must have been of aquatic habit and crustacean affinity, the fancy of the phylogenist therefore turns naturally, and not without reason, to the Trilobita for their ultimate source. In the evolution of the insects a terrestrial stage must have preceded the acquisition of powers of flight. Some clue to the condition during this stage may possibly be supplied by the centipedes, which exhibit fundamental resemblances to them in their detailed anatomy and development.

Though the known insects from the Carboniferous cannot be placed in any of the existing orders they provide conditions from which the latter could have been derived. The most primitive group (Palæodictyoptera) is typically represented by the genus *Stenodictya* (U. Carb.). In addition to having two pairs of fully-formed wings (Fig. 210) it carries small wing-like projections upon the first thoracic and eight of the abdominal segments. These may have served a parachute-like function, as the creature glided through the air. The wings proper were capable only of an up and down movement. The fore and hind wings were of equal size and were strengthened, as in modern insects, by chitinous thickenings (nervures) arranged like the veins of a leaf. The main nervures arose from the base of attachment of the wing. Those in front ran parallel to the anterior margin, those behind diverged outwards to the tips and hinder margin. The central nervures tended to bifurcate and thus give more adequate support to the wing membrane. The intervening spaces were occupied with a meshwork of fine nervules.

Along with the Palæodictyoptera there existed other forms (Fig. 211) which must have been derived from such a stock, but which exhibited modifications of it that tended in the direction of familiar existing types. Thus *Eubleptus* (C. M.) foreshadowed the May flies, *Œdischia* (C. M.), the Locusts; *Eucænus* (C. M.), the cockroaches; and *Meganeura* (C. M.), the dragonflies. This last named was the largest insect known, for it had a stretch of two feet from tip to tip of the wings. Those of the cockroach type, however, exceeded all the others in numbers. This may of course be merely an accident of preservation, for their heavy bodies prevented them from being very efficient fliers, whilst their stout walking limbs fitted them for moving easily through rank and rotting vegetation upon which they fed. With such a habitat they were more likely to be entombed than were the other types. Between the venation of their wings and that of some of the leaves of the coal-measure plants there is a similarity which invites speculation upon mimicry among Palæozoic insects. All the insects referred to above belong to the Endopterygota. With the possible exception of the beetles, the Exopterygota do not appear to have been represented during the Carboniferous period.

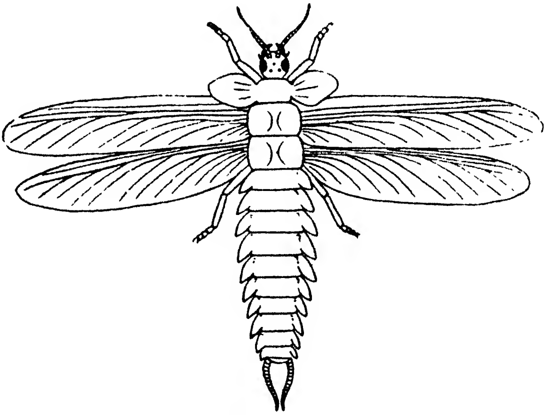


FIG. 210.—*Stenodictya* (after Handlirsch).

The passage from Palæozoic to Mesozoic times was marked by the disappearance of the Palæodictyoptera, and by the assumption of a more typically modern structure with consequent loss of palæodictyopteroid characters by the descendants of the other Carboniferous forms. Nevertheless, these exhibit even at the present day the same multiplicity of nervures and their branches as did the Palæodictyoptera.

In Upper Permian rocks there have been found the earliest-known representatives of exopterygote types in which, on the whole, there was a tendency towards the reduction in numbers and a wider spacing of the nervures. These Permian insects resemble the scorpion flies (*Mecoptera*) and alder flies (*Megaloptera*). Both types attained their maximum development during the Mesozoic. These primitive Permian insects of the alder fly type appear to have given origin to the caddis flies (*Trichoptera*) and the butterflies and moths (*Lepidoptera*). The latter are uncommon in the fossil state, but are known from the Jurassic onwards.

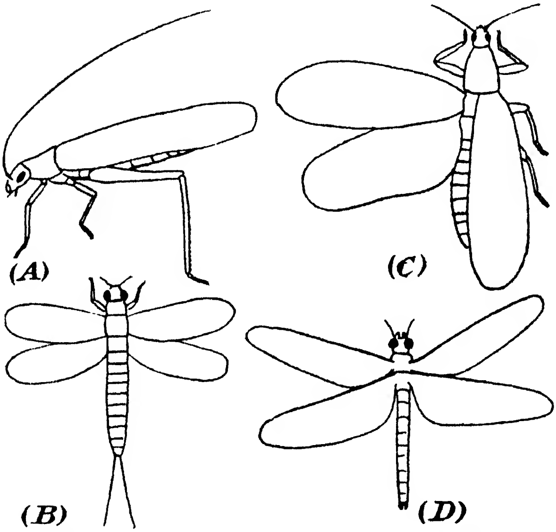


FIG. 211.—Various Carboniferous Insects.

(*A*) *Œdischia.* (*B*) *Eubleptus.* (*C*) *Eucænus.* (All after Handlirsch.) (*D*) *Meganeura.* (Brongniart).

Traces of the existence of bees, ants and flies are likewise known from the Mesozoic rocks; it was not, however, until the Tertiary period that they assumed the same position of importance in the insect world as they hold to-day. Meanwhile, those Exopterygota and the primitive Endopterygota, which were the dominant insects during the Mesozoic era, declined and sank into a position of secondary importance.

SECTION XII

VERTEBRATA

General Characteristics.—The Vertebrata occupy the most conspicuous place among living animals. This is largely because they include the dominant inhabitants of the land, whereas the representatives of other phyla are mainly marine. It is natural, therefore, that man, himself a land animal, should have a more intimate knowledge of the vertebrates than of any other type. The rigid framework or skeleton (Fig. 212) which supports the vertebrate body, unlike that of the Arthropoda, is imbedded in the soft parts. It is built upon a very simple general plan, having one portion which lies along the axis of the body and another which is placed within the limbs. The axial skeleton consists of the skull, with jaw bones, and the vertebral column, which is made up of a large number of separate bones, or vertebræ, serially arranged. Ribs may also be present. There are never more than two pairs of limbs, the skeleton of each consisting of a series of bones supporting the limb itself and of a rigid base of attachment, the limb girdle.

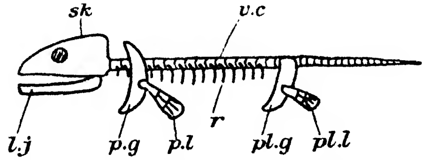


FIG. 212.—Diagram to show the General Plan of Structure of the Vertebrate Skeleton.

v.c, vertebral column. *sk*, skull. *l.j*, lower jaw. *p.g*, pectoral girdle. *p.l*, pectoral limb. *pl.g*, pelvic girdle. *pl.l*, pelvic limb. *r*, rib.

In its soft parts the vertebrate is characterized by the presence of a nervous system lying along the dorsal side of the body and of the axial skeleton (Fig. 214). Anteriorly this is enlarged to form a brain; the remainder is the spinal cord. The alimentary canal and other organs lie ventral to the main axial skeleton. In invertebrates these relationships are reversed. The earliest, like the lowliest living vertebrates, were the fishes (Pisces). These spend the whole of life in water, and breathe by means of gills. Their skins are moist and slimy, and their eggs numerous and small. Owing to the limited food supply in the egg the young hatch early, as larvæ. Undoubted fishes appear upon the scene at least as early as the Middle Ordovician. From the Silurian onwards they have occupied a prominent place in the life of the sea.

During the Devonian some vertebrates had begun to breathe air by means of lungs, and had thus become capable of going up on to the land. These earliest land animals are represented to-day by such creatures as frogs and newts which still retain moist, slimy skins; they lay small and numerous eggs, which, having no efficiently protective covering to prevent them from drying up, must be laid in water or in very damp situations. This limitation causes the animal to spend at least the early portion of its life in the water, hence the name Amphibia for this group of vertebrates. The Amphibia attained the acme of their development, as indicated by the variety of kinds and adaptations, during the Upper Carboniferous, Permian and Trias.

By the close of the Carboniferous period the bondage to an aquatic life was broken by some branches of the stock. In conjunction with certain structural features, this was made possible by a great increase in size, and reduction in the number, of eggs laid by individuals; and by the existence of a covering to each egg which protected it from drying. It thus became possible to deposit the eggs safely in dry and warm situations. There was a long period of incubation (Fig. 213), during which the embryo was nourished from the abundant yolk, and the waste products of the body passed into a bag-like organ called the *Allantois*. The bag itself being richly provided with blood vessels functioned as a respiratory organ. Development advanced to a late stage, so that, when the little creature hatched out, it closely resembled its parents, and was able to breathe and run about almost immediately. This new type of land animal evolved along two main lines represented to-day by the reptiles and birds on one hand, and the mammals on the other.

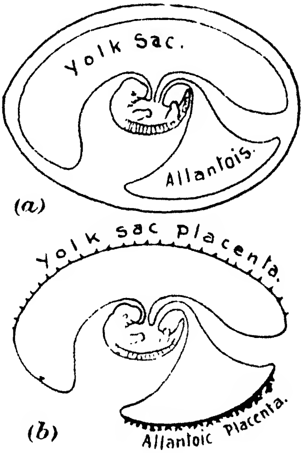


FIG. 213.—Diagram showing Early Stage in the Development of (*a*) a Reptile or Bird, (*b*) a Mammal.

The reptiles on the whole retained their egg-laying habits through all their modifications. Their skin, however, lost its moisture-secreting glands, and thus evaporation from the body surface was reduced to a minimum. Thus equipped for a terrestrial mode of life, they replaced the Amphibia as the dominant land animals and, during the Mesozoic period, exhibited such a wonderful diversity of forms and adaptations that it has come to be spoken of as the Age of reptiles. During Jurassic times this stock gave rise to that perfect flying machine, the Bird. The change was accompanied by the conversion of certain surface projections into feathers. Birds (Aves) are in their heyday at the present time.

In the mammalian line, the skin lost its slimy character, but retained its moisture-producing glands, *i.e.* sweat glands. At the same time it developed a hairy covering, the fur. The earliest mammals, like the lowly Duckmole (*Ornithorhynchus*), which lives in Australia to-day, must have laid eggs. There came a time, however, when some discarded this habit, and retained the egg within the body. The embryo, or fœtus, now derived its nourishment, as in the Kangaroo, partly from the yolk of the unlaid egg, and partly from the parent by means of a skin enveloping the yolk. This skin assumed for a while an intimate relation to tissues of the organ within which the fœtus lay, and thus formed a yolk placenta. Later, as in the majority of living mammals, the formation of the abundant yolk was omitted. The allantois now became the chief organ by means of which the oxygen and nourishment required by the fœtus were obtained from the parent. In other words, this became the *allantoic placenta.* In both kinds of placental mammals the offspring, at birth, presents a close resemblance to the parent, and for a while is further nourished on milk secreted by the mammary glands.

TABLE X.—The main Classificatory Characters and Divisions of Vertebrates and their Order of Appearance in Time.

		ACRANIATA	CRANIATA							
			Agnatha	Gnathostomata						
				Pisces			Terrestrial animals			
				Placodermi	Chondrichthyes	Osteichthyes	Amphibia	Reptilia and Aves	Mammalia	
Present										
Tertiary						Progressive increase of bone with loss of cartilage			Placenta, milk and fur	
Mesozoic								Feathers		MAIN TRENDS OF CHANGE IN VERTEBRATE EVOLUTION ↑
Palaeozoic	Permian and Carboniferous				Progressive increase of cartilage with loss of bone			Large eggs with shells		
	Devonian						Legs and Lungs			
	Silurian			Cartilage bones, Membrane bones, Jaws and Fins						
	Pre-silurian		Cartilaginous skeleton. Cranium							

The points just studied are not ones which are of value to the palæontologist in dealing with fossils. Nevertheless, they form the basis of classification of mammals, and they are associated with skeletal peculiarities by which the systematic position, even of fossils, may be recognized. It is thus possible to state that the Prototheria or egg-laying mammals existed as early as Rhætic times, that the remains of Metatheria, or mammals which do not lay eggs, and have a transitory placenta, are found in the Stonesfield slate. It was not, however, until the close of the Mesozoic era that mammals began to become a prominent item in the land fauna. The Eutheria, which have a placenta for a long time during development, became, during the Tertiary, what the reptiles had been during the Mesozoic. They have since declined to some extent, but are nevertheless still the dominant forms on the land.

The General History of the Vertebrate Skeleton.—The vertebrate skeleton, like that of the Arthropoda, reflects the structure of the organism as a whole in such detail that its evolution provides a reliable guide to that of the vertebrates. A portion of it occupies a superficial position below the skin ; this is the outer skeleton or exoskeleton. The remainder is deeply seated, and is called the inner skeleton or endoskeleton.

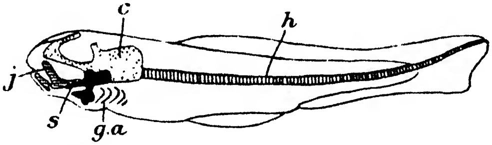


FIG. 214.—Diagram of the Skeleton in a very young Vertebrate (Stickleback). *h*, notochord. *c*, cranium (dotted). *j*, jaws (lined). *s*, suspending apparatus for jaws (black). *g.a*, gill arches.

In the development of the individual the endoskeleton consists at the outset of an elastic rod (notochord), which extends along the axis of the body for practically its whole length. This condition persists on into adult life to-day in the small fish, *Amphioxus*. Animals at the same lowly grade must have existed in all ages back to, or even earlier than, the Silurian, but their fossils have not been found. As development proceeds there is laid around the notochord the foundation of the main axial skeleton. This is made of cartilage, which resembles gristle in appearance. Under the microscope (Fig. 215) it is seen to consist of isolated cells imbedded in a structureless matrix. It decomposes comparatively rapidly, and for this reason rarely occurs in the fossil state. Not infrequently lime is deposited in the matrix. The cartilage is then said to be calcified, and in this state is often preserved.

The cartilaginous skeleton appears in the form of rings, called centra, around the notochord. From these paired outgrowths arise; those on the dorsal side unite to form the neural arch which encloses the spinal cord, while those on the ventral side in the tail region form the hæmal arch which encloses blood vessels. Long median processes may arise on the crests of the arches; these are the neural and hæmal spines. In the head region (Fig. 214) the cartilage first appears as a pair of stout rods lying alongside of and projecting beyond the anterior end of the notochord. From these a framework of cartilage grows upwards around the brain, and forms the brain case (cranium), hence the name *Craniata* for these vertebrates, as opposed to *Acraniata*, which like *Amphioxus* possess only a notochord.

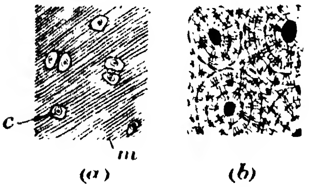


FIG. 215.—Diagrammatic Sections of (*a*) Cartilage, (*b*) Bone. *m*, structureless matrix. *c*, cell.

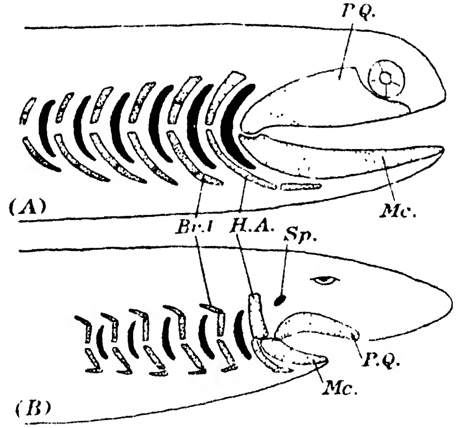


FIG. 216.—Visceral Head Skeleton in relation to the Mouth and Gill Clefts. (*A*) *Acanthodes* (adapted from Watson). (*B*) *Scyllium*. Dotted areas = skeleton. Black areas = gill clefts. Br. branchial arch. H.A. hyoid arch. Mc. Meckel's cartilage. P.Q. palatoquadrate. Sp. spiracle.

Beneath the cranium another framework forms around the mouth cavity and throat. This, the visceral head skeleton, is intimately associated with certain openings, the gill clefts, by which in the adult fish water that has entered the mouth escapes to the exterior once more. The fleshy walls of these clefts, which are filled and richly supplied with blood vessels, function as gills. The gill clefts, of which there are usually four or five pairs, lie behind the mouth (Fig. 216). In sharks and their allies another cleft, reduced to a small hole known as the *spiracle* is situated further forward below the eye. Behind each cleft there is a branchial arch made up of a more or less vertical series of four cartilages. That behind the spiracle is the hyoid arch. It is of stouter build and consists of only two pieces. The upper, the *hyomandibular*, is attached to the cranium above and to the hinder end of the jaws below. It thus serves the purposes of a *suspensorium* or suspensory apparatus for the jaws. These also consist of two stout cartilages nearly horizontally placed ; the upper is called the *palatoquadrate* ; the lower, *Meckel's cartilage*.

In *Acanthodes*, and its relatives (Late Sil.–Dev.) the hyoid arch presents a closer resemblance to a branchial arch and is separated from the jaws by a fully developed gill cleft, the homologue of the spiracle. This condition suggests that in later types the mouth has extended backwards and, by encroaching on the hyoid cleft, has reduced it to a vestigeal condition seen in the spiracle. At the same time the jaws have become linked up with the hyoid arch.

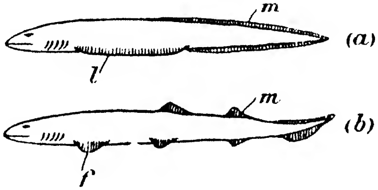


Fig. 217.—Diagram of Hypothetical Fish with (*a*) continuous lateral Finfold, (*b*) with paired Fins.

l, lateral finfold. *f*, paired fins. *m*, median fins. (*a*, After Balfour.)

In the Upper Silurian genus *Kieraspis* the mouth is small and without jaws. Behind it there are nine pairs of gill openings. In this fish the head is enclosed in a bony shield which also incorporates the cranium. Within this there are impressions made by the brain, nerves and other structures. A detailed study of these shows that the first pair of gill openings, and possibly also the second, lie in front of the hyoid cleft. These and other facts support the view that the primitive mouth evolved by extending backwards along the side of the head and by the modification of the anterior branchial arches into jaws. This extension involved the suppression of the front gill pouches and clefts. Thus the jawless fishes, the *Agnatha*, gave rise to the jawed fishes or *Gnathostomata*. Among the latter the *Placodermi* which include *Acanthodes* and its allies represents a more primitive grade of structure than that seen in all other fishes.

The limbs in lower vertebrates or fishes are fins (Fig. 217*b*). They consist of folds of skin supported in varying proportions by elements derived from both the outer and the inner skeleton. One fold, or series of folds, lies in the median plane and forms the median fin. Embryological evidence suggests that this fold originally extended continuously (Fig. 217*a*) along the dorsal line round the tip of the tail, and forward along the ventral line to the trunk region; and that at this point it was replaced by a pair of fin folds which continued, one on either side of the trunk, and ended just behind the head. Anteriorly and posteriorly each of these lateral fin folds then enlarged (Fig. 218*a*, *b*, *c*), but at the same time the central portion became reduced, and ultimately suppressed. Thus the two pairs of fins came into being. The palæontological evidence concerning the origin of paired limbs is very fragmentary, nevertheless much of it finds its simplest explanation in this lateral finfold theory.

With the adoption of the terrestrial mode of life the paired limbs became modified into legs. In these the skeleton consists of three sections; upper and middle which were lever-like and arranged so as to enable the animal to lift its body; and a spreading terminal portion, consisting of five digits, which rested flat upon the ground. The transitional stages from the fin condition to this pentadactyle walking limb were probably passed through during late Devonian, and the change was completed before Upper Carboniferous time.

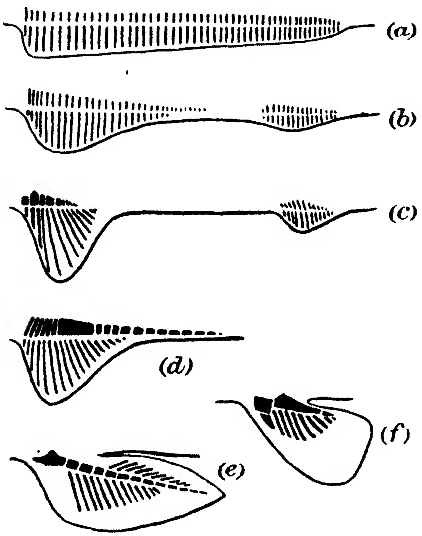


FIG. 218.—Diagram illustrating Phases in Evolution of paired Fins in Cartilaginous Fishes.

(*a*) Hypothetical—continuous lateral finfold. (*b*) Hypothetical—reduction of fold where the body bends laterally, enlargement at extremities. (*c*) Fins of *Cladoselache*. (*d*) Pect. fin of *Cladodus*. (*e*) Pect. fin of *Pleuracanthus*. (*f*) Pect. fin of modern shark.

In the early stages of vertebrate evolution, as in development, cartilage was probably the only material used in building up the endoskeleton, and it became the only material in an important section of fishes, the Chondrichthyes or cartilaginous fishes. These have persisted as an important group until the present day. In the acanthodian fishes, which were among the earliest gnathostomes, much of the cartilaginous endoskeleton of the head was already converted into bone. Now bone is as superior to cartilage, as iron is to wood, because for a given bulk it has much greater strength. The process of bone formation (ossification) differs from calcification in that the cartilage is gradually replaced and ultimately disappears. Nevertheless, such bone is called cartilage bone, because it is preformed in cartilage. It differs from cartilage, however, in the presence of a complicated system of canals (Fig. 215) and canaliculi along which nutritive fluids are conveyed to the most deep-seated portions. Bone resists decomposition for a much longer time than cartilage, and is, therefore, more frequently preserved in the fossil state. In Devonian fishes, as in early development, bone was little more than a superficial covering to the cartilage, but in some Carboniferous fishes it almost wholly replaced the cartilage. Thus the evolution of land animals, which require a more rigid skeleton, became a possibility.

During the Silurian and Devonian the exoskeleton manifested every gradation in development (Figs. 222, 223) from a continuous bony armour, enclosing the head and part of the trunk, through a covering made up of small bones or of placoid scales (Fig. 219) consisting of dentine coated with hard shiny enamel, to a condition in which it was quite absent. In many, even of the early fishes, plates of bone were formed by the ossification of fibrous tissue in the skin. Over the trunk and tail these remained small and formed a flexible covering of scales, but on the head they fused together and formed larger plates. These plates are called *membrane bones*. In later fishes the scaly covering of the body was always an important feature, but in land animals only a few membrane bones which became related to the endoskeleton of limb girdles and head remained.

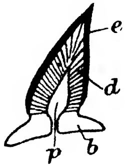


FIG. 219.—Diagrammatic section of Placoid Scale.

e, enamel. *d*, dentine. *p*, pulp cavity. *b*, basal plate.

PISCES

Form and Function in Fishes.—The normal shape for a fish is that of a spindle slightly flattened from side to side (Fig. 220), a form which is eminently adapted for slipping through water without producing those eddies which are the chief hindrance to rapid progress. The stoutest and most rigid portion of the spindle is situated anteriorly, where the head and trunk with the vital organs are placed. The front end is bluntly conical and acts as a cut-water. The elongated hinder portion, or tail, of the spindle, tapers gently, is pliable, and well suited to its function as the chief or only organ of propulsion.

When a fish of the form just described swims at full speed it drives itself forward by a rapid sculling movement of the tail, aided by the median fins which the tail bears. All the other fins either lie flat against the body, or have their margins projecting slightly as keels. It is evident, therefore, that normally they do not act as propelling organs. Directly the fish attempts to slow down or to execute a turning motion these fins are brought into action. In the former case the paired fins are extended with their planes athwart the line of movement, thus producing eddies and acting as brakes (Fig. 220). In turning, however, only those fins are extended which lie on the side towards which the fish desires to wheel. At the same time the dorsal fin is erected to its fullest extent, and thus, by increasing the depth of the body, provides a stable fulcrum round which the whole body rotates.

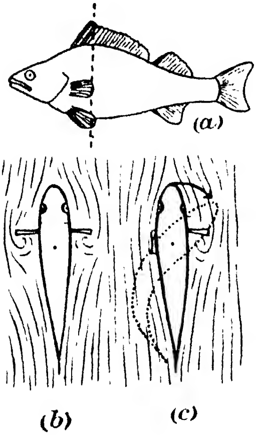


FIG. 220.—Diagrams illustrating the Mechanics of Swimming.

(*a*) Side view of fish showing axis of turning, and attitude of the dorsal fin when turning takes place. (*b*) Dorsal view of fish with paired fins extended to act as brakes; n.b. swirl behind fins. (*c*) Dorsal view of fish with one fin extended to enable fish to turn sharply to one side.

The function of the paired fin has not always been that of a brake, on the contrary it has varied according to the stage of evolution attained. If the continuous finfold stage was ever passed through that fold probably helped propulsion by executing an undulatory movement similar to that of the long fins in some modern fishes. The paired fin at first had a broad base parallel to the axis of the body, and could only have functioned as a keel (Fig. 218*c*, *d*.). Later the fin became freed by elongating outwards and shortening along its base from behind forwards. It was now able to act also as a lateral rudder (cp. "aileron" in aerodynamics) enabling the fish to rise and sink and even to turn over on to its back (cp. shark). By a further narrowing of the base, or by the rotation of this into a vertical plane (Fig. 220*a*), it became possible for the fish to use the fin as a brake.

The form of body described above is that of a fish that spends most of its time swimming freely to and fro in the open water. But other shapes corresponding to other conditions of life are assumed (Fig. 221). Thus fishes which remain stationary in the water, basking in the sunshine near the surface (*e.g.* Perch, Bream) tend to develop a compressed and elevated form. This reaches its extreme development in many small fishes of tropical seas, which flit like butterflies over flowery expanses of coral polypes and sea mosses. Others, like the Pike, lie in wait hidden by weeds, and then suddenly dart forth with terrific velocity upon their prey. The form of body is long and arrow-shaped, and the powerful stroke that is needed for developing speed so rapidly is largely due to the close association of median with tail fins. A more common habit is that of the Angler fish and Skate which keep close to and lie upon the sea-floor. In such cases the body becomes depressed and expanded, and the eyes are situated well on to the dorsal side of the head; the tail also becomes subject to reduction.

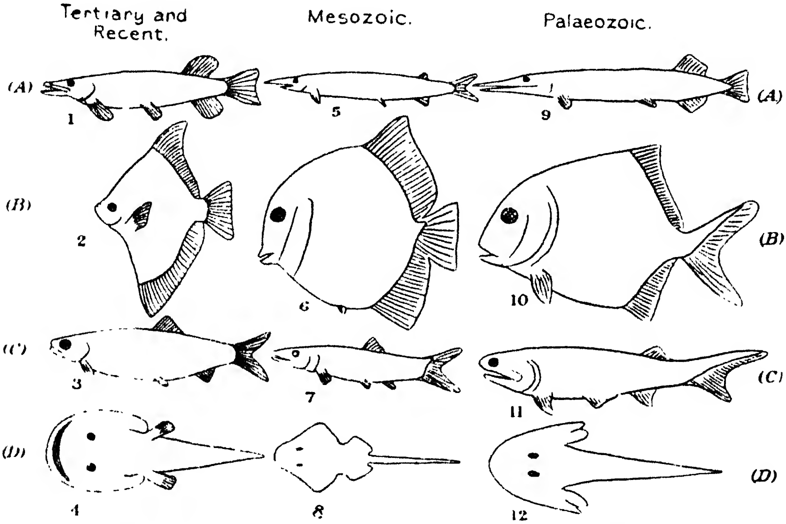


FIG. 221.—Diagrams showing the Repetition of the same Adaptational Forms in Fishes belonging to different Periods.

Those in the same vertical column belong to the same period. Those in the same horizontal line have the same adaptational form but are not related to one another.

(*A*) Arrow-shaped fish. (*B*) Deep bodied fish. (*C*) Normally-shaped fish. (*D*) Depressed fishes.

1, *Esox* (Pike). 2, *Psettus*. 3, *Leptolepus*. 4, *Chirolophus* (angler fish). 5, *Aspidorhynchus*. 6, *Pycnodus*. 7, *Eugnathus*. 8, *Squatina*. 9, *Belonorhynchus*. 10, *Platysomus*. 11, *Palæoniscus*. 12, *Cephalaspis*.

With the passage of time one evolutionary type of fish rose to predominance, declined and was succeeded by another. Yet each type in its turn exhibited the same adaptational forms, for though the living organism evolved, the physical conditions of their surroundings remained practically constant down through the ages.

The Earliest Fishes.—Rocks of late Silurian and Devonian ages have yielded remains of a rich and very varied fish fauna which implies the existence of allied forms in yet earlier times. The Agnatha, which make up an important section of that fauna, were, for the most part, small fish only a few inches long which exhibited a wide range of adaptational forms. They owe their preservation largely to the possession of a well-developed exoskeleton (Figs. 222,

224) and on that account are often spoken of collectively as the *Ostracodermi*.

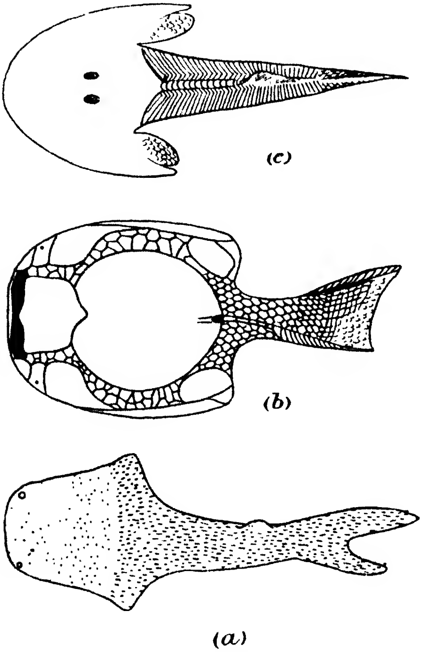


FIG. 222.—Ostracoderms.

(*a*) *Thelodus* (U. Silurian. Lanarkshire after Traquair). (*b*) *Drepanaspis* (U. Devon. Rhein. Prussia after Traquair). (*c*) *Cephalaspis* (L. Devon. Forfar, adapted from Lankester).

Kieraspis (U. Sil.), *Cephalaspis* (Dev.), and their allies, had a depressed form with the head completely enclosed in a rigid bony shield. The mouth and gill openings were on the underside and the eyes lay close together in the middle of the upper surface. The remainder of the body was covered with scale-like plates. The tail was tilted upwards (heterocercal) with a fin along its lower margin. Pectoral fins were present.

Pterolepis represents a group of laterally compressed free-swimming forms closely allied to *Cephalaspis*. The head was enclosed in numerous small plates and the tail was tilted downwards (hypocercal) with the fin along its upper margin.

Pteraspis and *Drepanaspis* belong to another group with the head and front part of the trunk depressed (Fig. 223*a*) and covered above and below with large plates consisting of an outer layer of dentine, a middle zone pierced by canals, and an inner pearly lining. As distinct from *Cephalaspis* true bone cells were absent. The mouth was ventral, but the gill openings were arranged along the sides and hidden from view by long lateral plates. The rest of the body was laterally compressed and covered with scales. The tail was hypocercal.

Thelodus belongs to a small and little-known group having a body form not unlike that of the cephalaspids. The eyes were far apart and situated along the front margin of the head. The whole body was armed with numerous tiny stud-shaped scales with an essentially placoid structure. Examples of these have long been known from the Ludlow bone beds.

Towards the close of the Devonian the Agnatha declined rapidly and so far as fossil evidence is available seem to have become extinct. The present-day Lamprey (*Petromyzon*) and its marine relatives prove that a small section survived. The Gnathostomata, on the other hand, underwent a variety of profound modifications and became the forerunners of that vast multitude of vertebrates which to-day dominate water, land and air.

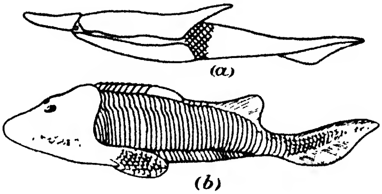


FIG. 223.—(*a*) *Pteraspis*. (*b*) *Cephalaspis*. (After Brit. Mus. Cat.)

Among these early gnathostomes the *Placodermi* (*Aphetohyoidea*) are of peculiar interest because, as already seen, they retain a very primitive condition of the jaw apparatus and the hyoid arch. Apart from this they present an even greater range of adaptive modification than did the Ostracoderms.

The normal type of adaptational form is presented by those predaceous types formerly known as the acanthodian sharks (Fig. 230) which ranged from the Upper Silurian to the Permian. It is interesting to note that in them the endoskeleton of the head was extensively ossified and the exoskeleton of all parts of the body consisted of small closely packed rhomboidal plates. Both median and paired fins were membranous and were strengthened along their anterior margins by stout spines. In *Climatius* (U. Sil.–Dev.) a series of such spines extended from the pectoral to the pelvic regions and supplied the nearest approach to a continuous lateral finfold among fossils. In *Acanthodes* (U. Dev.–Perm.) itself all the intermediate spines have gone.

The *Arthrodira* (Dev.) had a stout armour. That enclosing the head was not continuous with the trunk but connected with this by a peg and socket articulation situated on either side of the body.

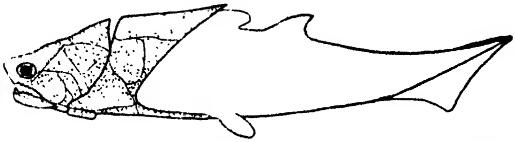


FIG. 224.—Restoration of *Coccosteus decipiens* (O.R.S.). Modified after Jaekel and Woodward.

As a rule the pectoral limbs were absent, and the pelvic greatly reduced. In some, *e.g.* *Coccosteus* (Fig. 224), the bones of this armour were sculptured and decorated with enamel. In others, *e.g.* *Dinichthys*, which sometimes grew to gigantic proportions, the bones had apparently sunk beneath the skin, and had lost both external marking and enamel. Nothing is known of the *Arthrodira* before the Devonian, and at the close of that period they disappeared entirely.

Pterichthys (M. Dev.) and *Bothriolepis* (U. Dev.) (Fig. 225) represent another type in which the armature which encloses the fore part of the body consists of a number of large symmetrically-arranged plates and has attached to it a pair of armoured appendages of unknown function. In the earlier genus the rest of the body is covered with rounded overlapping scales. In the later the scaly covering seems to have degenerated and disappeared, leaving the trunk and tail naked. Thus at this early date and in this lowly ostracoderm type, the exoskeleton exhibits practically all the modifications seen in later branches of the piscine stock.

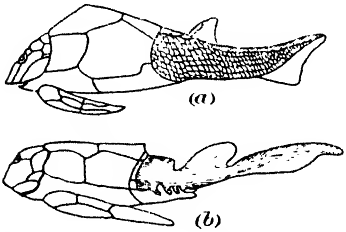


FIG. 225.—(*a*) *Pterichthys*, Devonian (after Traquair). (*b*) *Bothriolepsis*, U. Devonian 'after Patten).

At the other extreme to the forms just described lies the tiny naked fish *Palæospondylus* (M.O.R.S.) (Fig. 226). This fish possessed a cranium, a visceral skeleton and possibly jaws. It also had a vertebral column with indications of calcified vertebræ. Neural and hæmal arches were present, and in the tail region these were prolonged into median spines. No traces of teeth or of paired limbs have been found.

The other groups occupied a much less prominent place in the fauna of Devonian times than those just considered. Since, however, they open new and distinct chapters of piscine history that range far across subsequent geological ages, they may be most conveniently dealt with in separate sections. They fall naturally into two main divisions, the cartilaginous fishes or *Chondrichthyes* and the bony fishes or *Osteichthyes*.

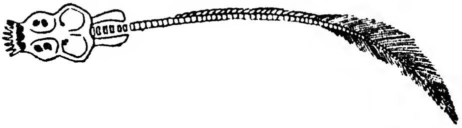


FIG. 226.—*Palæospondylus* (after Traquair). O.R.S.

Sharks and their Predecessors (Elasmobranchii or Chondrichthyes).—Among familiar living fishes Sharks (Euselachii) represent the boneless type whose endoskeleton consists of cartilage, and exoskeleton of placoid scales. They are strong swimmers and are generally of normal shape (Fig. 227) with the head slightly depressed. The tail is long and slender. Both pectoral and pelvic fins are present, but being only slightly movable they function mainly as "ailerons." All the fins are covered with placoid scales (Fig. 240*a*) and supported by numerous slender horny rays called ceratotrichs.

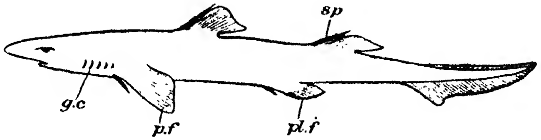


FIG. 227.—Side View of a Shark.
g.c, gill clefts. *p.f*, pectoral fin. *pl.f*, plevic fin. *sp*. fin spine.

Skates and Rays (Fig. 228*c*) are shark-like fish which have assumed a depressed adaptational form of body. The pectoral fins are enormously enlarged, and may extend as far forwards as the snout, and as far backwards as the hind fins. The fish propels itself by an undulatory movement of the pectoral fin margin. The tail, being no longer the chief organ of propulsion, is greatly reduced. A form of body intermediate between that of the sharks and that of the skates is exhibited by *Squatina* (Lithographic limestone, U. Jur.).

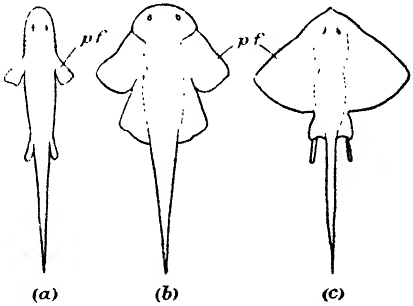


FIG. 228.—Diagram comparing Shark with Ray.
(*a*) Shark. (*b*) Monkfish. (*c*) Ray.
Dotted line = outline of body.

Among cartilaginous fishes the relationship of the jaws to the cranium (Fig. 229) constitutes a classificatory feature of great importance. The upper jaw consists of a pair of stout cartilages called the *palatoquadrates*. The lower jaw consists of a similar pair known as Meckel's cartilages. In the majority of Euselachii the articular ends of these cartilages are linked to the cranium by the upper or ***hyomandibular*** portion of the first gill arch. This method of suspension of the jaws is described as ***hyostylic*** (Fig. 229*a*). In one small group of cartilaginous fishes (Chimæroids) the upper jaw cartilages are fused with the base of the skull along their whole length (Fig. 229*b*). In this case the lower jaw is articulated only with the upper, and the hyomandibular has no share in its suspension. This is described as ***autostylic***. In the primitive living shark, *Notidanus*, the upper jaw both articulates directly with the cranium (Fig. 229*c*) and receives support from the hyomandibular. This is described as the ***amphistylic*** condition. Fishes having the hyostylic type of suspensorium existed in Palæozoic times, but they did not become a prominent constituent of the fauna until the Mesozoic era. To-day they are dominant. On the other hand the amphistylic type, which to-day is exhibited by only a few forms such as *Notidanus* and *Cestracion* (Port Jackson Shark), was supreme in Palæozoic times.

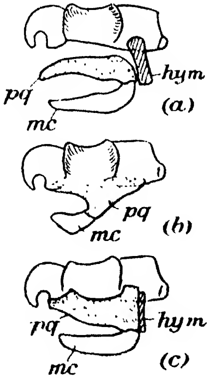


FIG. 229.—Diagrams showing Mode of Suspension of Jaws in Fishes.

(*a*) Hyostylic. (*b*) Autostylic. (*c*) Amphistylic. Palatoquadrate (dotted), *pq*. Hyomandibular (lined), *hym*. Meckel's cartilage, *mc*.

The paired fins furnish a second important basis of classification. In the Palæozoic sharks they had not yet settled down to that almost fixed plan of structure which characterized the Mesozoic and later boneless fishes.

In *Cladoselache* (U. Dev., Figs. 218*c*, 231*a*) the paired fins were lobe-shaped keels, broad based and supported by a series of parallel cartilaginous rods or radials articulating with a similar series of rods, the basals, imbedded in the body walls. These fins exhibit just that structure which might be expected in isolated and enlarged portions of what was once a continuous finfold. *Cladodus* (Fig. 218*d*) had similar fins. In the genus, *Pleuracanthus* (Carb.-Perm., Fig. 231*b*), the fin with its basals seems to have been rotated outwards from the body wall (Fig. 218*e*), thus producing a more movable narrow based fin. In the pelvic fin cartilaginous radials were borne only on the outer or anterior margin of the basal series, but in the pectoral fin some radials exist on the posterior margin, thus producing a biserial arrangement. In the Euselachii (Jura.-Pres., Fig. 218*f*) the paired fins settled down to a uniserial condition like that of the pelvic of *Pleuracanthus*. In this case, however, the series of basal cartilages is represented by one long stout cartilage.

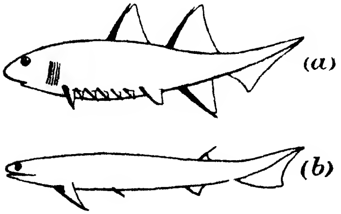


FIG. 230.—Acanthodian Sharks.

(*a*) *Climatius* (after Woodward. Brit. Mus. Guide). (*b*) *Acanthodes* (after Fritsch).

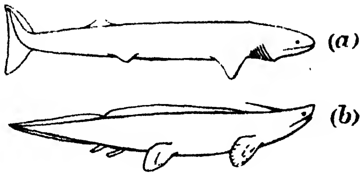


FIG. 231.—Other Palæozoic Sharks.

(*a*) *Cladoselache* (U. Devonian, adapted from Dean). (*b*) *Pleuracanthus* (L. Permian, adapted from Fritsch).

In all types up to early Mesozoic times the axial skeleton consisted of a continuous, unconstricted notochord bearing both neural and hæmal arches. In *Pleuracanthus* it extended to the tip of the tail without any marked upward bend posteriorly. This is the condition of tail described as *diphycercal.* In other selachians there was a more or less well-developed upward tilt, which was much exaggerated in *Cladoselache* (Fig. 231*a*). This feature, together with the enlarged fin lobe in the ventral side, characterizes the heterocercal condition.

Among Liassic selachians, *e.g. Palæospinax*, ring-like cartilaginous vertebræ (cp. Fig. 243) existed which by inward growth had constricted the notochord. The innermost layer of the vertebra was calcified in the form of an hour-glass shaped cylinder, a condition described as cyclospondylous. In late Jurassic and Cretaceous times this was strengthened by the calcification of other portions of the cartilaginous vertebræ by a series either of concentric cylinders, or of radially arranged longitudinal laminæ.

The Euselachii have attained their acme to-day and include some of the largest and most powerful of fishes.

Boneless Fishes. Teeth and Spines.—A covering of placoid scales has characterized the boneless fishes from the earliest times.

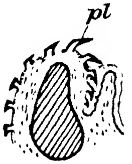


FIG. 232.—Diagrammatic section through the Jaw of the Dogfish, showing the Position of the Teeth (adapted from Goodrich).

pl, placoid scale used as a tooth.

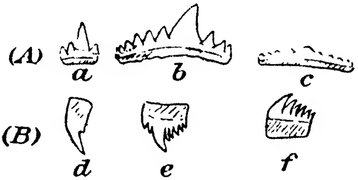


FIG. 233.—(*A*) *Synechodus* (U. Cret). (After Brit. Mus. Cat.)

a, Teeth near the middle line. *b*, Teeth some distance from the middle line. *c*, Back teeth.

(*B*) *Notidanus* (adapted from Gunther).

d, Upper front teeth from near the middle line. *e*, Upper front teeth some distance from the middle line. *f*, Lower front teeth some distance from the middle line.

In living selachians the skin passes over the margin to the inside of the mouth (Fig. 232), and the scales which cover it function as teeth. Thus the normal teeth of sharks were always merely enlarged placoid scales, varying in pattern from those with a variable number of small points or cusps (*Notidanus*), through those with one large central and a few lateral cusps (*Synechodus*, *Odontaspis*, Cret.-Tert.), to those which consisted of one large cusp without laterals

(*Oxyrhina*). Such slightly modified teeth occur commonly as fossils from the Jurassic onwards.

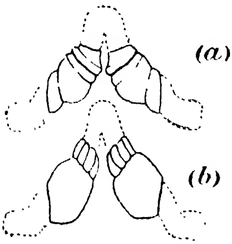


FIG. 234.—Carboniferous Teeth.

(*a*) *Cochliodus*, (*b*) *Psephodus* (adapted from Woodward). Dotted line represents the probable outline of the jaws, cp. *Cestracion*.

Within the limits of one jaw the teeth may show a considerable difference. Those near the middle line and in front may be pointed and prehensile, whilst those upon the hinder portions of the jaw tend to be blunt and to develop broad flat crowns for crushing (Fig. 236*a*). In some predaceous sharks (*Notidanus*, Jur.–Pres.) the chief object is the seizure and swallowing of active prey. In such the hind teeth are small and the front are large and trenchant (Fig. 233*b*). Other sharks gather food from the floor of the sea in the form of shell fish. These have the front teeth strong and sharp (Fig. 236*a*), and adapted for tearing the attached food from rocks and stones. The hind teeth, however, assume a broad surface more suited for cracking and crushing shells (*Cestracion*, Jur.–Pres.). In *Ptychodus* (Cret.) (Fig. 236*a*) and *Myliobatis* (Fig. 235) (Tert.–Rec.) another type of dentition occurs, in which the front teeth are most specialized for crushing, and the hind teeth are reduced.

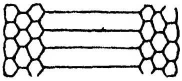


FIG. 235.—*Myliobatis* (adapted from Owen).

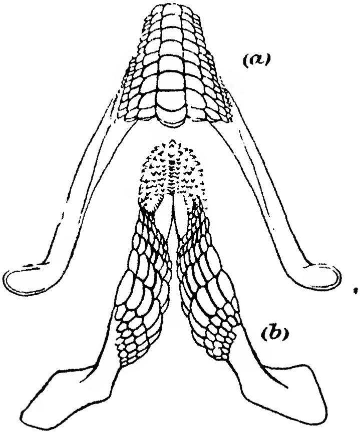


FIG. 236.—Lower Jaws of Sharks.

(*a*) *Ptychodus*, Lower Jaw (Cretaceous (adapted rom Woodward). (*b*) *Cestracion*, Upper Jaw (adapted from Owen).

The Carboniferous *Bradyodonti* exhibit parallel modifications to the above but sometimes carried to a further extreme. In *Cochliodus* and *Psephodus* (Fig. 234) the lateral teeth were fused together into large crushing plates. In *Edestus* the piercing teeth of the front middle line were enormously developed. The teeth of *Psammodus* were more comparable with those of *Myliobatis*.

Spines are of two main kinds, one associated with fins and the other occurring upon the head. The fin spines are situated at the front margin of the fins (Fig. 227 *sp.*) and serve the purposes of a cut-water. Those belonging to the median fins are bilaterally symmetrical, those of the paired fins asymmetrical. It is not improbable that they originated by the fusion of scales. This may account for the tuberculations on the surface of some spines (Fig. 237). Head spines are less common. Being medianly placed they are usually symmetrical. On the whole they have more excrescences, and are more irregular in outline than the fin spines.

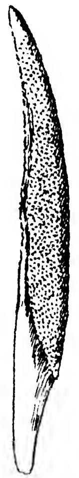


FIG. 237.—Fish Spine. *Asteracanthus* spine, Oxfordian.

Structural Changes in Fishes with Bone (Osteichthyes.)—In any given evolutionary series of Osteichthyes the earlier form of scale is the rhomboidal (Fig. 238*a*). Gradually the hinder and lower margins of the scales extend over adjoining scales until only a quarter of each scale is visible. Meanwhile the scale becomes thinner and assumes a rounded outline, it then being described as cycloidal (Fig. 238*b*). On the whole the rhomboidal shape predominates during the Palæozoic and early Mesozoic, and the cycloidal during the Cretaceous and later periods.

The minute structure of scales changes much more slowly than their shape, and each stage therefore is characteristic of a larger group, and a longer period of time (Fig. 239). The majority of the Devonian, and many of the Carboniferous scales, belong to what is called the cosmoid type (Fig. 239*a*). These consisted of an inner laminated bony layer similar to the base of a placoid scale; a middle spongy, or cancellous, layer; and an outer layer of cosmine in the form of denticles of dentine covered with enamel. They grew only by additions to the margins and inner surface. In some Carboniferous and the majority of Permian and early Mesozoic scales the layer of dentine became insignificant, and was buried under a fourth layer consisting of a continuous coating of an enamel-like substance called ganoine. This type, the true ganoid scale, grew by addition to the outer surface as well as to the margins and inner face.

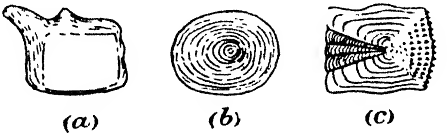

(*a*) (*b*) (*c*)

FIG. 238.—Types of Scales.
(*a*) Rhombic scale with processes which underlie adjoining scales. (*b*) Cycloid scale. (*c*) Ctenoid scale.

In later Mesozoic times the ganoine disappeared (Fig. 239*d*) along with the dentinal and cancellous layers. Thus in the majority of scales of this and subsequent periods only a thin bony plate remained. Such was the constitution of the true cycloidal scale. In certain highly specialized fishes the exposed surface of this scale is armed with denticles and thus the ctenoid scale (Fig. 238*c*) was produced.

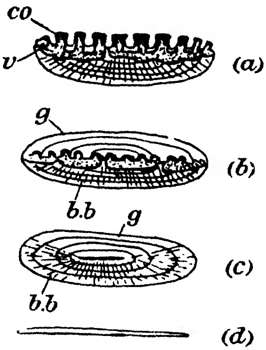
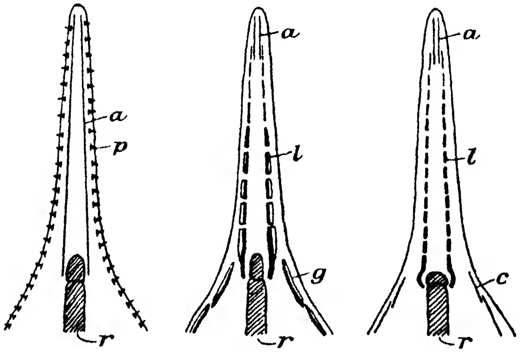


FIG. 239.—Diagrammatic Sections through different Types of Scales (adapted after Goodrich).

(*a*) Cosmoid scale. (*b*) Ganoid scale—with cosmine. (*c*) Ganoid scale—without cosmine. (*d*) Cycloid scale.

co, cosmine. *v*, vascular canals—cancellous layer. *g*, ganoine. *b.b*, bony base.



(*a*) (*b*) (*c*)

FIG. 240.—Diagrammatic Sections through the Dorsal Fin of various Fishes (after Goodrich).

(*a*) *Scyllium*. (*b*) *Lepidosteus*. (*c*) *Teleost*.

r, Endoskeletal fin ray, radial. *a*, ceratotrich. *l*, lepidotrich. *c*, cycloid scale. *p*, placoid scale. *g*, ganoid scale.

In the head region the scaly covering had already become modified, probably by fusion, to form a helmet of bony plates as early as the Devonian. These bones usually had enamelled and sculptured surfaces as long as they lay actually at the surface of the body. There was, however, a tendency, especially marked in late Mesozoic times, for the bones to sink in from the surface and to lose their enamel and ornamentation. In the Osteichthyes both the endoskeleton and the horny dermal rays or *ceratotrichs* played a gradually diminishing part in the support of the fins. On the other hand the minute scales which covered them increased in importance. Already in Devonian times these scales had assumed a lineal arrangement, and each linear series formed with its counterpart of the opposite side a jointed fin ray or *lepidotrich* (Fig. 240*b*). During the Devonian and Carboniferous period the number of lepidotrichs or scaly dermal rays in the fin usually exceeded the number of endoskeletal rays. In a few cases, however, the number was the same; a condition which became predominant in post-Carboniferous times.

The tail fin in its simplest or diphycercal condition (Fig. 241*a*) was divided almost equally into upper and lower portions by the tapering end of the body. It seems, however (cp. Fig. 252), to have arisen generally by degenerative change. In the *heterocercal* condition (Fig. 241*b*) which was dominant during the Palæozoic, the tail was tilted slightly upwards, the upper lobe of the fin was absent and the lower lobe enlarged. Along many lines of descent progressive change continued in the same direction; the tilted-up body portion became increasingly upturned, and much reduced; the ventral lobe became relatively much larger. This, the *hemiheterocercal* condition (Fig. 241*c*), arose during the Permian, and was common up to the close of the Jurassic, when the *homocercal* condition arose (Fig. 241*d*). In it the tilted end of the body became reduced to minute proportions, and the tail fin consisted almost exclusively of the morphological ventral lobe. During the Cretaceous period this condition came still more into vogue, and to-day it is almost the only one found.

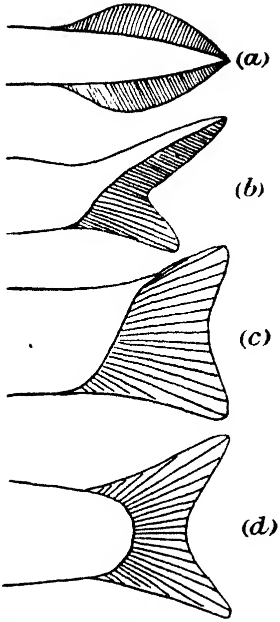


FIG. 241.—Diagram of the Tail Fin in various Stages in Evolution.

(*a*) Diphycercal. (*b*) Heterocercal (*c*) Hemiheterocercal. (*d*) Homocercal.

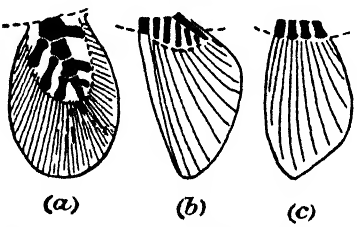


FIG. 242.—Diagrams showing Different Types of Paired Fin among Osteichthyes.

(*a*) Crossopterygian (from Goodrich. (*b*) Primitive Actinopterygian. (*c*) Advanced Actinopterygian.

Black = endoskeleton. Broken line = body boundary. Rayed portion = part of fin supported by dermal fin rays.

The paired fins, during the Devonian period, were often still largely supported by endodermal skeleton. Externally this fact was indicated by the presence of an axial portion made up of a blunt or sharp lobe-like extension of the body wall covered with ordinary body scales (Fig. 242*a*). Around the lobe the dermal rays formed a kind of fringe; hence the descriptive term *crossopterygian* for this kind of paired fin. At that time there existed, however, a few fishes in which the body lobe had become greatly reduced, and dermal rays supported the major portion of the fin. This is described as *actinopterygian type* (Fig. 242*b*). It became important during the Carboniferous period and has been the dominant type in all subsequent periods.

Until Carboniferous times the notochord remained but little altered (Fig. 243*a*), and then a slight tendency set in towards the formation of ring-like ossified vertebræ thickened by inward growth until the notochord was constricted to the condition of a string of bead-like swellings connected by a thread (Fig. 243*c*). This was exhibited by many Cretaceous and later fishes in which the vertebræ were amphicœlous or concave at both ends. The endoskeleton of the head remained largely cartilaginous throughout Palæozoic times and is consequently little known. Ossification, however, set in during late Palæozoic and progressed until in some fishes of the Cretaceous a very largely ossified internal head skeleton was produced.

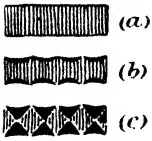


FIG. 243.—Diagrammatic Longitudinal Section of the Vertebral Column at successive Stages in Early Evolution.

Lined area = notochord. Black = bone or cartilage of the vertebral body.
(*a*) Unconstricted notochord. (*b*) Slightly constricted notochord with cylindrical or nearly hour-glass shaped vertebræ. (*c*) Completely constricted notochord, vertebræ biconcave or amphicœlous.

Devonian Bony Fishes and their Later Representatives.—With the exception of one genus, the Devonian Osteichthyes had fins which conformed to the crossopterygian pattern, and they fall into three orders centring round the genera *Osteolepis* (*Osteolepidoti*),

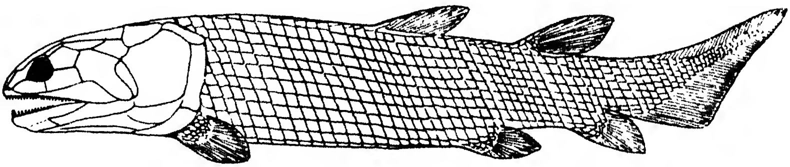


FIG. 244.—Restoration of *Osteolepsis macrolepidotus* (O.R.S. Caithness, after Traquair and Watson).

Cœlacanthus (*Cœlacanthini*) and *Dipterus* (*Dipnoi*). All were at their acme during the Devonian, but subsequently experienced rapid decline.

Osteolepis (Fig. 244) was of normal shape and covered with rhombic cosmoid scales. It had numerous bones on the roof of the skull arranged mainly in pairs (Fig. 248B), of which only the nasals, frontals, and parietals need be mentioned. The bones seen in side view (Fig. 245) may be grouped into (1) jaw bones associated with the mouth; (2) opercular bones, occupying the fold of skin which covers the gills; (3) cheek bones, between the operculum and the eye; and (4) the snout bones lying in front of the eye. Owing to the forward position of this organ the snout is short. The cheek is more extensive and is occupied by several large bones of which the squamosal is the chief. The upper margin of the mouth is bounded by two pairs of bones, the large maxilla and small premaxilla. The lower margin has only the dentary. These bones are all armed with small teeth, though larger more trenchant teeth lie just within the margin. The fins of *Osteolepis* are supported by lepidotrichs. The tail is heterocercal. The paired fins conform to the crossopterygian pattern, but because their fleshy scale-covered portion is short and rounded, they are described as bluntly lobed in contrast to the long pointed acutely lobed condition of other forms.

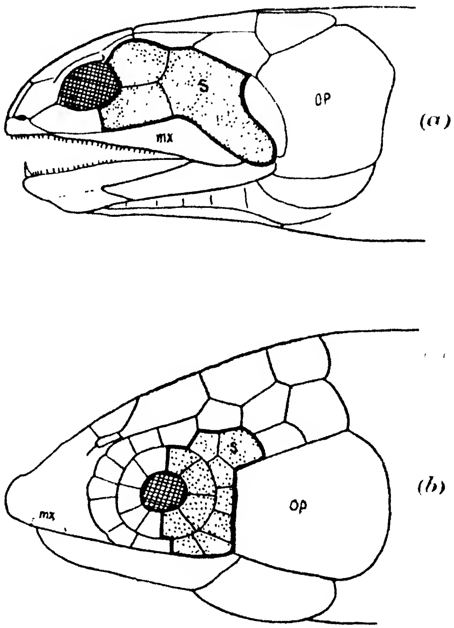


FIG. 245.—Restorations of Skulls of (*a*) *Osteolepis* (adapted from Watson), (*b*) *Dipterus* (adapted from Traquair).

Dotted area = cheek region. Compare large upper jaw bones in *Osteolepis* with their absence or much reduced state in *Dipterus*. The probable size and position in the latter taken from *Phaneropleuron*. *mx* = maxilla. *s* = squamosal. *op* operculum.

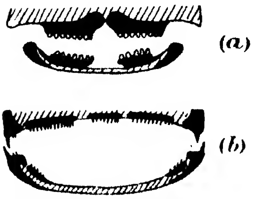


FIG. 246.—Diagrammatic Sections across the Mouth Cavity and Upper and Lower Jaws of (*a*) *Dipterus* type, (*b*) *Osteolepis* type to show difference in relative Development of Teeth on margin and inside the Mouth.

Black areas are the teeth-bearing bones.

The other members of this order differ from *Osteolepis* chiefly in minor details. Thus in *Holoptychius* (U.O.R.S.) (Fig. 247*a*) the scales are cycloidal in form though covered with a thin wrinkled coating of cosmine; the teeth have the enamel folded into the dentine, and the fins are acutely lobed. *Glyptopomus* (Dev.) (Fig. 247*b*) exhibits a tendency to assume a pike-like form of body with its median fins concentrated in the tail region. During the Carboniferous period this order was still an important section of the fish fauna. *Megalichthys* was a close ally of *Osteolepis*. *Rhizodus* and

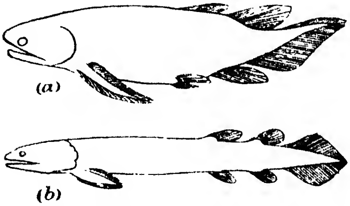


FIG. 247.—Outline Restorations of (*a*) *Holoptychius* (O.R.S.) after Traquair; (*b*) *Glyptopomus* (Devonian) after Huxley. Note the pike-like form and large mouth.

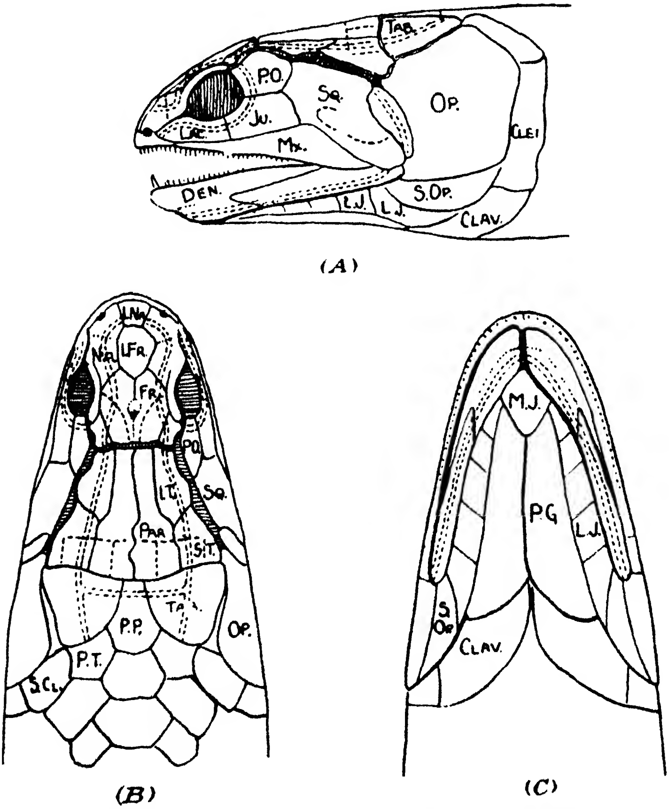


FIG. 248.—Cranial Bones of *Osteolepis* (by Watson).

Dotted lines, uncertain suture. Broken lines, lines of pit. organ. Double broken lines, lateral line canals.

(*A*) Side view. (*B*) Dorsal view. (*C*) Central view. *Fr* = frontal. Opening for median or pineal eye lies on its inner margin. *Par* = parietal.

Rhizodopsis had cycloid scales and ossified ring-shaped vertebræ. The order died out in the Permian with the genus *Megalichthys*.

Cœlacanthus (Carb.–Trias.) was a specialized Crossopterygian. In it the endoskeleton of the median and paired fins was completely ossified. The tail fin was diphycercal and had three lobes. The order to which it belongs had a long range in time being represented in the Devonian by *Nesides*; in the Jurassic, by *Undina*; in the Cretaceous, by *Macropoma*; and exists still in the genus *Latimeria*.

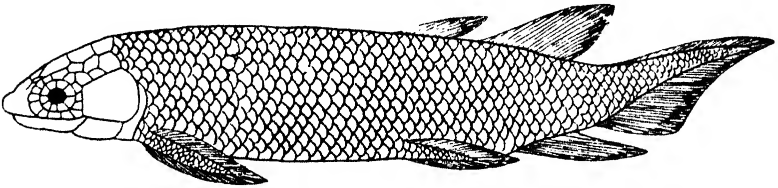


FIG. 249.—Restoration of *Dipterus valenciennse* (L.O.R.S. After Traquair)

Dipterus belongs to the crossopterygian order of the *Dipnoi*, so called on account of their close affinity with the existing mud fishes, of which *Ceratodus* is an example. This fish lives in the rivers of Australia where at certain seasons the water becomes stagnant and putrid with rotting vegetation, and unsuited for oxygenating the blood. The fish then rises to the surface, and breathes air into its lung-like air bladder. Its food consists of crustacea, shellfish, and other small creatures living in the vegetation. The endoskeleton of the head is largely cartilaginous, and the upper

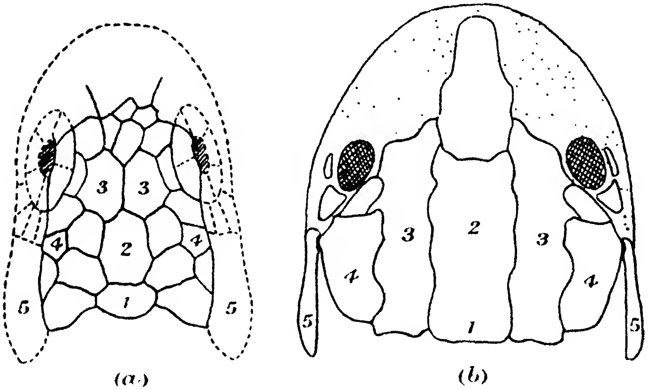


FIG. 250.—Roof of Skull of (*a*) *Dipterus* (O.R.S.) adapted from Watson, broken lines from other figures; (*b*) *Ceratodus*—dotted area is without bones.

1 = post-parietal. 2 = parietal. 3 = frontal. 4 = squamosal. 5 = operculum.
Note the tendency towards an unpaired arrangement of the centrally-placed bones. Compare this with the paired arrangement in *Osteolepis* (Fig. 248B). Note also fewness of bones in Ceratodus as compared with Dipterus.

jaw is united to the cranium in a typically autostylic manner (Fig. 229*b*). There are no teeth on the marginal bones of the mouth, but there are large dental plates (Fig. 246*a*, 251) with coarse ridges, formed during development by the fusion of teeth, upon the palatoquadrate, and upon the inner bones of the lower jaw. This dental apparatus is well suited for breaking shells and crushing food. The skull is roofed (Fig. 250) above by a few large bony plates, of which two are unpaired and occupy the middle line.

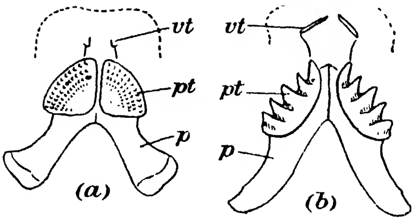


FIG. 251.—The Palates of (*a*) *Dipterus*, (*b*) *Ceratodus*, showing the palatal and vomerine Teeth.

Note many denticles on the plate of *Dipterus*; similar denticles occur in the young of *Ceratodus*, but they fuse to form the ridges in the adult (b).

p, palatoquadrate. *pt*, dental plates. *vt*, vomerine teeth.

Dipterus (M.O.R.S.) (Fig. 249) is one of the more primitive of the Devonian Dipnoi. At first sight it bears a striking resemblance to members of the *Osteolepis* group, such as *Holoptychius*, in the shape of the body, the subdivision of the median fins, and the heterocercal tail. An inspection of the head (Fig. 250*b*), however, shows that its affinities are with *Ceratodus*. The mouth is small, without marginal teeth but armed internally with similar stout crushing dental plates. These plates bear numerous ridges (Fig. 251*a*) made up of separate denticles, thus recalling an early stage in the development of these plates in *Ceratodus*. In association with the shortness of the jaws the cheek region is considerably reduced (Fig. 245*b*). The roof of the skull of *Dipterus* (Fig. 250) resembles that of *Osteolepis* in the number of bony plates, but it differs in the presence of unpaired plates in the middle line.

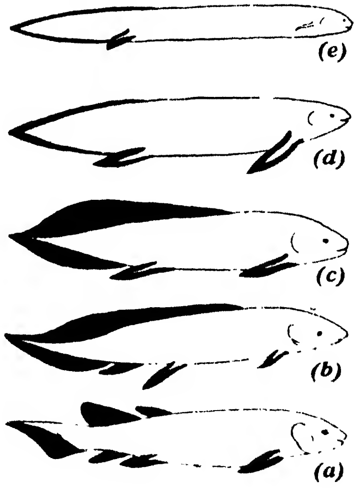


FIG. 252.—Series of Dipnoans showing the Tendency to assume an Eel-like adaptation Form with the passage of time (after Dollo).

(*a*) *Dipterus* (L. Dev.) (*b*) *Phaneropleuron* (U. Dev.). (*c*) *Uronemus* (L. Carb.). (*d*) *Ceratodus* (Present, Australia). (*e*) *Lepidosiren* (present, S. America).

Note the secondary loss of the heterocercal condition, the union of the median fins, the ultimate reduction of paired fins.

The Dipnoi were at their acme during the Devonian. They declined during the Carboniferous and were represented by *Ceratodus*-like forms from the Trias onwards. During the Trias the latter appear to have been world-wide in their distribution. The story of the decline of the Dipnoi is not merely a matter of reduction in number of bones but also of degeneration in other ways. This was manifested, for example, by a gradual assumption of an eel-like adaptation form (Fig. 252). This first became evident in Devonian and Lower Carboniferous in the progressive extension and union of the median fins to form a continuous finfold like that of *Ceratodus*. At the same time the tail lost its heterocercality and became secondarily diphycercal, *i.e. gephyrocercal*. This tendency reaches its extreme expression in the living Lepidosiren (S. America)—in which the paired fins have become greatly reduced.

Sturgeons and their Late Palæozoic Allies.—The Sturgeon or *Acipenser* (Fig. 253) may be taken as the first type for the Actinopterygii. Its head is moderately depressed, and is drawn out anteriorly into a long snout. The mouth is small and protrusible and has the appearance of being situated far back on the under side, being suctorial it is devoid of teeth. These features are associated with the habit of grubbing for food in the mud.

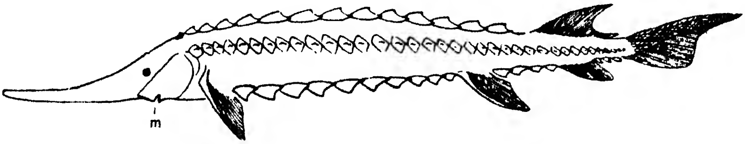


FIG. 253.—*Acipenser* (modified from Cuvier).
Note Rhombic scales on tail.

The trunk is also slightly depressed anteriorly, but posteriorly it is cylindrical, and tapers off gradually into an elongated tail. The hinder end of the latter is tilted slightly upwards and produces the same degree of heterocercality of fin as in sharks. The dorsal surface of the head is protected by numerous bony plates, but the cheek region is naked and the opercular region is occupied by only one bone. The trunk and tail are also naked except for five longitudinal rows of bony plates, and for rhombic plates upon the upturned hinder portion. The fins are supported by lepidotrichs which in the median fins considerably outnumbered the corresponding endodermal rays. The front borders of dorsal and caudal fins are greatly strengthened by a double series of long overlapping scales called fin fulcra. The paired fins are typically *actinopterygian*.

The vertebral column consists of a stout unconstricted notochord, upon which the cartilaginous basal portions of the neural and hæmal arches find support. The endoskeleton of the limbs and limb girdles is likewise cartilaginous (Fig. 242*b*). The combination of an almost completely cartilaginous endoskeleton with a reduced bony exoskeleton has led to the name Chondrostei for the Sturgeons and their liassic ancestor *Chondrosteus*. These fish were a degenerate offshoot of the *Palæoniscoidea*, a virile group of strong swimmers of predaceous habit that dominated the fresh waters of Carboniferous and Permian times.

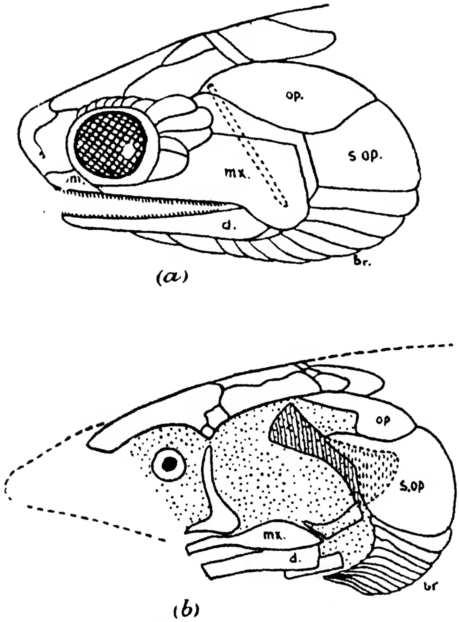


FIG. 254.—Restoration of Skulls of (*a*) *Palæoniscus* (U. Perm.), after Traquair; (*b*) *Chondrosteus* (L. Lias), adapted from Traquair.

Dotted area = region from which bones which are present in Palæoniscus have disappeared. Lined area = Hyomandibular. Note its backward slope.

mx, maxilla. *op*, operculum. *s.op*, suboperculum. *br*, branchiostegal rays. *d*, dentary. *pm*, premaxilla.

Broken lines indicate the position and backward inclination of Hyomandibular.

The earliest representative of this group was *Cheirolepis* (Dev.) which was also the first and most primitive member of the Actinopterygii. *Palæoniscus* (Perm.) is much more fully known (Figs. 221, [11], 254*a*). In its head the snout projected a little beyond a capacious mouth armed with numerous teeth. The bony plates forming the cheek and covering the suspensorium show a marked backward displacement. The maxilla was large and closely united above and behind with the preoperculum. The rest of the body was covered with rhomboid scales. In the fins the dermal rays were more numerous than their endoskeletal supports. The tail was heterocercal and projected backwards beyond the large ventral fin lobe (cp. Fig. 253). *Gonatodus* and *Elonichthys* (Carb.) were similar, but *Platysomus* (Carb.–Trias.) was deep bodied and laterally compressed (Fig. 221, [10]). In *Canobius* (Carb.) the projection of the snout was reduced and the suspensorium almost vertical. These differences went a step further in *Haplolepis* (Carb.) which represented a section of the Palæoniscids which showed modifications parallel to those characteristic of later fishes. During the Trias the Palæoniscoidea declined rapidly and persisted only as a rare element in the fauna until the Upper Cretaceous.

Belonorhynchus (Trias.–Lias., Fig. 221, [9]) is believed to be allied to the Palæoniscidæ, but the details of its skeleton are imperfectly known. Meanwhile its pike-like adaptation form should be noted.

A point of general interest arising out of the above study is that specialization appears often to affect the posterior organs, or parts of organs, less quickly than the anterior. Thus in *Chondrosteus* and *Acipenser* the scales upon the tail remain rhombic whilst those in front are modified or suppressed. In *Chondrosteus* the opercular and branchiostegal rays are complete, whilst cheek and jaws degenerate. Again, it is the front dermal rays of each fin which are most liable to become enlarged and strengthened.

Mesozoic Fishes.—The decline of the palæoniscids was accompanied by the appearance of a rich variety of forms which may be provisionally included in two orders, the *Subholostei* and the *Holostei.*

The Subholostei were world-wide in distribution during Triassic times. They include representatives of a number of lines of descent which exhibit structural differences of the kind already noted in the palæoniscids, but they carry the grade of evolution in these respects nearer to that seen in the later Holostei. Thus in *Catopterus*, which is otherwise a typical palæoniscid, the tail is almost truly hemiheterocercal, and the paired fins have the dermal rays reduced in number almost to that of the endodermal rays. *Cleithrolepis* shows similar changes but is deep bodied like *Platysomus.* The Pycnodont fishes (Fig. 221, [6]), *Mesodon* (Lias.–Cret.), *Mesturus* (Jur.) and *Gyrodus* (U. Jur.), appear like a persistent relic of the same type. They had a small mouth and well-developed crushing teeth.

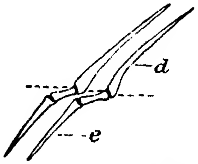


FIG. 255. — Diagram showing the Relation between Dermal and Endodermal Rays in Holostei and higher Actinopterygii.

d, dermal ray. *e*, endodermal ray. Note the equality in number. Dotted line shows body boundary.

The Holostei were dominant during the Jurassic and the Cretaceous. They also include sections of several lines of descent derived either directly from the Palæoniscoidea or indirectly through the Subholostei. They had advanced to a yet further grade in the evolution of various characters. The endoskeleton was more completely ossified; the tail was quite hemiheterocercal; the dermal rays were equal in number to the endodermal; the eye was further back on the cheek; the suspensorium was vertical or even forwardly inclined; the maxilla was separated from the preoperculum, and another bone, the interoperculum, lay between; the scales had become typically ganoid. The majority of the Holostei may be grouped around two outstanding genera—*Lepidotus* and *Eugnathus.*

Lepidotus (Fig. 257*a*) (Trias.–L. Cret.) differs from *Eugnathus* chiefly in the smallness of its mouth. It was a large, moderately deep-bodied fish with its body encased in stout rhombic ganoid scales. The head was completely encased in bones, and the cheek region was much restricted (Fig. 256*a*). The teeth upon the margins of the mouth were small, but those situated inside upon the palate and splenial had hemispherical crowns adapted for crushing, like those of the modern wolf-fish, which feeds upon molluscs and star-fish. In the early species of this genus the notochord was unconstricted; in the later, ring-shaped bony vertebræ were present.

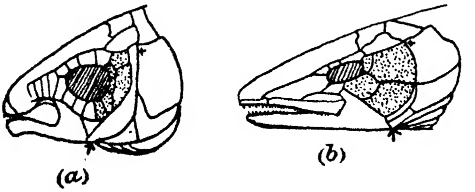


FIG. 256.—Restoration of Head of (*a*) *Lepidotus* (after Brit. Mus. Cat.) and (*b*) *Eugnathus* (modified after Woodward).

Dotted area is the cheek region. → indicates position of jaw articulation. Note the small mouth in *Lepidotus* and large one in *Eugnathus*. + indicates position of articulation of operculum on hyomandibular.

Acentrophorus (Perm.) and *Semionotus* (Trias.) were the earliest representatives of this small-mouthed Lepidotus type of fish.

The slight tendency towards the deepening and compression of the body shown in these three genera was carried to an extreme in *Dapedius* (Fig. 257*b*) (Trias.-Lias.). *Ætheolepis* (Jur.) is a *Dapedius*-like form in which the scales of the tail region have become deeply overlapping and cycloid. Every grade between the rhombic and the cycloidal type of scale occurs on the body of this fish, a fact which shows how unimportant these structures are for broad classificatory purposes.

Eugnathus (Lias.–Jur., Fig. 257*c*, 256*b*) and its allies appear to have originated from the Palæoniscoidea through forms like *Parasemionotus* (Trias.). They occupied the same place in the fauna of the Mesozoic seas as did the palæoniscids in later Palæozoic seas. The large gape, armed with numerous teeth, combined with torpedo-like body and powerful tail, must have made them highly efficient enemies of smaller fry. *Eugnathus* was covered with thick rhombic ganoid scales, but in the closely similar *Caturus* (Trias. and U. Juras.) the scales were thin, deeply overlapping and had only a delicate coating of ganoine. In both genera the notochord was unconstricted, or at the most only enclosed in ring-shaped vertebræ. In *Eurycormus* (U. Jur.) the vertebral column was more advanced in its ossification.

Amia, a fish which lives in the fresh waters of North America, may be regarded as the sole survivor of the eugnathid stock. It differs from its Mesozoic relatives in the yet more complete ossification of the trunk vertebræ, and in the loss of the fin fulcra. *Amia* itself is unknown before the Tertiary, but the closely similar *Megalurus* occurs in the Kimmeridgian.

Reduction of fin fulcra took place independently in another group which included *Pachycormus* (Lias.), *Hypsocormus* (U. Jur.), and *Protosphyræna* (Cret.). These were all agile forms with cycloid scales and a tendency for the snout to project beyond the gape.

Lepidosteus is another holostean which has survived to the present day. It lives in the same regions as *Amia* and, like that, furnishes yet another example of the last members of ancient types finding a refuge in fresh waters of rivers and lakes. *Lepidosteus* differs from other Holostei in the complete ossification of the vertebral column. Along with the extinct genera *Aspidorhynchus* (Fig. 221, [5]) (Jur.) and *Belonostomus* (U. Jur.–Cret.) it repeats the adaptive form of body of the Pike.

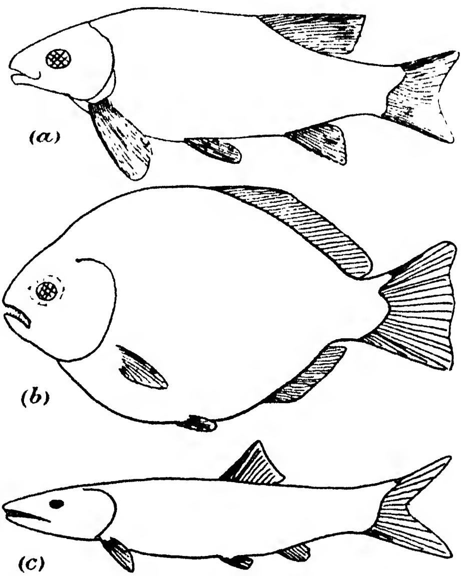


FIG. 257.—Outline Restorations of (*a*) *Lepidotus*, (*b*) *Dapedius*, (*c*) *Eugnathus*.
[Modified (*a*) from Woodward, (*b* and *c*) from Brit. Mus. Cat.]

In *Pholidophorus* (Trias.–Jur.) the lower jaw has nearly, if not quite, attained the simplicity of later Teleostei, but fin fulcra are still present. Its scales, though thin and overlapping, are rhombic in outline and covered with ganoine. In the closely similar *Oligopleurus* (U. Jur.–Cret.) the vertebræ are quite well ossified. In *Leptolepis* (Fig. 259*b*, U. Jur.), the lower jaw is typically teleostean and fin fulcra have disappeared ; though the notochord is continuous, it is enclosed by a series of well ossified vertebræ shaped like constricted cylinders. The scales still have a thin coating of ganoine.

The Perfecting of the Bony Fish.—Just as the Palæoniscoidea declined and gave place to the Subholostei and Holostei at the opening of the Mesozoic, so these also, in their turn, sank to insignificance and gave place, from the late Cretaceous onwards, to the Teleostei. In a typical teleostean, such as the herring or trout, the trunk and tail region are covered by typical cycloid scales. The tail is now homocercal; that is to say, the fin itself consists entirely of what in the heterocercal condition was the ventral lobe. The paired fins are typically actinopterygian (Fig. 258). The endodermal elements of the pectoral fin are reduced in number to four or five and in the pelvic fin they are almost wholly suppressed. Fin fulcra are absent. In the head the membrane bones have all sunk deeply below the skin and have lost all traces of enamel covering or of sculpturing on the surface. In the lower jaw the bones have settled down to the fixed number of three pairs. The chondrocranium is now largely ossified. One bone, the supra-occipital (Fig. 260), is especially characteristic of the order. It is situated at the posterior end of the mid dorsal line. The constriction of the notochord by well ossified biconcave vertebræ is now the rule and not the exception.

FIG. 258.—Diagram of Actinopterygian fin showing fin fulcra on Anterior Border.

Broken line is body boundary.

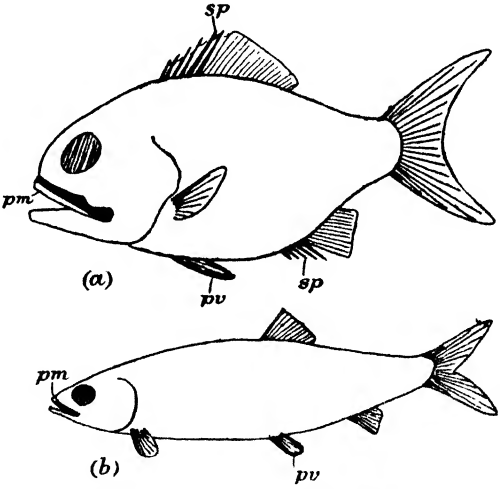


FIG. 259.—Diagrams of the more obvious Differences between a primitive Teleost (*b*) *Leptolepis* and a specialized Teleost (*a*) *Hoplopteryx* Cret.

Black area is maxilla excluded from gape in *a*.
sp, spiny fin ray in *a* only. *pv*, pelvic fin—far forward in *a*. *pm*, premaxilla.
(After Brit. Mus. Cat.)

Post-Jurassic teleosts are extraordinarily varied and numerous, and show almost every conceivable adaptation to the wide range of conditions of life in the sea and rivers. They show, however, certain progressive changes from the primitive condition inherited directly from the Holostei to that of the most specialized member of the order. Only a few of these need be mentioned (Fig. 259*a*, *b*). The head increases in size in proportion to the body. In the mouth margin the premaxilla extends backwards under the maxilla, and eventually excludes this from the gape. In the roof of the skull the parietal bones, which at the outset are in contact with one another, become completely separated by the forward growth of the supraoccipital (Fig. 260). Each dermal fin ray is usually made up of separate scales which, in some cases, unite to form a stiff sharply pointed spine. The pelvic fin shifts forwards, with advancing specialization, from its position near the junction of the trunk and tail to one close to the pectoral fin. In the endoskeleton, cartilage disappears almost entirely, hence the name Teleostei for the order.

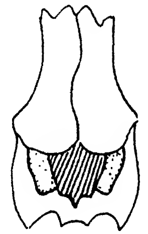


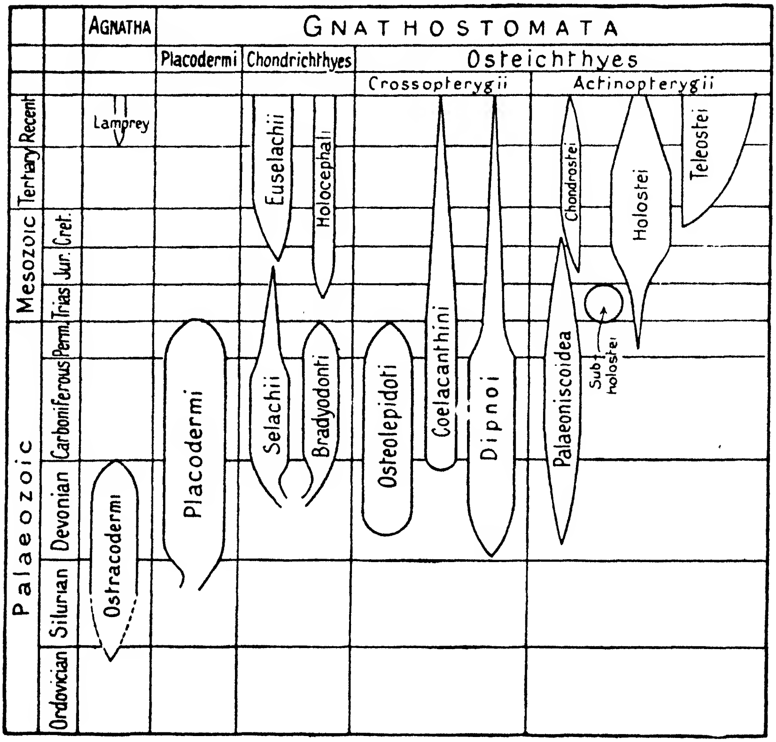
FIG. 260.—Diagram of Part of the Roof of the Skull of a specialized Teleost. Lined area shows the large supra-occipital bone separating the parietal bones (dotted).

Primitive Teleosts, such as the *Herring*, *Elops*, *Saurodon*, *Pike*, were in the ascendancy during the Cretaceous and early Tertiary times. But even at that early date a few highly specialized genera, *e.g.* *Beryx* and *Sparus*, existed. In later Tertiary times specialized fishes increased in number, and to-day they dominate the water as completely as the birds dominate the air.

In the light of what has gone before, a brief survey of the development of such a specialized bony fish as the stickleback is instructive. The skeleton of a newly-hatched stickleback consists of a simple notochord with the first beginnings of a cranium, jaws and gill arches in cartilage. The limbs and girdles likewise consist only of cartilage at their first inception. These facts suggest a stage in evolution when as yet the earliest ancestors of the Bony fishes had no bones. Up to the present no fossil evidence is forthcoming from the Silurian either against or in support of this view. At a later stage vertebræ appear around the notochord as short cylinders of bone slightly constricted centrally, and this constriction increases as the bone thickens until the biconcave condition of the adult is attained. This sequence of events (Fig. 243) accords well with that revealed by Mesozoic fishes.

In the tail the notochord is at first straight (Fig. 261, cp. Fig. 241), and divides the fin into equal dorsal and ventral portions. Gradually

TABLE XI.—Relationships and Distribution in Time of the Main Divisions of Fishes.



the end of the notochord tilts upwards and a ventral lobe develops in the hitherto continuous finfold. The tilt increases, but this portion of the notochord ceases to keep pace with the growth of the fish as a whole and thus becomes relatively more and more insignificant. Meanwhile, the ventral lobe increases until it forms the whole of the adult fin to the complete exclusion of the larval fin. These changes also present a striking parallelism to those passed through during the course of evolution. Nevertheless, it is merely a parallelism in broad outline. Many details in the evolutionary sequence are

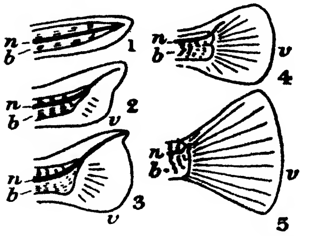


FIG. 261.—Diagrams showing Stages in Development of the Tail in a Stickleback. Compare with Fig. 241. 1 with *a*. 2 and 3 with *b*. 4 with *c*. 5 with *d*.

n, notochord. *b*, fleshy axis of tail. *v*, ventral lobe.

omitted in the developmental sequence, such as the dorsal dermal rays, the fin fulcra, the rhombic scales.

When the development of other parts of the skeleton is compared in detail with their evolution as revealed by fossils, the similarity, which at first seems so striking, becomes elusive and difficult to define. Whilst at first sight development of the individual appears to recapitulate the evolution of the race to which it belongs, a more careful comparison of the two sets of phenomena shows that it only tends to recapitulate, in general outline, the evolution of the several parts separately but independently so that the collective appearance of all the characters at any developmental stage may differ markedly from that of the adult individual at the presumed corresponding evolutionary stage.

AMPHIBIA

Modern Amphibia.—The Frog and Newt represent the lowliest group of living terrestrial vertebrates, namely the Amphibia. They begin life as purely aquatic animals breathing by means of plume-like gills (Fig. 262*a*). As the larva or tadpole grows lungs develop, and it then comes to the surface of the water to breathe air; at the same time the legs appear. At first these are mere stumps, and as they grow into typical walking limbs they pass through no stage comparable with a fin. Ultimately the young creature ventures on to the land, where, as in terrestrial animals generally, the tail is replaced by the legs as the main organ of propulsion. The adult amphibian resembles fishes in the moist condition of its skin, and in the small size and great number of its eggs. The latter have no effective covering, and are therefore liable to be dried up when exposed to the air. Their close affinity with terrestrial vertebrates is proved, however, by the presence of legs, and lungs, and of nostrils opening internally on the roof of the mouth.

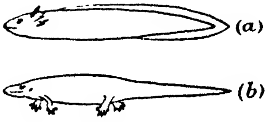


FIG. 262.—Outline Diagram of (*a*) Larval newt, (*b*) Adult newt.

FIG. 263.—Vertebra of Newt. (*a*) anterior end of centrum.

The back bone of a frog is highly specialized, but that of the newt is normal and, in common with that of other terrestrial animals, is long and consists of numerous vertebræ. These fall into four groups, viz. those of the neck, the trunk, the sacrum (to which the pelvis is attached), and the tail. The centra (Fig. 263) are ossified, and are convex in front and concave behind, and thus articulate with one another by a ball-and-socket type of joint. The skull of the frog is more normal (Fig. 264). Its endoskeleton is, however, mainly cartilaginous. Thus in the region surrounding the foramen magnum (Fig. 265), the opening through which the brain passes into the spinal cord, it has only a pair of bones (exoccipitals) on either side, instead of the usual four present in other terrestrial vertebrates. Similarly the jaw articulation is cartilaginous, for the quadrate and articular bones of the reptiles are unrepresented. In the exoskeletal portion of the skull the bones are few, and situated beneath the skin. Unlike the condition in Fishes many are reduced to mere splints and are separated from one another by wide spaces.

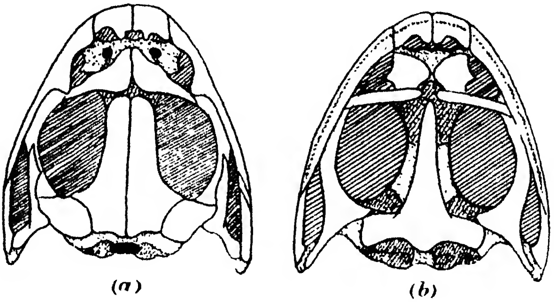


Fig. 264.—Skull of Frog (*Rana*).

(*a*) Dorsal view. (*b*) Ventral view.
Lined areas are openings or fenestræ. Dotted areas represent the endoskeleton; where this is lined it is ossified. White areas are membrane bones, which are nearly all narrow and splint-like. Note the extensive fenestration of both the roof of skull and the palate.

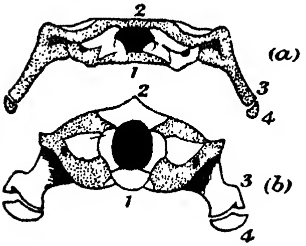


Fig. 265.—Posterior view of the Cranial Endoskeleton of (*a*) Frog, (*b*) Young Reptile, *Sphenodon*.

Observe the cartilaginous condition in the former and the ossified condition in the latter of the following regions:—
(1) Basioccipital. (2) Supraoccipital. (3) Quadrate, (4) Articular.
Dotted areas = cartilage. White areas = cartilage bone. Black areas = foramen magnum.

The pectoral limb girdle (Fig. 266*a*) is mainly cartilaginous. Above the glenoid cavity or surface for the articulation of the limb, it is called the *scapula*; below, the *coracoid*. Such ossifications as are present are named after these portions. The pelvic girdle (Fig. 266*b*) is similarly divided by the *acetabulum*, or facet for the articulation of the hind limb. The upper portion is called the *ilium*. The lower consists of an anterior *pubis* and a posterior *ischium*. In modern Amphibia the pubis alone is not ossified. Both fore and hind limbs are built upon the same plan (Fig. 267). They have an upper portion containing one long rod-like bone, and a lower with two long bones lying side by side. At the further end of these is a flexible mosaic of small bones, which lies in the wrist and ankle. Beyond this is the hand or foot with five digits, each of which has several segments. Thus each limb ends in an extended surface by means of which the creature may stand, even upon soft ground, without sinking.

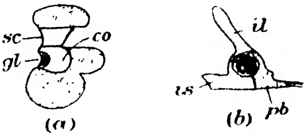


FIG. 266.—Diagram of (*a*) Shoulder Girdle, (*b*) Pelvic Girdle of Newt-like Amphibian.

gl, glenoid cavity. *sc*, scapula. *co*, coracoid. *il*, ilium. *is*, ischium. *pb* pubis.

Frog-like Amphibia are called *Anura*. They are rare as fossils and have not been found in rocks of earlier age than the Upper Jurassic.

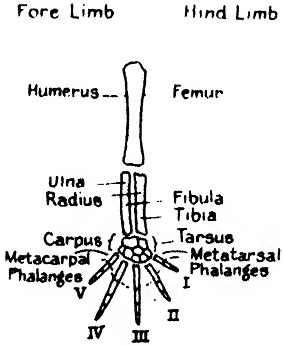


FIG. 267.—Diagram of the Limb Skeleton of a Typical Land Animal.

I-V. Digits.

Newt-like Amphibia are called *Urodela*. Fossils of these also are rare. One genus, *Hylæobatrachus*, comes from the Lower Cretaceous rocks.

The Smaller Fossil Amphibia.—Remains of fossil Amphibia occur at various levels from the Carboniferous to the Triassic. In them the roof of the skull like that in fishes has a continuous bony covering (Fig. 268), and they are therefore classed as the *Stegocephalia*. Small Stegocephalia have been found in comparative abundance in both upper Carboniferous and Permian rocks. Normally these are like the newt in size and shape, and they probably led a similar mode of life. Some were less normal, and had the head much enlarged and the tail greatly reduced, or the body very long and the limbs small or even absent (Fig. 269). The two chief types of small Stegocephalia are the *Phyllospondyli* and the *Lepospondyli*.

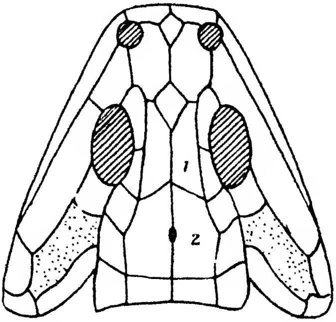


FIG. 268.—Roof of the Skull of a Stegocephalian.

Compare Fig. 264*a*, a similar view for the modern Amphibia. Note the absence of fenestræ, more numerous bones, and the otic notch in the posterior border. Dotted area is squamosal bone.

1, Frontal. 2, Parietal. Dark spot = position of median or pineal eye. (Modified after Watson.)

Branchiosaurus (L. Perm., Fig. 269) is the type for the former. It was only four inches long. In its axial skeleton the notochord was continuous and only slightly constricted. The vertebræ were hollow and cylindrical and divided longitudinally into three parts by sutures along the lateral and midventral lines (Fig. 270*a*). The exoskeleton of the head, like that of the *Crossopterygii*, formed a complete covering for the roof, and the surface of the bones was sculptured, thus indicating that they lay at or near the surface. The roof of the mouth, however, recalls that of the living Amphibia in the presence of large spaces between and the slender character of, the bones. In the limb girdles the coracoid and pelvic regions remained cartilaginous. The pectoral girdle had three membrane bones along its anterior border, a large median interclavicle and a pair of clavicles. The whole of the under surface of the trunk and limbs was covered with similar but smaller bones.

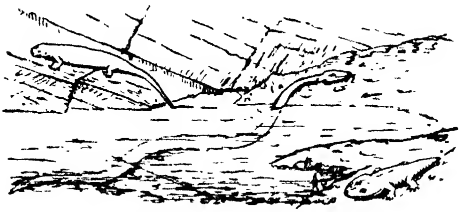


FIG. 269.—Restorations showing some of the Adaptation Forms of smaller Stegocephalia.

From left to right the amphibia are *Hylonomus*, *Dolichosoma*, *Branchiosaurus*.

The limbs of *Branchiosaurus* were typically terrestrial in plan and could only have been derived from a post-piscine ancestor that was adapted for life upon the land. But the cartilaginous condition of the carpus and tarsus, and of the articular ends of the large bones, shows that the limbs were too weak to support the body, and that probably a secondary return to an aquatic mode of life had taken place. The earliest forerunners of the modern amphibia may be sought among such forms as these.

In the Lepospondyli (U. Carb., L. Perm.) also the notochord was continuous, but the hour-glass shaped vertebræ were not divided into separate parts (Fig. 270*b*). They exhibited a great variety of adaptive forms (Fig. 269) including some like newts *e.g. Hylonomus* and others like snakes *e.g. Dolichosoma*.

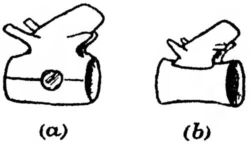


FIG. 270.—Vertebræ of (*a*) *Branchiosaurus*, (*b*) *Hylonomus*.

[From Woodward after Credner.

The Larger Fossil Amphibia.—Some of the Amphibia of the late Palæozoic and early Mesozoic attained large proportions, being not uncommonly eight or nine feet long. They all appear to be closely related to one another, not merely in size but in structural peculiarities, and are therefore classed together as a natural subdivision of the Stegocephalia, the *Labyrinthodontia*. This name refers to the fact that the enamelled covering of the teeth is folded into the underlying dentine, sometimes in a complex manner.

The Labyrinthodontia were heavy, clumsily built creatures (Fig. 271) with large heads, bulky bodies and stumpy tails. Their limbs were so short and weak that their bodies must have rested directly upon the ground. In the axial skeleton the notochord was continuous. In the earliest forms it was of almost uniform calibre, but with the passage of time it became gradually more constricted. Each vertebra consists of several separate pieces Fig. 272), the arrangement and relative development of which is so varied that they furnish one of the bases for detailed classification.

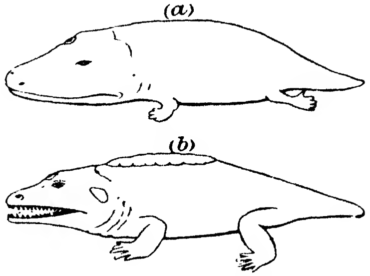


FIG. 271.—Outline Restorations of Labyrinthodonts.

(*a*) *Mastodonsaurus* (U. Trias), after Abel. (*b*) *Cacops* (Permian), after Williston.

Note the large, more powerful limb in the earlier form.

In general shape the head of the labyrinthodonts exhibits certain adaptive modifications which recur in the successive periods. In the central *Capitosaurus* (Trias.) type (Fig. 273*a*) the skull is not much longer than it is broad. Thus in *Eryops* (Perm.) it is two feet long by one and a half wide. In front the muzzle also is wide. The orbits are small and quite near to one another on the hinder half of the roof. In the second or *Archegosaurus* (L. Perm.) type (Fig. 273*b*) the snout is elongated as in creatures which lead an aquatic life and prey on fish. The third type (Fig. 273*c*) is exhibited by *Lydekkerina* (L. Trias.). In this the skull was much flattened, and the eyes were far forward and close together. This also is regarded as an aquatic form. The fourth or *Micropholis* (Trias.) type (Fig. 273*d*) is more distinctive. The head was flat-topped. The eyes lay near the lateral margin, and tended to face laterally as in land animals generally. The notches for the drum of the ear at the back of the skull were also similarly placed.

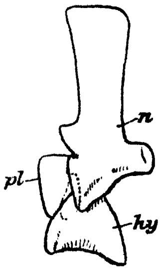


FIG. 272.—Vertebra of a Labyrinthodon (*Eryops*).

n, neural arch. *pl*, pleurocentrum. *hy*, hypocentrum (after Broili).

While the roof of the skull remained typically stegocephalian that of the mouth underwent progressive change. Thus in the Carboniferous forms there were no vacuities piercing it (Fig. 274A), in early Permian forms the vacuities were small and the bones extensive, but in the late Triassic genera they were large and the bones correspondingly reduced and splint-like (Fig. 274C, cp. Fig. 264*b*). A retrogressive change took place also in the back portion of the cartilaginous head-skeleton (cp. Fig. 265). In the earlier labyrinthodonts the ossification was more complete, for basi-occipital, supraoccipital, quadrate and articular bones were all present. In Triassic forms these bones were suppressed. Similar degenerative changes took place in the limbs and girdles. In the earlier labyrinthodonts, *e.g. Eryops* (L. Perm.), these parts were well ossified, as is usual in land animals. In Triassic genera, *e.g. Mastodonsaurus*, the scapular and coracoid bones were reduced, the pubis had lost its ossification and the carpus and tarsus were mainly cartilaginous. These changes were no doubt associated with the fact that the weight of the body was no longer borne by the limbs but was buoyed up in the water.

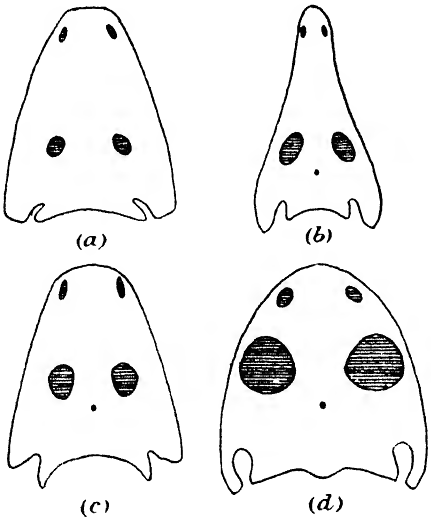


FIG. 273.—Outline Restorations of the Heads of Labyrinthodonts showing the chief Adaptational Forms.

(*a*) *Capitosaurus* type	modified after	Zittel.
(*b*) *Archegosaurus* type		Woodward.
(*c*) *Lydekkerina* type		Woodward.
(*d*) *Micropholis* type		Watson.

The resemblances between the Triassic labyrinthodonts on the

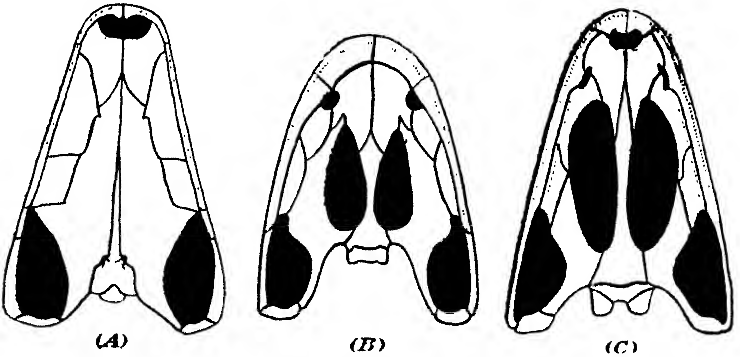


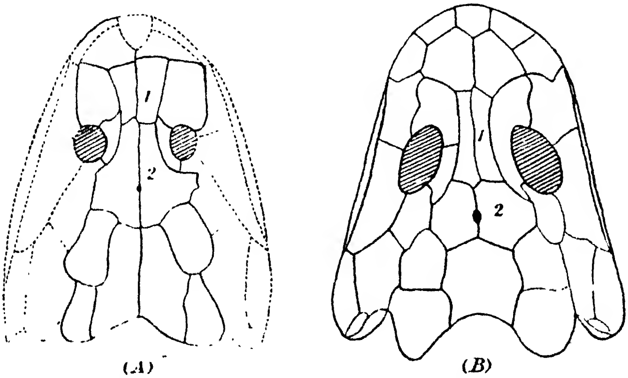
FIG. 274.—Restorations of the Palate in Labyrinthodonts.

(*A*) *Loxomma*—Carboniferous (modified from Watson). (*B*) *Eryops*—Permian (modified from Watson after Broom). (*C*) *Capitosaurus*—Triassic (modified from Watson).
Note the more extended fenestræ and splint-like bones in the latest form.

one hand and the Phyllospondyli and the modern Amphibia on the other, in the roof of the mouth, and in the reduced ossification of the head skeleton, and of the joints of the limbs, are not due to community of origin but to degenerative changes along parallel lines consequent upon the secondary resumption of amphibious or even aquatic habits in adult life. Looking at the history of the Amphibia as a whole they appear to be a branch of terrestrial animals which, because it has failed to shake off the necessity for its young to hatch and develop in water, has likewise failed to produce true denizens of the land. For the Amphibia it has always been easier to slip back into the water than to become permanently adapted to the conditions on dry land.

The Origin of the Four-footed Animals. The earliest remains of recognizable land vertebrates have been found in the Upper Devonian of Greenland. Up to that period of time the fishes had been the only vertebrates in existence. It is evident, therefore, that they alone could have provided the ancestral stock from which the land animals arose.

The fact that bone is an invariable constituent of the skeleton of land animals excludes the cartilaginous fishes from further consideration, and limits discussion to the Osteichthyes. Of these only the Crossopterygii and the Palæoniscid section of the Actinopterygii need be mentioned, for they alone were in existence during the Devonian. The Actinopterygii may be excluded, because among them the tendency of evolution in the fins was towards the increase of the dermal and decrease of the endodermal skeleton. Such a tendency would not be likely to produce a leg in which only endo-



(A) (B)

FIG. 275.—Roof of the Skulls of the Earliest Stegocephalia.

(*A*) *Elpistostege*. (*B*) *Ichthyostega*.
1 = frontal. 2 = parietal. Black spot = opening for pineal eye (after Westoll). Cp. Figs. 248B and 268.

skeletal elements are present. In the other two orders of fishes the endoskeleton plays an important part, and moreover it exhibits just that variability that would be required by a piscine stock which had to produce a new type of limb.

As yet there is no fossil evidence forthcoming which shows the steps in the transition from fins to legs. Attempts have been made to trace homologies between the elements of the limb skeleton of certain Amphibia and of the Crossopterygii, but with only partial success.

In other parts of the body it is found that the head skeleton, especially of the Stegocephalia, resembles that of the Osteolepidoti more closely than that of any other Crossopterygii (cp. Fig. 268 with 248B). In these, as in all terrestrial animals, the bones near the middle line of the skull roof are paired, the marginal bones of the mouth are well developed and bear the functionally most important teeth.

The two types differ, however, in that the orbits and the paired bones associated with the opening for the pineal eye lie far forwards in *Osteolepis* and far backwards in the Stegocephalia (Fig. 268). Incidentally it should be noticed that, notwithstanding the discrepancy in the naming of these bones they are strictly homologous in both types.

The remains from Greenland referred to above include the skulls of the two phyllospondylous genera *Ichthyostega* (High U. Dev.) and *Elpistostege* (Lowest U. Dev.). In these the eyes and paired bones occupy positions that are intermediate between the two extremes just described (Fig. 275). The former approaches more nearly to the Stegocephalia. The latter resembles *Osteolepis* more closely and may be regarded as the earliest-known terrestrial vertebrate, the forerunner of four-footed animals.

REPTILIA AND AVES

Primitive Reptiles.—Fragmentary remains of reptiles have been found as low down as the Upper Carboniferous rocks of North America. A richer but slightly later fauna has been yielded by the Permian of Texas and South Africa.

FIG. 276.—Restoration of *Labidosaurus*, a primitive Permian Reptile (after Williston).

The genus *Seymouria* (L. Perm. Texas) has much in common with the most primitive reptiles, but still retains typically stegocephalian characters in the region of the ears and the lower jaws. Opinions therefore still differ as to its rightful position. *Labidosaurus* (Fig. 276) from the Lower Permian of Texas still resembles the Stegocephalia in such features as the complete bony covering for the head (Fig. 277), the numerous elements which make up the lower jaw and the relatively short ribs. In other respects, however, it is typically reptilian. Its head is relatively small, and the eyes are laterally placed. The hinder portion of the head skeleton is more completely ossified, for both the basi- and supra-occipital bones are present. The jaw articulations are likewise well ossified, having a quadrate above and an articular below. Both these bones are invariably present in Reptiles. The vertebral column in this primitive form is also typically reptilian in that each vertebral centrum consists mainly of one piece. This is a short hour-glass shaped cylinder, which completely constricts the notochord centrally (cp. 243*c*). Owing to the presence of cushions of notochordal substances between and in the

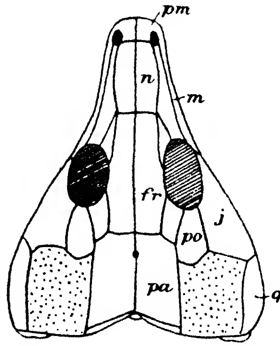


FIG. 277.—Roof of the Skull of *Labidosaurus*.

Cp. the Stegocephalian Skull, Fig. 268, and note that though the roof is equally complete, it has fewer bones, and the otic notch is absent. The dotted area in both is the squamosal.

n, nasal. *fr*, frontal. *pa*, parietal. *pm*, premaxilla. *m*, maxilla. *j*, jugal. *qj*, quadratojugal. *po*, postorbital. (Modified from Williston.)

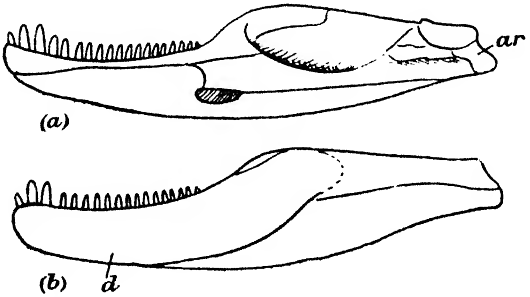


FIG. 278.—The Lower Jaw of *Labidosaurus*.

(*a*) Inside view. (*b*) Outside view.
Note the number of bones present.
d = dentary. *ar* = articular (after Williston).

hollow ends of the vertebræ, the backbone as a whole must still have retained much of its primitive flexibility.

The clumsy form of these Permian reptiles, which gives them a superficial resemblance to the Labyrinthodonts, is not to be regarded as a primitive feature, but as an adaptational form associated with life in swampy surroundings. The more slender form described as lizard-like approximates more closely to the primeval body-shape. This was possessed by *Aræoscelis* (Fig. 307), a contemporary of *Labidosaurus* and *Seymouria*, and also by the Lepospondyli (Fig. 269), which as already seen, include the earliest-known four-footed animals.

The Early Changes in the Reptilian Skull.—Already in Lower Permian times the reptilian organization showed modification in several directions. This fact proves that the stock must have had a long previous history dating back probably to the beginning of the Carboniferous period. As yet this section of their history is unknown. In these early modifications the skull roof underwent several series of changes which diverged from the ancestral condition seen in the Stegocephalia. These were most marked in the *temporal region*, that is the area which lies behind the eyes, and roofs over the space occupied by the massive muscles which work the jaw.

In *Seymouria* (Fig. 279*b*) as in the Stegocephalia (Fig. 279*a*), the hinder part of the head was covered by four pairs of horizontal rows of bones. The topmost pairs lay alongside one another in the middle line. They consisted of the *frontals*, the *parietals* and the *post-parietals* and formed the roof to the cranium proper. The remaining rows covered the temporal region. Of these the uppermost had four elements, the *tabular* being the hindmost. The next row below had two elements, the *post-orbital* and the *squamosal*. The bottom row also had two, the *jugal* and the *quadratojugal*.

Among Lower Permian reptiles two main changes took place in the temporal region. In the first the identity of some of the bones was lost as the result of suppression or of fusion. In the second openings, called *temporal fossæ*, were formed in one or both of two clearly defined positions. When a bone disappears during evolution it never reappears, and thus the presence or absence of certain elements is a differential character of some importance. Thus *Labidosaurus* (Fig. 279*c*), which has a quadratojugal, could not have been derived from a form-like *Aræoscelis* (Fig. 279*d*) in which it is absent. Similarly the latter has a tabular and, therefore, could not have been derived from *Labidosaurus* which does not possess one. The temporal fossæ furnish another valuable differential character. In *Aræoscelis* (Fig. 279*d*) the single fossa is situated between the parietal above and the post-orbital and squamosal below. In *Mycterosaurus* (Fig. 279*e*) it occupies a quite different position below these two bones and at their line of junction with the jugal. These two positions could not possibly be derived the one from the other. By such facts and reasoning it is proved that already as early as the

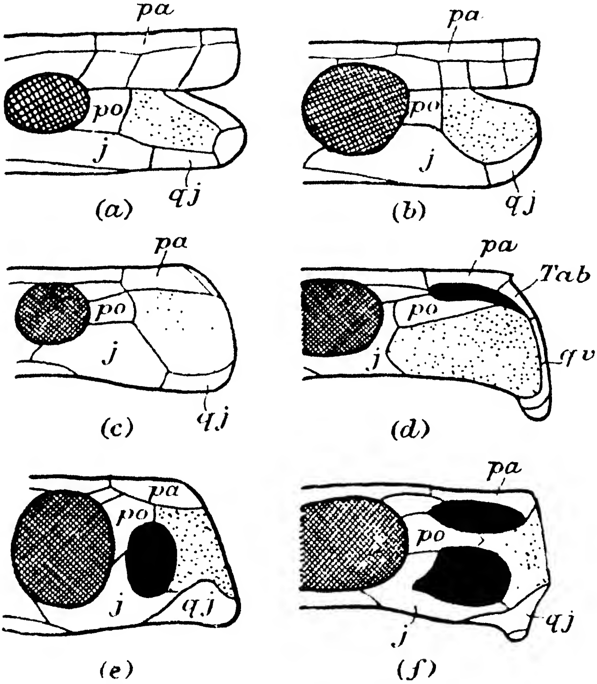


FIG. 279.—Diagrams showing the typical Conditions of Temporal Region found in Early Reptilian Skulls.

(*a*) Primitive Stegocephalian (adapted from Watson). (*b*) *Seymouria* (note the otic notch). (*c*) *Labidosaurus*. (*d*) *Aræoscelis*. (*e*) *Mycterosaurus* (all adapted from Williston). (*f*) *Sphenodon*.

(*a–c*) are Anapsidan, *i.e.* without temporal fossæ. (*d*) Parapsidan, fossa above post-orbital and squamosal. (*e*) Synapsidan, fossa below these. (*f*) Diapsidan, both fossæ present. Dotted area = squamosal.

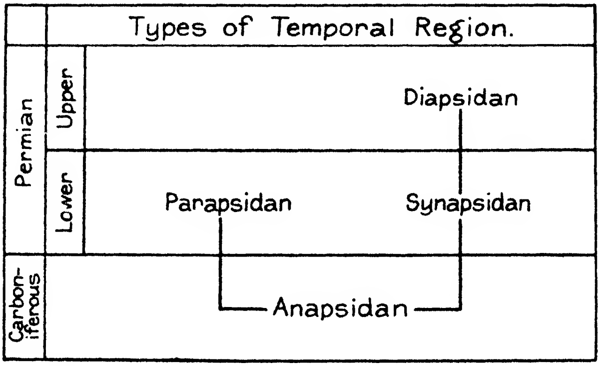
j, jugal. *pa*, parietal. *po*, is post-orbital. *qj*, quadratojugal. *qv*, quadrate. *Tab*, tabular.

Lower Permian times the Reptiles had diverged along several distinct lines of development.

In Upper Permian times the temporal region manifested another condition which is well seen in the living *Sphenodon*. In it both fossæ are present in one and the same skull (Fig. 279*f*). The presence of the quadratojugal bone points back to the condition shown by *Mycterosaurus* as the ancestral one for this type. The condition of the temporal region in *Sphenodon* is described as *diapsidan* ; that in

Mycterosaurus as *synapsidan*; that in *Aræoscelis* as *parapsidan*; and that in *Seymouria* and *Labidosaurus* as *anapsidan*. The morphological and time relationships of these types of temporal region to one another is shown in Table XII.

Table XII.



Progressive Changes in Arms and Legs.—The fact that land animals had piscine ancestors endowed them with structures and habits which imposed upon them, at the outset, the limitation of habitat to a moist or even wet situation, which limitation still binds the majority of Amphibia. This necessitated the scrambling over soft or even sloppy surfaces, especially at those periods when the individuals were passing out of the larval state, or returning to the water to breed. For progress upon such a surface the tail was of little value. The fleshy portion of the fins, however, supported as they were by stiff skeletal rods, provided a means for shoving the body along the ground. The proximal portion of the fin naturally acted as a lever, and any elongation of it led to an increase in speed. The distal portion remained broad and flat, so that it might rest upon, without sinking into, the mud. Meanwhile, its free edge became digitate and thus provided a means for gaining a hold upon the ground, either by sticking the digits into it, or hooking them on to irregularities of the surface or on to weeds.

At first the limbs spread out sideways, so that the creature merely sprawled along. Such seems to have been the posture even of primitive reptiles, *e.g. Limnoscelis* (cp. Figs. 280*a* and 283). The next step in progress was the lifting of the body from the ground so that friction might be reduced, and obstacles more easily cleared (Fig. 280*b*). This was accomplished by a downward rotation of the lower limb, which was thus brought into a more or less vertical position. The feet of the opposite sides were necessarily still far apart, and the creature moved along with a waddling gait. The plane, in which both upper and lower portions of the limbs lay, was next rotated from a position at right angles to one which was parallel to the median plane of the body. Fore and hind limbs rotated in opposite directions, so that the elbow and the knee were brought into juxtaposition (Fig. 281) with one another and lay against the animal's flanks. The upper part of the limb now swung in the same vertical plane with the rest of the limb ; and its length became effective, both for raising the body yet higher from the ground, and for increasing the length of stride. At the same time the feet of opposite sides were brought close together, and more directly under the centre of gravity of the body (Fig. 280*c*, *d*).

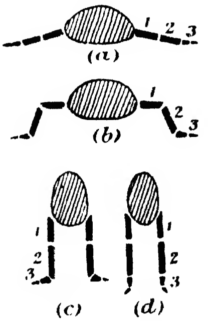


FIG. 280.—Diagram to illustrate the Changes which took place in the Attitude of the Limb with advancing Adaptation to Terrestrial Life.

(*a*) Limbs sprawling sideways. (*b*) Lower portions of limb vertical and thus body is raised from ground. (*c*) Upper portions of limb vertical, thus raising body higher and producing longer stride. Whole of foot still on ground. (*d*) Only digits rest upon ground. Stride correspondingly lengthened.

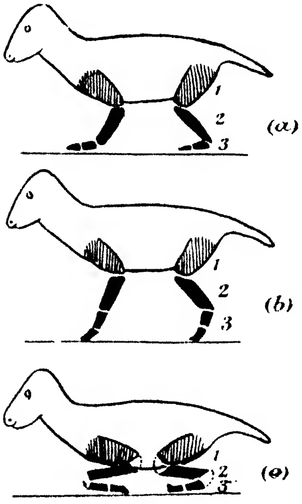


FIG. 281.—Diagram showing 280*c* and *d* in side view.

Note the juxtaposition of elbow and knee and the fact that all parts of the limb now swing in a vertical plane.

Up to this stage the animal was *plantigrade*, that is to say the whole of both the hands and the feet rested upon the ground (Figs. 281*a*, 280*c*). The maximum length of stride and, therefore, greatest speed was eventually secured by raising first the palm and sole, and then the greater part of the digits off the ground, until finally the creature rested only upon the tips of one or two of the digits of each foot or hand (Figs. 280*d*, 281*b*). This extreme *digitigrade* condition entailed the reduction of the surface of contact between feet and ground to a minimum which was possible only to animals that lived on firm dry land.

Hitherto all four limbs have been concerned equally in the support of the body. As the main work of propulsion fell upon the hind limbs, it is not surprising to find that sometimes the whole burden of supporting, as well as of propelling, the body was thrown upon these (Fig. 282). The fore part of the body was then lifted higher and the corresponding limbs adapted in some lines for flying.

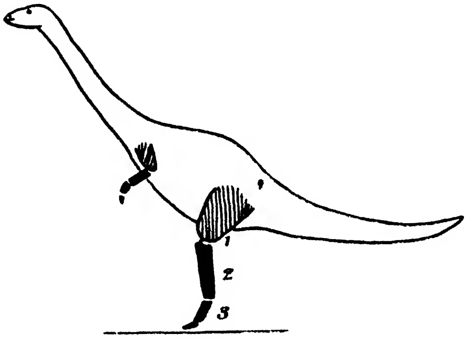


FIG. 282.—Diagram of Bipedal Gait.

An Early Reptilian Radiation.—The earliest reptilian fauna known with any degree of fullness has been unearthed from rocks of Lower Permian age in Texas, and of later Permian and Triassic age in South Africa. Fragments of the same fauna have been found in Brazil, the British Isles and Russia. Already at the opening of the Permian the first-known reptilian radiation had commenced, that is to say their organization had begun to differentiate in several directions, and to become adapted to the varied habitats which the land provided.

An important portion of this primitive fauna consisted of a conservative stock, the Cotylosauria. These had an anapsidan temporal region and were, for the most part, clumsy slow-moving animals. *Seymouria* presents peculiarities of limb-bones and of feet suggestive of a burrowing habit. *Limnoscelis* (Fig. 283) was more active but still retained a sprawling gait. *Labidosaurus* (Fig. 276) was similar but was probably able to lift its body clear of the ground. The later Permian Cotylosauria included *Pariasaurus* from South Africa and Russia. It had a massive body and walked with a waddling manner. *Elginia*, from the Permian of Scotland, was allied to *Pariasaurus*, but its skull bore spine-like bony tubercles not unlike those of certain lizards which live to-day in the deserts of the Deccan in India. With *Procolophon*, from the Upper Trias, the cotylosaurian race died out. It was small, lizard-like and active. *Telerpeton* from the British Trias was similar.

FIG. 283.—Restoration of *Limnoscelis* (after Lull).

This ancient fauna also included more progressive stocks of cotylosaurian origin, but already differentiated in several directions.

Many of these can be classed together in one division, the *Pelycosauria*, in which the reptilian organization was just entering upon great series of changes. One series produced the *Therapsida*, or Mammal-like reptiles, which became dominant during the Trias and eventually attained a consummation in the Mammalia. Other divisions gave origin to the diapsidan and parapsidan Reptiles which dominated the earth during the Jurassic and Cretaceous periods and, through their descendants, the birds, effected the first genuine conquest of the air.

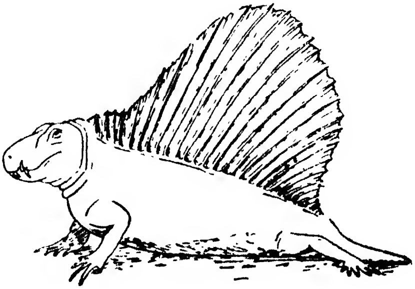


FIG. 284.—Restoration of *Dimetrodon* (after Gilmore).

Dimetrodon (L. Per.–Trias.) (Fig. 284) was a typical advanced Pelycosaurian. Its jaws were armed in front with large incisors and long trenchant tusks, and behind with teeth having serrated edges. It was therefore well fitted for seizing the animals upon which it preyed. Its neural spines on the trunk vertebræ were greatly elevated and together with a covering of skin provided an enormous fin-like structure the purpose of which defies the imagination. *Casea* was a clumsy slow-moving form which fed upon soft vegetation. The more primitive *Myctero-saurus* had teeth of uniform size and ordinary character.

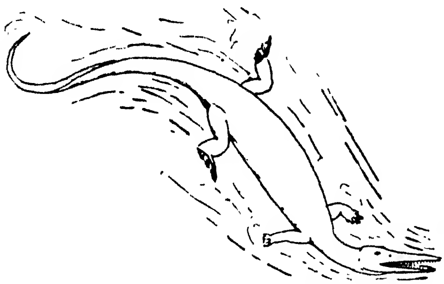


FIG. 285.—Restoration of *Mesosaurus* (modified from Williston).

Some Permian reptiles stand alone as the only traces yet discovered of other great groups. Thus *Mesosaurus* (Fig. 285) was a small animal as perfectly adapted for an aquatic life as a seal. *Aræoscelis* (Fig. 307) with its parapsidan temporal region may possibly have been the prototype of modern lizards. Lastly *Eunotosaurus* seems to have had a similar relationship to the Tortoises.

Reptiles and Mammalia Compared.—In order to appreciate the steps by which the Cotylosaurian stage of organization became transformed into that of the mammal, it is necessary to study the chief differences between these extremes. For this purpose the head skeleton is the most illuminating. The most outstanding differences are associated with the greater size of brain and the more varied function of the teeth. The mammalian brain in consequence of its increase in size (Fig. 286) has expanded upwards and outwards beyond the limits of the original cartilaginous cranium, which with the ear-capsules becomes ventrally placed. The squamosal bone has accordingly been requisitioned from the temporal roof to help in forming the cranial wall. The parietal bones, which in reptiles usually lie flat, here form an arched, sometimes crested, roof to which the jaw-muscles are attached. In the temporal region there is one widely open fossa bounded externally by a single arch, the *zygomatic* arch, formed by the jugal and a process from the squamosal.

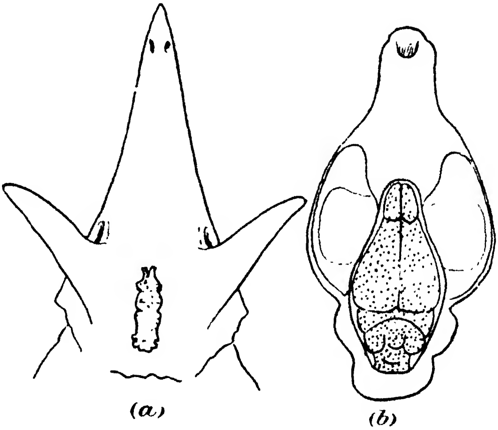


FIG. 286.—Diagram illustrating the relative Size of Brain in (*a*) a successful Reptile and in (*b*) a primitive Mammal.

The teeth in the reptile are numerous, simply shaped and conical, and show as a rule but little variation in size and form (cp. Fig. 278). Their function is mainly prehensile, for the reptile having seized its food generally swallows it whole. The majority of mammals, however, crush and grind their food, or cut it up into small pieces whilst still within the mouth; their teeth, though few in number, are accordingly more varied in form and function (cp. Fig. 332). Those inserted into the premaxilla are used chiefly for gnawing small pieces of flesh off bones, or the soft parts off plants, and are called incisors. The canines lie at the junction of the premaxilla and maxilla. They retain the primitive reptilian pattern, and in predaceous forms become long and trenchant. The premolars and molars are placed behind these, in the maxillary region. They lie hidden from view by the fleshy cheek which serves the purpose of preventing the food from falling out sideways during mastication. Associated with this same difference in the treatment of food is the regular presence in mammals of a false palate; formed by a shelf-like ingrowth from the maxilla, and the palatine bones (Fig. 287). Its presence enables the animal to breathe and triturate its food simultaneously.

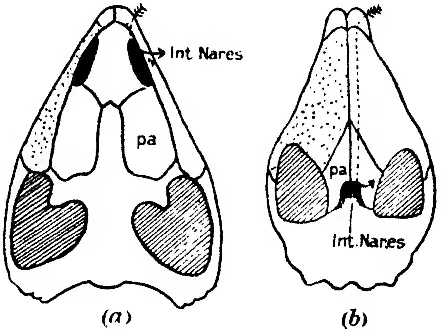


FIG. 287.—Diagram illustrating the Difference between the Palates of Typical Reptiles (*a*) and Mammalia (*b*).

In the former the internal nares open near the front. In the latter the maxillæ (dotted) and the palatines (*pa*) have formed shelf-like ingrowths which meet in the middle line and form a passage which takes the internal nares to the back of the palate.

The reptilian jaw (Fig. 278), like that of the fishes and the amphibians, consists of many bones of which the largest, the dentary, lies in front, while the chief cartilage bone, the articular, lies behind. In Mammalia the lower jaw (Fig. 332) consists of but one bone, the dentary, which in addition to carrying all the teeth provides both the stout upstanding coronoid process for the attachment of the jaw muscles and the articular surface. This latter fits into a facet on the under surface of the zygomatic process of the squamosal (Fig. 288), and that most diagnostic of all bones in the reptile, namely the quadrate, is absent or unrecognizable. The mammalian limbs have almost invariably attained to the posture in which the elbows and knees lie against the flanks. Within these limits they exhibit every phase of advancement from the plantigrade to the digitigrade and bipedal. In reptiles the longest digit is the fourth, in mammals it is the third. The number of phalanges in successive digits in the former is 2, 3, 4, 5, 4; in the latter, 2, 3, 3, 3, 3.

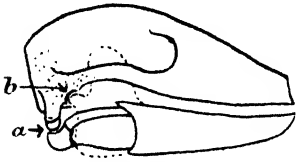


FIG. 288.—Diagram showing the Difference in the position of the Jaw Articulation in Reptiles (*a*) and Mammals (*b*).

In the former the quadrate and articular, in the latter the dentary and squamosal bones are concerned.
Dotted area = Squamosal. Broken line = Outline of mammalian jaw.

Mammal-like Reptiles.—In South Africa rocks of from Middle Permian to Rhætic ages have yielded the remains of a number of small Therapsidan reptiles, which exhibit modifications of the Pelycosaurian condition in directions approaching that of Mammalia. In their skulls the space between the temporal fossæ exhibits various gradations from the more primitive condition in which it is still moderately wide and flat to one in which the parietals arch over the cranial cavity and even rise into a crest as in the Mammalia.

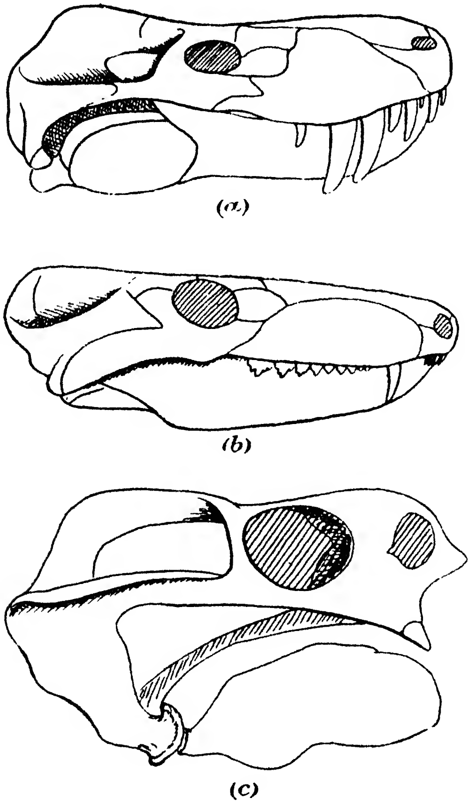


FIG. 289.—Diagrams of the Skulls of various Therapsida.

(*a*) *Lycosuchus*, a therocephalian (after Broom); (*b*) *Cynognathus*, a cynodont (Broom). (*c*) *Gordonia* (after Newton).

The teeth are moderately numerous and differentiated into incisors, canines and cheek teeth (Fig. 289). They are still usually conical and pointed, or at the most slightly compressed. In the lower jaw the dentary has increased at the expense of the other bones and has developed a coronoid process. A quadrate bone is present, but is reduced in size. On the other hand the squamosal bone has increased.

This type of reptile gave rise to several stocks. The closely allied *Therocephalia* and *Cynodontia* (Fig. 289*a*, *b*) exhibited a closer approximation to a mammalian combination of characters. They had a false palate (Fig. 290). The quadrate was very insignificant. In the lower jaw the bones, other than the greatly enlarged dentary, were on the verge of disappearance. In some the cheek teeth were sharp-edged and pointed, and adapted to a carnivorous diet. In others they were flat-topped, and suited to the consumption of herbaceous food (Fig. 290). The Ictidosauria approached the Mammalia most closely. In them the squamosal took part along with the quadrate in the jaw articulation.

In the *Dicynodontia* (Fig. 289*c*) the skeleton as a whole exhibited a strikingly mammalian condition, but the skull became highly modified, especially in the teeth. These underwent degeneration and ultimate suppression. The incisors went first, then the cheek teeth ; finally the canines disappeared in all but a few individuals believed to be males, in which they became very large. Meanwhile both upper and lower jaws became clothed with *horn* as in tortoises and birds. *Lystrosaurus* was a dicynodont adapted to an amphibious life. Its eyes and nostrils were placed high up on the head so that the animal could float, like a hippopotamus, with all parts of its body except those organs submerged.

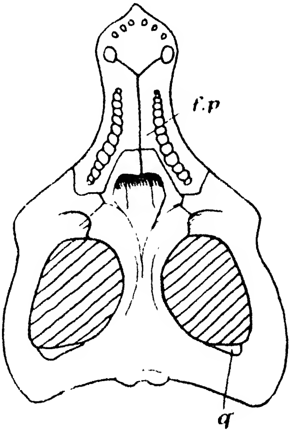


FIG. 290.—Palate of a Cynodont Reptile *Gomphognathus*. Note crushing teeth and false palate. (After Broom.)

q = quadrate. *f.p*, false palate.

The *Dicynodontia* were not only very varied in genera and species, but were also widely distributed over the world. They are represented in the Triassic rocks of Elgin in Scotland by the genera *Geikia* and *Gordonia*.

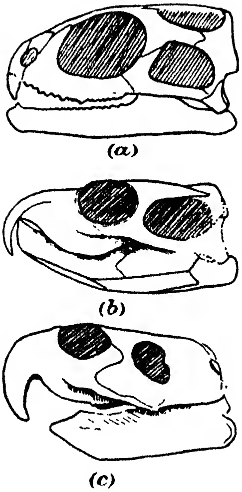


FIG. 291.—Skulls of Rhynchocephalia.

(*a*) *Sphenodon*. (*b*) *Rhynchosaurus*. (*c*) *Hyperodapedon*. (*b*) and (*c*) after Woodward.

The New Zealand Lizard and its Allies.—Sphenodon is a lizard-like animal which lives to-day on a small island to the north of New Zealand. Its most familiar feature of interest is the well-preserved vestige of a median eye, with lens and retina complete, situated under the skin on the top of the head. In the skull its presence is indicated by an opening, the parietal foramen, placed between the parietal bones. This opening forms a prominent feature in the skull of many extinct reptiles. The skull of *Sphenodon* is typically diapsidan (Fig. 291*a*). The quadrate bone is large and roughly triradiate in form, and is held firmly in place by stanchions attached to each radius (Fig. 292). Its anterior ray is fixed to the pterygoid ; its upper posterior ray to the squamosal on the outside, and to a process of the ear capsule on the inside. Its lower posterior ray provides the surface on which the lower jaw articulates, and is held in place by the jugal and quadratojugal bones. The premaxillary teeth are slightly enlarged, a peculiarity which is more emphasized in fossil forms and gives the appearance of a curved beak (Fig. 291). This has suggested the name *Rhynchocephalia* (beak-headed) for the order to which these reptiles belong.

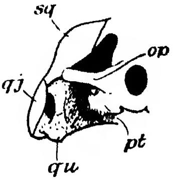


FIG. 292. — Diagram showing the relationships of a Fixed Quadrate to adjoining Bones.

sq, squamosal. *qj*, quadrate jugal. *qu*, quadrate. *pt*, pterygoid. *op*, process from otic capsule.

The order probably originated from a section of the Cotylsaurian stock, which did not show any marked tendencies towards mammal-like modifications. It reached its maximum development during the Triassic period. *Rhynchosaurus* (Keup. Brit.) was strikingly like Sphenodon, but in its expanded coracoid and small foramen between the ischium and pubis retained a more primitive condition. Its orbits tended to face upwards, a feature which indicates a partial adoption of amphibious habits. Its premaxillary teeth were long and curved like a beak. This feature was greatly exaggerated in *Hyperodapedon* (Trias. Brit.), a much larger animal.

In later periods the order sank to relative insignificance. *Saphæosaurus* (Solenhofen Slates) closely resembled Sphenodon. *Champsosaurus* (Cret.–L. Tert.) was from four to five feet long and of semiaquatic habits. Its snout, like that of certain crocodiles which live by catching fish, was long and armed with many sharp teeth.

Crocodiles and their Fossil Allies.—In the Crocodiles, as in *Sphenodon*, the temporal region is typically diapsidan, and the quadrate is stout and fixed. Crocodiles exhibit, however, differences, certain of which may be summed up under three headings. Firstly, there are those due to the adoption by the Crocodiles of an amphibious mode of life. Thus the eyes lie close to one another on the top of the head (Fig. 296*a*). Between them and the nostrils the snout tends to become elongated. They have a secondary palate in which the pterygoids take part as well as the maxillæ and the palatines (Fig. 293*c*). This carries the internal nares into a very backwardly placed position.

Secondly there are differences due to the attainment of more advanced stages along those lines of development common to other groups. Thus the vertebræ have gone beyond the amphicœlous to the procœlous stage, so that the flexibility of the vertebral column as a whole is due to a ball-and-socket articulation between the vertebræ. Finally, there are differences due to specialization along lines peculiar to the crocodilian type. Thus the ilium is expanded

(Fig. 294) antero-posteriorly; in both fore and hind feet the first three digits are enlarged. There are also those general proportions of body which give the creature its characteristic appearance.

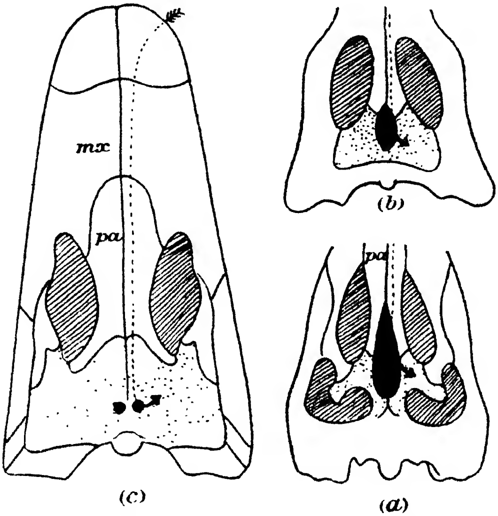


Fig. 293.—Diagrams of the Palate of Crocodiles showing the backward shifting of the Internal Nares.

(*a*) *Pelagosaurus* (Lias). (*b*) *Theriosuchus* (Purbeck, modified from Woodward). (*c*) Crocodile (present).
Lining = vacuities. Black = internal nares. Dotting = pterygoid. Broken arrow shows the course of the passage from the external to internal nares. *pa*, palatine. *mx*, maxilla.

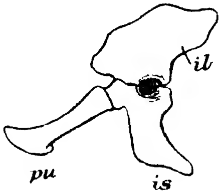


Fig. 294.—Pelvic Girdle of Crocodile showing the expanded Ilium (*il*).
pu = pubis. *is* = ischium.

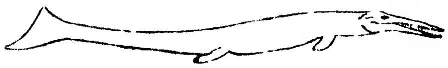


Fig. 295.—Outline Restoration of *Geosaurus* (U. Jurassic), a marine crocodile (after Fraas).

Broad-snouted crocodiles appeared as early as the Upper Cretaceous. Long-snouted forms with more completely webbed feet, such as those which live in Borneo to-day, also existed during the Cretaceous. Forms allied to the *Gavial* of India, which feeds upon fish, lived in the Pliocene, and grew to a length as great as fifty feet. During the Jurassic period there lived a long-snouted but more primitive type of crocodile, in which the vertebræ were still amphicœlous. In *Teleosaurus* the formation of the secondary palate had only reached a stage in which the palatines were incompletely united, and the nares were situated between them. In *Goniopholis* (Purbeck–Wealden) the union of the palatines was complete and the internal nares lay further back.

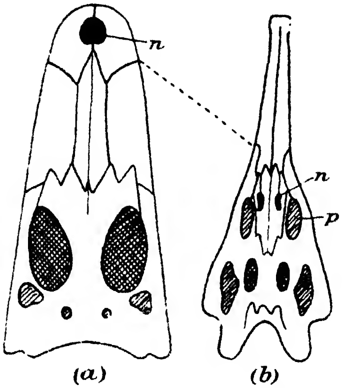


FIG. 296.—Diagram of the Roof of the Skull to show that the Snout is elongated behind the Nostrils *n* in the Crocodile (*a*) and in front of the Nostrils in a Phytosaur *Belodon* (*b*).

Note the two pre-orbital fossæ *p* in the latter. Cross-lined areas = eyes.

All the crocodiles mentioned above were amphibious and confined to fresh waters. The Jurassic *Geosaurus* (Fig. 295), however, arose at an early stage in the evolution of the group, and became perfectly adapted for a life in the open sea. Its limbs were flipper-like, and the tip of its tail bore a fleshy fin-shaped lobe. Concerning the yet earlier history of the crocodiles nothing certain is known, but during Triassic times their place in nature seems to have been occupied by the *Phytosauria*, which resembled them in shape both of the body and the head. In these, however, the elongation of the snout took place in front of the nostrils (Fig. 296*b*), so that the internal nares already occupied a posterior position in the mouth and a secondary palate was not needed. A special feature was the presence of a vacuity, the pre-orbital fossa, in front of the orbits.

The Dinosauria.—During Triassic times, when mammal-like reptiles had begun to wane, there arose a race, the Dinosauria, which in their way were just as perfectly adapted for easy and even rapid progress on the land. These became both the dominant reptiles and the dominant land animals of the late Trias, the Jurassic and the Cretaceous periods, a stretch of time which may with equal truth be called the "Age of Reptiles," or the "Age of Dinosaurs." The dinosaurs had a common ancestry with the crocodiles in some group not far removed from the Phytosauria, and possibly represented by the tiny *Ætosaurus* (Fig. 297). All these had a diapsidan type of temporal region and a large fixed quadrate, but the dinosaurs shared with the phytosaurs

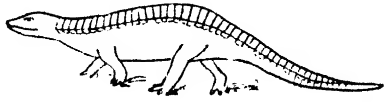


FIG. 297.—Outline Restoration of *Ætosaurus* (after Lull).

This is closely allied to the ancestral stock of the phytosaurs and dinosaurs. Note quadrupedal gait.

the possession of a pre-orbital fossa, and the absence of a secondary palate.

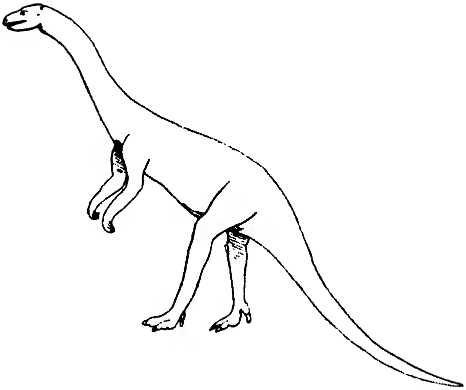


Fig. 298.—Outline Restoration of *Anchisaurus* (from Schuchert after Lull). A primitive dinosaur with bipedal gait.

The distinctive feature of the order was a bipedal gait (Fig. 298). This determined many of the other structural peculiarities. With the whole weight of the body thrown upon the hind limbs the attachment of the girdle to the backbone had to become greatly strengthened. In the earlier forms the ilium was united to only three vertebræ; in Jurassic and Cretaceous genera, to four or even five. Triassic dinosaurs were already digitigrade, and later advance consisted in an elongation of the metatarsal bones, and a suppression of one or other of the digits I and V.

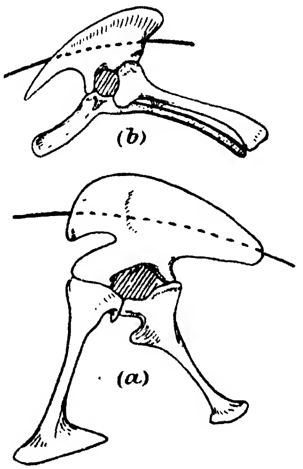


Fig. 299.—Pelvic Girdles of two types of Dinosaur.

(*a*) *Saurischia*. (*b*) *Ornithischia*. Thick broken line = axis of vertebral column. Dotted area with thick outline = process of pubes.

Two types of dinosaurs, characterized by differences in the hip girdle, are recognized. These diverged from one another possibly as early as the Trias. In one type, the *Saurischia* (Fig. 299*a*), the pubic bone was simple, like that of reptiles generally. In the other type, the *Ornithischia* (Fig. 299*b*), it carried a long stout process at its upper end, which projected backwards parallel to the ischium, and so presented a superficial similarity to that in birds.

In the Saurischia the jaws bore teeth along the whole of their margins (Fig. 300*a*), or when these were reduced in number they disappeared only at the hinder end (Fig. 300*b*, *c*). In the Ornithischia (Fig. 301) it was the hind teeth that persisted; the front ones were suppressed and replaced functionally by a beak-like horny covering of this region of the jaws. In the lower jaw this covering was supported by a special half-moon-shaped bone called the ***pre-dentary***. On the whole the Saurischia, *e.g. Tyrannosaurus* (Cret.),

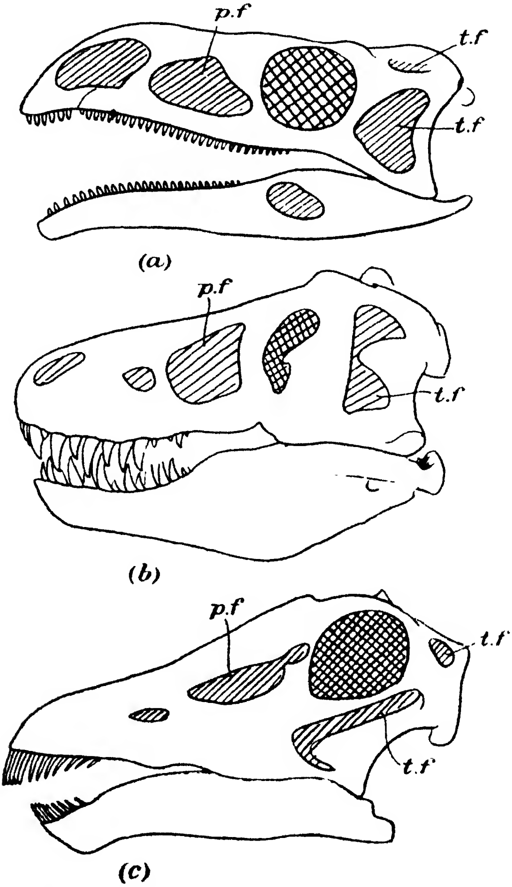


FIG. 300.—Diagrams of the Skulls of three Saurischian Dinosaurs.

(*a*) ***Plateosaurus*** (after Jaekel), a primitive Triassic dinosaur. Note the presence of teeth along the whole mouth margin. (*b*) *Tyrannosaurus* (after Osborn). A carnivorous dinosaur. Note the trenchant character of the teeth and their more limited extent. (*c*) *Diplodocus* (after Marsh). A gigantic quadrupedal saurischian dinosaur. Note the limitation of teeth to the front of the mouth margin.

Cross hatching = eye. *pf*, pre-orbitalf ossa. *t.* , temporal ossa.

were carnivorous (Fig. 300*b*), the Ornithischia, *e.g.* *Iguanodon* (Wealden), herbivorous (Fig. 301).

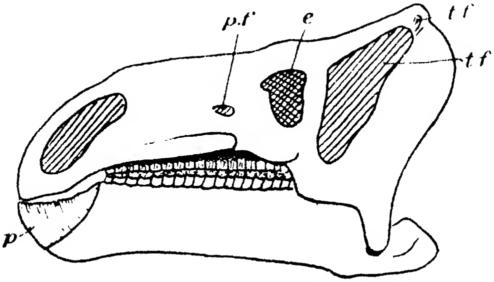


FIG. 301.—Diagram of the Skull of an Ornithischian Dinosaur, *Iguanodon* (adapted from Dollo).

p, predentary bone. *p.f*, pre-orbital fossa. *e*, eye. *t.f*, temporal fossa.
Note the absence of teeth in front, and the grinding character of the teeth at the side.

Some sections of both divisions reverted secondarily to a quadrupedal habit. Among the Saurischia, those which did this, *e.g.* *Diplodocus* (U. Jur.), and *Brontosaurus* (U. Jur.) became gigantic and massive (Fig. 302). The joints of their limbs were loose and had a cartilaginous covering on the articular surfaces, conditions which imply amphibious habits. Among the Ornithischia the quadrupedal gait was adopted by forms which acquired weapons of defence and offence. Thus *Stegosaurus* (Jur.) had large plates on its back and spines on its tail, and *Triceratops* (Cret., Fig. 303) had large horns and a shield-like bony rim upon its head.

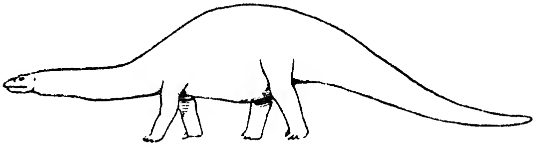


FIG. 302.—Outline Restoration of *Brontosaurus* (from Schuchert after Lull).
A Saurischian dinosaur which has reassumed secondarily a quadrupedal habit.

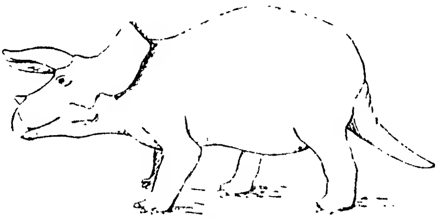


FIG. 303.—Outline Restoration of *Triceratops* (from Schuchert after Lull).
An Ornithischian dinosaur that has returned secondarily to quadrupedal habit. Note the horns.

The dinosaurs were not all of gigantic proportions. Thus *Scleromochlus* (Trias., Elgin) was no larger than, and not unlike, a large frog. *Compsognathus* (Jur.) was the size of a cat and just as active.

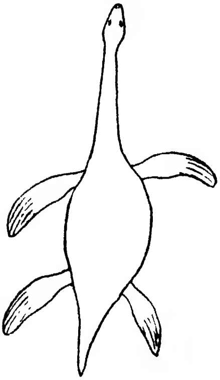


FIG. 304. — Outline Restoration of *Plesiosaurus*. (Lias)
Note the oar-like paddles.

Extinct Denizens of the Deep.—It has been seen that terrestrial animals had aquatic ancestors and that the essentials of their structure were evolved under aquatic conditions. Long after their organization had been adapted for life on the land it still possessed the capability of ready adjustment to life in the water, whenever this was readopted. Every period from the Permian onwards had its aquatic animals of terrestrial origin, and every great group of reptiles had some representatives that resorted to the water for their livelihood. There were, however, two great groups,t he *Sauropterygia* and the *Ichthyosauria*, of which every known member led an aquatic existence, and which are so modified that their relationship to other orders is still an unsolved problem.

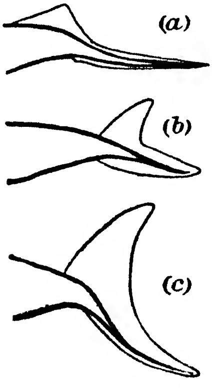


FIG. 306.—Diagrams illustrating the Evolution of the Tail Fin of Ichthyosauria.
(*a*) *Mixosaurus*, Trias. (*b*) *Ichthyosaurus*, Lias. (*c*) *Ichthyosaurus*, U. Jurassic. (All adapted from Abel.)
Note the topsy-turvy heterocercality.

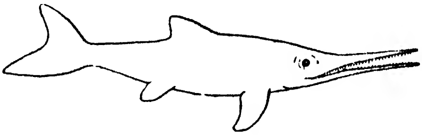


FIG. 305.—Outline Restoration of *Ichthyosaurus*. (Lias)
Note the keel-like paddles.

Plesiosaurus was a typical sauropterygian (Fig. 304). It had a wide depressed oval trunk with a short thin tail behind and a long tapering neck and small head in front. *Ichthyosaurus* (Fig. 305) on the other hand had as compact a body as a fish.

In both types the limbs were paddles. In *Plesiosaurus* they were attached by a narrow base and were used like oars. In *Ichthyosaurus* they were broad based, and functioned as keels, whilst the tail was used as the organ of propulsion, and during its evolution passed through a series of changes (Fig. 306) parallel to that already studied in fishes, but with the symmetry reversed. In *Lariosaurus*

(Fig. 308*a*), a Triassic sauropterygian, the terrestrial character of the limbs is still recognizable, the podial portion is short and the rest is long, the five digits have the normal length and number of phalanges. That aquatic adaptation has begun is shown by the shortening of the lower limb bones, by the looseness of the joints, and by the partly cartilaginous condition of the carpus and tarsus, the bones of which have become mere rounded nodules. The Permian *Aræoscelis* (Fig. 307) may represent the terrestrial forerunners of the Plesiosaurs.

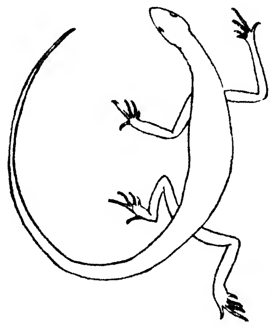


Fig. 307.—Outline Restoration of *Aræoscelis* (adapted from Williston).

In later Sauropterygia (Fig. 308*b*, *c*) these features became more emphasized until the elements of the lower limb were no larger than carpal or tarsal bones, and all articular movements between the bones were lost. A new tendency was an increase in the number of phalanges up to as many as fifteen in some digits. The podial portion now exceeded the remainder of the limb in extent. Even in the latest members of the Sauropterygia, *e.g.* *Polyptychodon* (Cret.), the limbs still functioned as the chief propelling organs. Among the ichthyosaurs this oar-like phase in evolution had been passed through completely, as early as the Trias. (Fig. 309*a*), so that in Liassic forms the upper limb bone was very short and stumpy (Fig. 309*b*), and the lower had merged into the mosaic of polygonal bones which make up the major part of the paddle. In some the number of digits had increased as well as the number of phalanges. In the latest genera, *e.g.* *Ophthalmosaurus* (Jur.) (Fig.

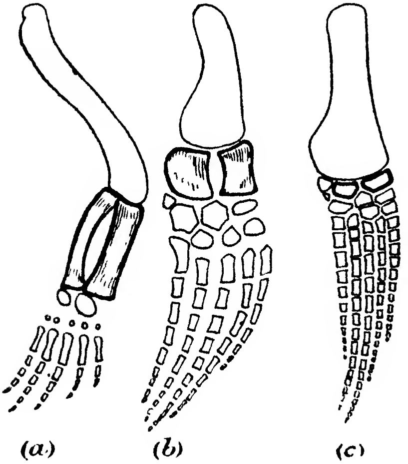


Fig. 308.—Diagrams of the Right Hind Limb of (*a*) *Lariosaurus*, Trias (adapted from Abel); (*b*) *Thaumatosaurus*, L. Juras. (adapted from Fraas); (*c*) *Trinacromerum*, Cret. (adapted from Williston).

Note the gradual reduction of the lower limb bones (black outlined) and the progressive increase in the number of phalanges.

309*c*), the bones of the mosaic were reduced to rounded discs imbedded in a matrix of cartilage.

It is not unlikely that the Sauropterygia, like living turtles, resorted to the shore to lay their eggs. In the Ichthyosauria the eggs were hatched within the body, and the young were born alive and ready to swim about. Thus the last link with the land was broken, and the ichthyosaurian was as free to roam the open seas as a whale or porpoise.

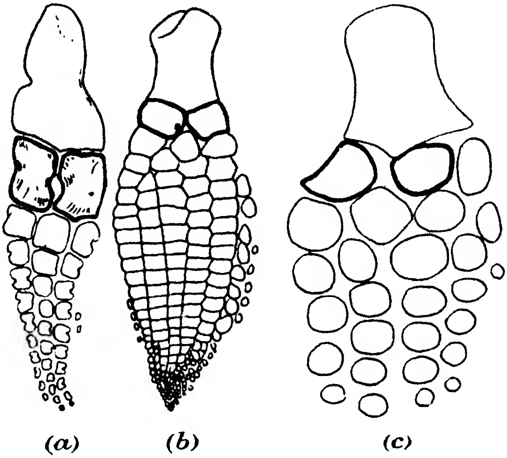


FIG. 309.—Diagrams of the Hind Limb of various Ichthyosauria.

(*a*) *Merriamia*, Trias (adapted from Merriam). (*b*) *Ichthyosaurus commune*, Juras. (adapted from Zittel). (*c*) *Ophthalmosaurus*, Oxfordian (adapted from Andrews).

Tortoises and Turtles.—Among existing reptiles the *Chelonia* (Tortoises and Turtles) are perhaps the most anomalous. Already in Triassic times they possessed all the essential characteristics of the order, such as the box-like bony casing (Fig. 310*a*), the absence of teeth, and the presence of a horny covering to the jaws. They had an anapsidan type of temporal region (Fig. 311), a fixed quadrate, a false palate to the mouth, and three phalanges in all except the first digits. They differed from living forms, however, in having amphicœlous vertebræ in the neck. The anapsidan condition of the temporal region points to the Cotylosauria as the ancestral stock, but as yet nothing is known of any of the transitional stages. *Eunotosaurus* (M. Perm.) with its flattened plate-like ribs may represent such a stage.

The early Chelonia, like the Cotylosauria, and many living forms, found a congenial home on the riverside plains. In such a habitat an amphibious existence like that led by modern " Snappers " was almost inevitable. It is not improbable that *Proganochelys* (Trias.), like a Snapper, had webbed feet and could both swim quickly in water and move actively on land. Before the close of the Jurassic some of the Chelonia migrated towards the sea. At first they kept to the littoral zone, but during the Cretaceous some, *e.g. Archelon*, went further and became at home in the open waters. Along with this change of habitat the skeleton underwent a corresponding change. The long bones of the limbs shortened and the phalanges increased in length, but not in number. The bony casing, or carapace, flattened and became fenestrated owing to the reduction of the paired bones. This latter process continued until the broad flat ribs were exposed. The series of changes is illustrated by the genera *Proganochelys* (Trias.), *Thalassemys* (Jur.), *Toxochelys* (Cret.), and *Archelon* (Cret., Fig. 310). The last was eleven feet long, and the largest and one of the most specialized chelonians known. Modern turtles probably originated in late Cretaceous times from a form in the *Toxochelys* stage of degeneration.

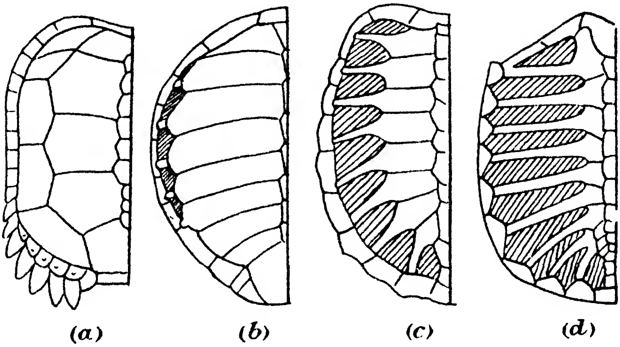


FIG. 310.—Diagrams showing the Change in Structure of Dorsal Carapace which takes place progressively in Chelonians which lead an aquatic Existence.

(*a*) *Proganochelys*, Trias (adapted from Fraas). (*b*) *Thalassemys*, Jurassic (adapted from Fraas). (*c*) *Toxochelys*, U. Cret. (after Wieland). (*d*) *Archelon*, U. Cret. (after Wieland). Note the gradual reduction of bony matter by the enlargement of fenestræ (lined).

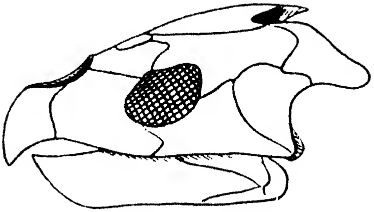


FIG. 311.—Diagram of the Skull of *Archelon*.

Note the absence of teeth and the anapsidan condition of the temporal region.

During the Early Tertiary some Chelonia migrated from the river-plains into the grasslands and gave rise to the tortoises. In these the carapace became thick and very convex and thus provided an effective protection from the newly-evolved mammalian carnivores. They reached their acme in numbers during the Miocene and Pliocene. Some attained an even greater stature than that of the Giant Tortoises of the Galapagos Islands.

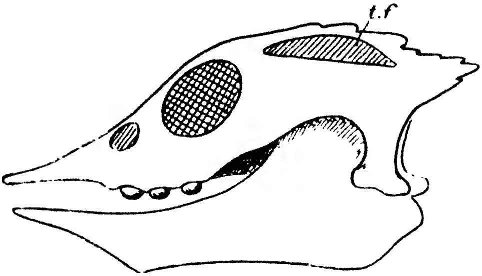


FIG. 312.—Diagram of the Skull of *Placochelys* (adapted after Jaekel), a Triassic Placodont.

Note the presence of crushing teeth, and the synapsidan condition of the temporal region. *tf*, temporal fossa.

During the Trias there also existed a group of Reptiles, the *Placodontia* of unknown affinity, which adopted a similar mode of life to that of the Chelonia, and likewise exhibited a remarkable similarity to them due to parallel evolution under like conditions. They, however, possessed a synapsidan temporal region, stout round crushing teeth, and had more numerous sets of bones in the carapace (Fig. 312).

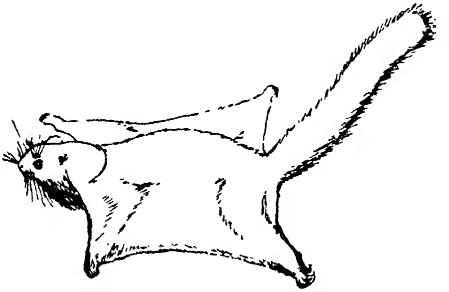


FIG. 313.—Diagram of Flying Squirrel (*Pteromys*, adapted from Flower after Haeckel), to show the method of using a Fold of Skin for a Parachute Glide or Flight.

Denizens of the Air.—The passage of the vertebrates into the air was probably made indirectly from the trees and other elevated situations, to which they had climbed and in which they learned to live. There they would often need to leap to the ground or from bough to bough or from tree to tree, and would have endless opportunities for trial flights. At first these would be no more than parachute glides, like those of the flying squirrel of to-day (Fig. 313). This creature has a fold of skin on either side of its body which it can extend by means of its limbs. It only requires a further extension of this fold and suitable movements of the limbs to convert the glide into a flight.

During the Middle and Late Mesozoic one branch of the Reptiles, the *Pterosauria* (Fig. 314), attained to this degree of skill in flying. They had a membranous fold of skin arising from the side of the body which was supported and extended by means of the fore-limbs and by a greatly elongated fifth digit. The other digits were normal, and provided with strong hooked claws of use for climbing. In forms like *Pterodactylus* (U. Jur.) the tail was short, but in others like *Rhamphorhynchus* (U. Jur.) it was long and provided at the end with a membrane of its own.

FIG. 314.—Diagrammatic Restoration of a Pterosaurian (*Pteranodon*).

Another unknown branch of the Reptiles gave rise to the birds or Aves, of which *Archæopteryx* (U. Jur., Fig. 316) was the earliest representative. In this the place of the membrane was taken by long stout feathers, formed by a modification of the ordinary papilla-like outgrowths of a reptile's skin. These feathers were situated along the hinder border of the forelimb and along either side of the lizard-like tail. There may also have been some behind the thighs (Fig. 315). This system of feathers when extended furnished a strong gliding plane.

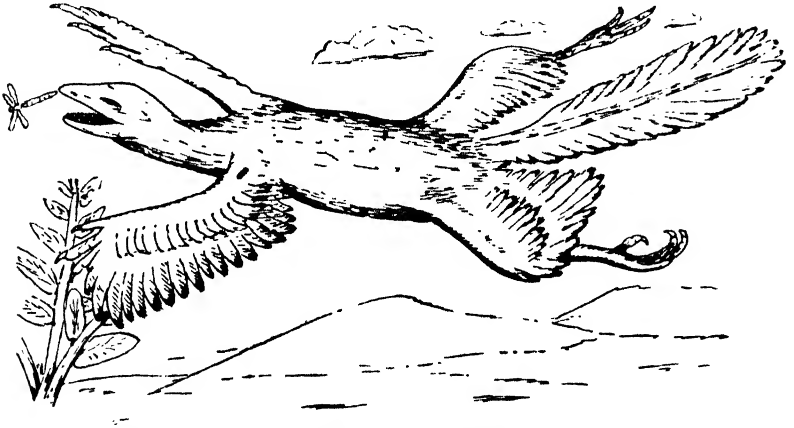


FIG. 315.—Diagrammatic Restoration of *Tetrapteryx* (after Beebe) illustrating the view that in the Parachute Phase in the Development of Flight among Birds there were large Feathers on the Hind as well as the Fore Limbs.

In *Archæopteryx* a flapping movement which changed this glide into a flight was also performed by the fore limbs. These (Fig. 317*a*) had only three digits (I–III), which were of normal size, and provided with strong claws for climbing and scrambling about the trees and bushes. Owing to the stoutness of the feathers there was no need for an elongation of the arms and digits. In true birds also there are only three fingers (Fig. 317*b*, *c*), which, however, have lost their claws and some of their phalanges. A firm foundation for the feathery plane is produced by a fusion of the bones of the lower arm with one another and with the metacarpals.

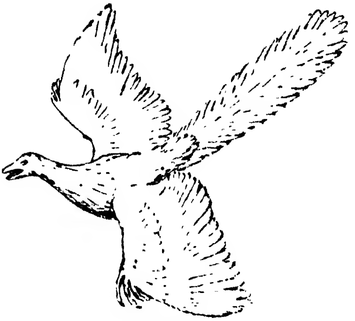


FIG. 316.—Diagrammatic Restoration of *Archæopteryx* in the Middle of a Parachute Glide.

The long feathers on the wings and tail provide the extended surface required.

The muscles which work the wings of a bird are attached to the breast bone, which is large and boat-shaped and bears a deep keel (Fig. 318). The fact that in Pterosauria and *Archæopteryx* this bone is small, and the keel shallow shows that they were weak fliers, and were little more than flapping parachutes. In birds the hind limbs and girdle bear a marked resemblance to those of the Dinosauria. This is, however, mainly due to parallel adaptation for similar habits. The first digit of the foot can often be opposed to the other digits (Fig. 315) so that with its aid they can grasp such a support as a branch. In *Archæopteryx* the foot was similarly available for perching.

The majority of pterosaurs had teeth, but in later genera these became reduced or even suppressed, *e.g.* *Pteranodon* (Cret.). Similarly among birds, *Archæopteryx* and all the known Cretaceous forms had teeth. In all Tertiary and present-day birds these are absent.

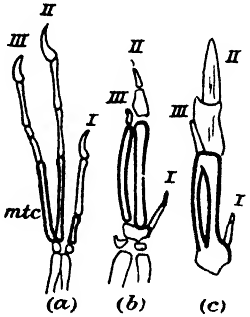


FIG. 317.—Diagrams illustrating the Difference between the Wing Skeleton of (*a*) *Archæopteryx*, (*b*) Sixteen-day Chick, (*c*) Adult Fowl.

I–III, digits. *mtc*, metacarpal bones.

In Cretaceous times true birds existed. *Ichthyornis* (Fig. 318) had an unusually deep keel, and was a strong flier. *Hesperornis* (Fig. 318) on the other hand had only vestigeal wings, but was a perfect diver. Among Tertiary birds reference need only be made to the giant flightless Moas of Madagascar and New Zealand. These like the Ostrich were as perfectly adapted for bipedal gait as any dinosaur. True flying birds are rare as fossils, but their history during Tertiary times must have been one of continual and successful progress since to-day, as judged by their number, their variety, and their adaptation to many different modes of life, they are at the floodtide of their evolution.

FIG. 318.—Diagrams illustrating the chief Structural Differences between the two Cretaceous Birds (left) *Ichthyornis*, (right) *Hesperornis*.

The former, a strong flier, has large wing and breast bone and has the first toe opposable to the others for perching. The latter, being a strong diver has a much reduced wing and breast-bone, but a large pelvis.

The Last Reptilian Radiation.—Among existing reptiles the lizards and the snakes are the most varied and ubiquitous. The latter, called the Ophidia, are specialized derivatives of the lizards or Lacertilia, and both are therefore classed together as the *Squamata*, a name which refers to the scale-like markings upon their skin. Little is known about the history of the Ophidia, for only scanty remains of them are found in the Cretaceous and Tertiary rocks.

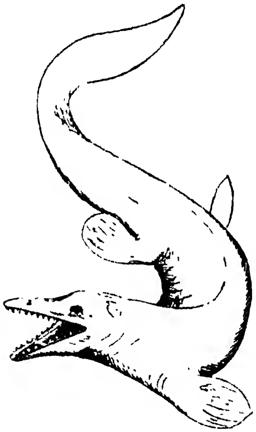


FIG. 319.—Outline Restoration of a Mosasaurian (*Clidastes*) (adapted from Williston).

With the opening of the Cretaceous the period of domination of the reptiles passed rapidly to a close. The Squamata, which may have evolved from the Rhyncocephalia, spread rapidly and became the supreme reptilian group. The most important among these Cretaceous squamates were the Mosasauria (Fig. 319). These were large forms, sometimes forty feet long, which occupied the same place in the economy of these late Mesozoic seas as did the Ichthyosauria in the Jurassic. They approximate to the same grade in lacertilian evolution as the Nile Lizard, *Varanus*, especially in the structure of the skull. The snout, however, was longer and more pointed. They had a curious joint in the lower jaw just behind the teeth (Fig. 320). Their limbs attained a stage analogous to that of the Triassic ichthyosaurs, but the wrist and ankle exhibited every grade from a completely bony to an almost cartilaginous condition. The *Aigalosauria* (L. Cret.) represent an early stage in the evolution of the mosasaurs when the limbs were still mainly terrestrial in character, but were webbed and without claws. The *Dolichosauria* (Cret.) were a semi-aquatic offshoot of the same stock characterized by an elongated neck.

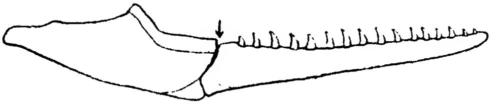


FIG. 320.—Lower Jaw of a Mosasaurian (adapted from Williston) to show Peculiar Joint ↓ in the Middle of its Length.

Information concerning the evolution of the lizards during the Tertiary period is scanty, but to-day they reproduce in a small way the adaptations exhibited by the Mesozoic Reptilia. The majority are quadrupedal, but a few are bipedal. Some climb rocks and trees and make parachute flights through the air, whilst others resort frequently to the water or live in the desert. The varied character of their food is reflected in their teeth which range from sharp piercing organs to round flat crushing plates. The name *Iguanodon* for a great Jurassic dinosaur recalls the similarity which its teeth bear to those of the lizard *Iguana*. Thus in the Squamata of late Mesozoic and subsequent times the reptiles experienced their last and least important radiation.

MAMMALIA

Teeth and their Modifications.—The evolution of the higher from the lower Vertebrates was accompanied by a reduction in the number of elements in the skeleton, so that in mammals, for example, the number in the roof of the skull, the lower jaw, the pectoral girdle, reached a minimum. Evolutionary energy now seems to have become concentrated on the perfecting of each element for the performance of its special function. This was particularly so in the case of the teeth.

In fishes the teeth were small and numerous, and new teeth grew up in the place of the old ones throughout life. In reptiles the number was greatly reduced, but the teeth were much larger, and new teeth still replaced old ones to an indefinite extent. In modern mammals the number of teeth reaches a maximum of only 44; in Man it is still smaller, being 32. Now, however, instead of the teeth being long, simple and uniform in shape, with only one root, nearly every tooth has its own characteristics, and they are grouped accordingly into incisors, canines, premolars and molars. The teeth of the young are called milk teeth and are smaller and fewer in number than in the adult. Thus in a child there are only two cheek teeth. Eventually these milk teeth drop out, and their places are taken by the adult or permanent dentition. Those which replace the two cheek teeth are called premolars, whilst three teeth which come up behind these and are unrepresented in childhood are the true molars. The teeth on one side of the mouth in man may be briefly described in a dental formula thus :—

Upper Jaw : 2 Incisors. 1 Canine. 2 Premolars. 3 Molars.
Lower Jaw : 2 Incisors. 1 Canine. 2 Premolars. 3 Molars.

This may be more briefly written thus : $\frac{2.1.2.3.}{2.1.2.3.}$ A similar replacement of temporary by permanent teeth in the adult takes place also in the other mammals.

In a typical tooth, *e.g.* a molar, the part which is sunk in the jaws is the fang or root ; that which can be seen in the mouth is the crown. This often bears tubercles or cusps on its upper surface. This specialization of the cheek teeth, so essentially characteristic of mammals, is no doubt associated with an increased tendency for the animal to cut up or pound its food before swallowing it. This new function demands a maximum of power for its performance and, therefore, fell naturally upon those teeth which lay nearest to the muscles and the fulcrum of the jaws. These teeth reflect with great sensitiveness the varying types of food, *e.g.* insects, flesh, fruit, vegetation, upon which mammals feed ; they are, therefore, one of the most highly instructive portions of the skeleton. At the same time, owing to the very resistant character of their substance, they are the most frequently preserved as fossils. The lowliest condition of the teeth is found in *Dromatherium* (Fig. 321B, Trias.), in which as in many lowly mammals the incisors, canines and even the premolars have still the simple reptilian form. In the molars, however,

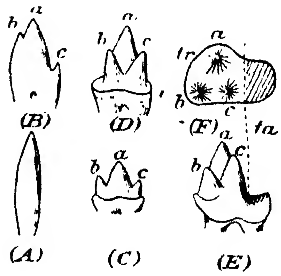


Fig. 321.—Types of Triassic and Jurassic Mammalian Lower Molar.

(*A*) Simple reptilian type. (*B*) *Dromatherium*, (*C*) *Amphilestes*, both Triconodont. (*D*) *Spalacotherium*, Tritubercular. (*E*) *Amphitherium*, side view. (*F*) Crown view, Tri-tuberculo-sectorial type. (All after Osborn.)

Letters *a*, *b*, *c*, show the relationships of the cones in different types to one another.
tr = trigonid. *ta* = talonid.

the root has begun to divide and the crown bears small cusps behind and in front of the main or reptilian cone.

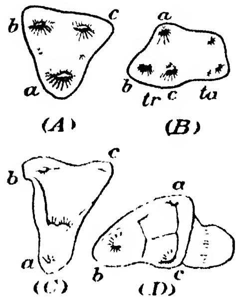


FIG. 322.—Trituberculo-sectorial Teeth of Cretaceous Mammals.

(*A*) Upper molar of *Ectoconodon*. (*B*) Lower molar of unknown genus (after Osborn). (*C*, *D*) Upper and Lower molars of *Deltatheridium* (after Gregory and Simpson).

Lower edge is inner side. Lettering as in Fig. 321.

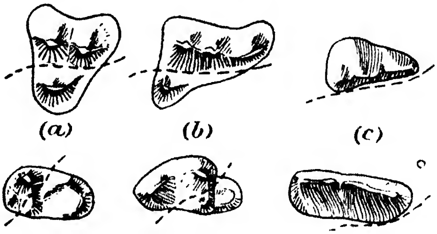


FIG. 323.—Method of Evolution of Carnassial Teeth from Tritubercular Type in Creodonts (after Osborn).

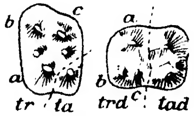
Upper row = upper molar. Lower row = lower molar.

(*a*) *Triisodon*. (*b*) *Oxyæna*. (*c*) *Hyænodon*.

Broken line marks off that portion of the teeth which becomes reduced and suppressed from that which remains and is modified.

In Lower Jurassic times, as represented by *Amphilestes* (Fig. 321C) these new cusps were in line with one another, and a slight swelling, called the *cingulum*, appeared around the base of the crown. *Amphitherium* (Fig. 321E, F, M. Jur.) and its allies also had three cusps on the lower molar, but these were arranged at the corners of a triangle called the *trigonid*. Another feature was present, namely, the heel or *talonid*, a table-like outgrowth from the base of the crown on its posterior margin. In *Melanodon*, (U. Jur.) the upper molars are also known. In plan the crown was obliquely triangular. It had a main cusp (*bc*) near the centre, a less prominent cusp (*a*) at the apex and accessory cusps round the margin. In *Deltatheridium* (Fig. 322), a primitive Cretaceous insectivore, the main cusp was divided into two at its apex. This seems to have been an early stage in the establishment of a tritubercular condition in the upper as well as in the lower molar. When in use the crown of the upper molar bit against the talonid of the lower and gave a crushing action. The trigonid, however, bit between the crowns of the upper teeth and thus acted as a cutting apparatus. Such a tooth is known as the *trituberculo-sectorial* tooth and provided the pattern upon which the description of most later types may be based. In Upper Cretaceous times the trituberculo-sectorial type of tooth still held sway, but the cusps on the trigonid were lower and more blunt, whilst the heel was extended a little and bore three small cusps (Fig. 322B). At this horizon upper jaws have also been found which show that the upper teeth have no heel and that the apex of the triangle of cusps upon the trigon points inwards (Fig. 322A). There are small cusps between the inner and two outer cusps so that these molars have attained a *quinquetubercular* condition.

From the Mesozoic tritubercular type of tooth most of the modifications found in the molars of Tertiary mammals can be derived. By reason of its sharp cusps it was eminently suited to an insect diet. In insectivorous mammals, therefore, it has undergone but little modification. When it was modified to form flesh cutting or carnassial teeth (Fig. 323) the heel and part of the trigon or trigonid became gradually reduced and ultimately suppressed. The remaining cusps—namely, the two outer in the upper and the two anterior in the lower jaw—became enlarged and formed sharp cutting edges which passed one another like the blades of a pair of scissors.



(*A*) (*B*)

Fig. 324.—Molars of Primitive Herbivore (*Tetraclænodon*, Basal Eocene).

(*A*) Upper M2. (*B*) Lower M2 (after Osborn).

a, *b*, *c*. Cusps of Primitive Tritubercular tooth. *ta* = talon. *tad* = talonid. *tr* = trigon. *trd* = trigonid. Note bunoid cusps.

In herbivorous mammals (Fig. 324*a*) the triangular upper molar in addition to becoming five-cusped developed a small heel upon which another or sixth cusp appeared. In the lower molar the cusps of the trigonid became blunt, whilst those upon the heel became equal to them in size. Thus a *hexatuberculate* condition was attained. In this case, however, the foremost and hindmost cusps were often subsequently suppressed and the tooth became quadritubercular. Further modification of the herbivorous molar followed (Fig. 325) three lines: (1) The addition of cusps at certain definite points on the edge of the crown; (2) the progressive deepening of the crown from the primitive shallow or brachydont condition to the specialized very high or hypsodont condition (Fig. 326); (3) the change of shape, and the union of the cusps with one another. The primitive condition was the *bunoid* (Fig. 324), in which the cusp was like a blunt cone. The specialized condition was the *selenoid*, in which the cusp became crescent-shaped (Fig. 327*a*); or the *lophoid*, in which the cusps became ridge-like and united one with another (Fig. 327*b*). Each cusp behaved as an independent entity and might or might not change along with its fellows. In omnivorous and fruit- or nut-eating forms the teeth usually remained brachydont and bunoid, but became quadritubercular.

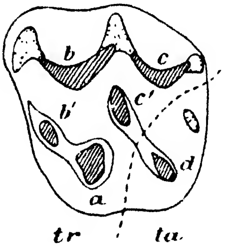


Fig. 325.—Crown of an Upper Molar of a Primitive Horse (*Anchitherium* (after Osborn).

Primary cusps lined, secondary cusps dotted.

b, *c*, crescentic or selenoid cusps. *b'a*, *c'd*, lophoid cusps.

The adaptive modifications of the molars described above were not each confined to any one line of descent. On the contrary the molars in the members of widely separated groups of mammals often became closely similar in several respects.

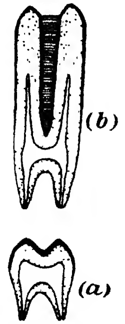


FIG. 326.—Diagrammatic section through (a) Shallow crowned or brachydont Molar. (b) High crowned or hypsodont Molar.
Dentine, dotted. Enamel, black. Cement, lined.

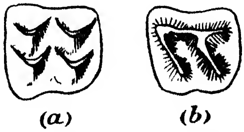


FIG. 327.—Typical Selenodont Tooth (*a*) and Lophodont Tooth (*b*).

Mesozoic Mammals.—Mammalian remains of a very fragmentary character have been found at several horizons in the Mesozoic rocks. For the early part of the period these consist almost solely of lower jaws. Those from the Cretaceous levels are more complete, and include fragments of upper jaws, and also of other portions of the skull. Fortunately such fragments are among the most instructive parts of the skeleton. During the Mesozoic period two types of mammals with quite distinct patterns of molars evolved side by side. The one had tritubercular molars, and the other molars with flattened crowns, often armed, with many cusps arranged in transverse and longitudinal rows (*multitubercular*). *Tritylodon* (Fig. 328a) (Trias, Africa) and *Triglyphus* (Fig. 328*b*) (Trias, Germany) are the earliest known members of the multituberculate type of mammal. The former had large canine-like incisors. Between these and the molars was a wide space without teeth, called the diastema, very characteristic of specialized herbivorous mammals. In the Cretaceous and basal Eocene members of the type these incisors were adapted for gnawing wood.

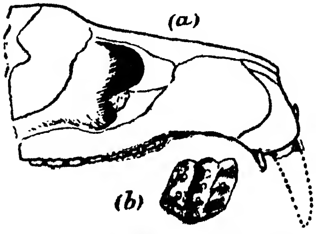


FIG. 328.—Side View of *Tritylodon* (*a*) (after Abel) and Crown of Tooth of *Triglyphus* (*b*).

During the late Mesozoic the Multituberculata differentiated in two directions, the one represented by *Polymastodon* (Fig. 329*a*) (Bas. Eoc., N. Amer.); the other by *Plagiaulax* (Fig. 329*b*) (U. Jur.–L. Cret., Eur. and N. Amer.). In the former, whilst the premolars degenerated, the molars became extended by the addition of fresh rows of tubercles at the hinder border. In the latter the premolars were larger and became laterally compressed forming a sharp cutting edge. In some cases the molars were small and hollow crowned, with irregularly arranged tubercles around the margin. This was the condition seen in the single tooth, *Microlestes* (Fig. 329*c*), which was found in the Rhætic of England, and which may be regarded as related to *Plagiaulax*. This degenerate molar bears some resemblance to certain vestigeal teeth which put in a transitory appearance in the development of the Australian egg-laying mammal *Ornithorhynchus* (Duckmole), and thus furnishes some justification for classifying the Multituberculata with the Prototheria. These low-grade mammals became extinct at the opening of the Eocene.

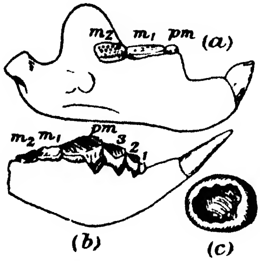


FIG. 329.—Lower Jaws and Teeth of Multituberculates.

(*a*) *Polymastodon*. (*b*) *Plagiaulax* (after Falconer). (*c*) Molar of *Microlestes* (after Osborn). pm_1, 2, 3, premolars. m_1, m_2, molars.

With regard to the trituberculate mammals enough has already been said about the teeth. The angle of the jaw of some of them exhibits a small shelf-like ingrowth (Fig. 330*a*). This feature occurs to-day only among the *Metatheria*, to which the Australian marsupials belong. The fact that a number of these have trituberculate molars increases the probability of relationship between this living fauna and the original owners of those Mesozoic jaws. In the remainder of the jaws *e.g. Amphitherium*, no such inflected angle occurs (Fig. 330*b*). Thus they anticipated the condition seen in the Eutherian grade of Mammalia. Among living forms the Insectivora furnish the truest picture of this Jurassic race.

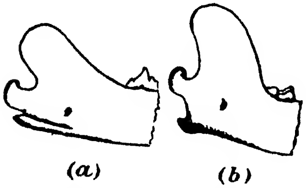


FIG. 330.—Inner View of the Angle of the Lower Jaw in a Metatherian (*a*) *Thylacinus* and an Eutherian (*b*) *Canis*.

The Mesozoic mammals hitherto discovered are usually of small size, being no larger than a rat or a rabbit, and subsisting apparently upon insects or soft plant tissues. The rarity of their remains as compared with those of contemporary reptiles indicates that they formed only an obscure portion of the land fauna of the period. During the time of their obscurity, however, they developed those improvements of brain, teeth and methods of reproduction which gave them the pre-eminence during Tertiary times.

Carnivora or Flesh-eating Mammals.—The small size of the Mesozoic Mammals and the sharply-pointed character of the cusps upon their teeth indicate that many of them, like the present-day hedgehogs and moles, got their living by feeding upon such diminutive creatures as insects and worms. At the opening of the Tertiary era appeared a race of larger animals which preyed upon their own kind. These were the flesh-eating mammals or *Carnivora*, represented at the present day by such familiar animals as dogs, cats and bears. The intervening history between those early and these later forms was not one of uniform modification and extension. On the contrary the early Tertiary carnivores differed to a marked degree from the later Tertiary and subsequent modernized forms, a fact which finds expression in the classificatory term *Creodonta* for the archaic and *Fissipedia* for the modern Carnivora.

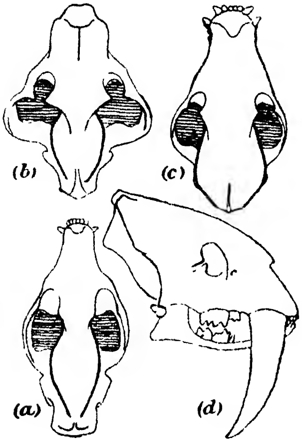


FIG. 331.—Outline Diagrams of Skulls of various Carnivores.

(*a*) *Cynohyænodon* = a creodont. (*b*) *Felis spelæus* (cave lion). (*c*) *Canis* (dog). (*d*) *Machairodus* (sabre-toothed tiger). *b–d* = fissipeds.

Both ancient and modern carnivores (Fig. 331) had clawed digits, carnassial cheek teeth, and a temporal arcade that was strongly arched to accommodate the powerful jaw muscles, required by creatures that had often to hold and carry a struggling prey in their mouths. The Creodonta, however, had much smaller brains (Fig. 331*a*) than had the Fissipedia (Fig. 331*b*, *c*). They always had a complete Eutherian dentition with the formula $\frac{3,1,4,3.}{3,1,4,3.}$. In the later forms the number and size of some of the teeth were very frequently reduced whilst in the Fissipedia (Figs. 332, 333) it was the fourth upper premolar and the first lower molar which underwent the carnassial modification; in the Creodonta any of the upper molars and the two lower molars could be so affected.

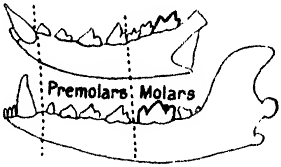


FIG. 332.—Diagrams of Lower Jaw of *Hyænodon*, Creodont (above), and of *Canis*, a Fissiped (below).

Black outlined tooth is the carnassial.

The Creodonta were in their heyday in Lower and Middle Eocene times, but they continued longer as a less important race and died out during the Middle Oligocene. The most primitive members of the sub-order, *e.g.* *Oxyclænus* (Bas. Eoc., Amer.), had teeth which still retained the tritubercular character of the Jurassic mammals. At the other extreme was *Hyænodon* (Figs. 332*a*, 333*a*) (Oligo.). This belonged to a successful type which survived long enough to be among the last of the Creodonta. Its second upper, and third lower molars had become typical large carnassial teeth. The two preceding teeth were also similarly modified, but to a lesser degree.

Other creodonts exhibited various adaptive modifications. Thus *Arctocyon* (Bas. Eoc., Eur.) had square crowned bluntly tuberculate molars, which like those of the bear were suited for an omnivorous diet. *Oxyæna* (L. Eoc., Amer.), like the Weasel, was suited for the pursuit of small prey. *Patriofelis* (M. Eoc., Amer.) had a long rather heavy body and short stout limbs and probably resembled the Otter both in its form and habits. *Mesonyx* (M. Eoc., Amer.) and *Pachyæna* (L. Eoc.) were both swift-running forms, the former had a large head in proportion to its body, the latter was a giant among creodonts. *Miacis* (Fig. 333*b*) (Eoc., Amer.) is a borderline form, which in its general organization is a creodont, but in some respects approaches modern carnivores. As in these its fourth upper premolar and first lower molar are the chief carnassial teeth. This genus belongs to that portion of the creodont stock, from which the Fissipedia arose.

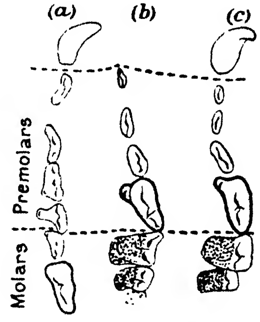


FIG. 333. — Diagrams showing Upper Teeth of (*a*) *Hyænodon*, (*b*) *Miacis*, (*c*) *Canis*.

Black outlined tooth is carnassial. Dotted areas are crushing regions.

True fissipeds appear as early as the Upper Eocene. They were at their maximum development from that date until the close of the Pliocene and persist to-day in only slightly diminished vigour. Among the earliest and most centrally placed is *Cynodictis* (Fig. 334*b*) (U. Eoc.). Its dentition does not differ greatly on the one hand from that of *Miacis*, and on the other from that possessed by dogs and dog-like animals the world over. From some such central generalized type modification proceeded in two main directions. In the one the cutting character of the cheek teeth was increased at the expense of the crushing character, *e.g.* *Proailurus*. In the other the crushing character was emphasized, *e.g.* *Amphicyon* (Fig. 334*c*).

In *Proailurus* (Mio. Oligo. Eur.) increase in size and importance among cheek teeth was confined to the carnassials; the remaining premolars and molars were reduced. These changes reached their acme in the cats, tigers and lions, whose dental formula is $\frac{3,1,3,1,}{3,1,3,1.}$

(Figs. 331*d*, 334*a*). Meanwhile the jaws shortened and the temporal arcades became still more strongly arched. The head thus assumed that short broad appearance which characterizes them (Fig. 331*b*). The claws became sharper and more hooked, and could be withdrawn from contact with the ground by rolling the last phalanx back on to the top of the digit. In addition to closely similar changes in teeth and skull *Nimravus* (L. Mio. Amer.) and *Machairodus* (Fig. 331*d*) (L. Plio.–Pleist.) exhibited an extraordinary increase of the upper canines.

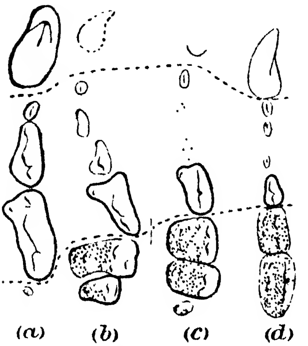


FIG. 334.—Diagrams of Upper Teeth of Fissipedia.

(*a*) *Felis spelæus* (cave lion). (*b*) *Cynodictis*. (*c*) *Amphicyon*. (*d*) *Ursus*.

In *Amphicyon* (U. Olig.–L. Plio.) the opposite type of modification was shown. The molars increased in size and became larger than the carnassials. In the Bear (*Ursus*, Plio.–Pres., Fig. 334*d*) the carnassials were further reduced and the molars became elongated by the addition of a tuberculated extension behind. In the Cave Bear (*Ursus*, *spelæus*, Pleist.) the first premolars had disappeared entirely. Throughout all these changes which characterize the bears, the canine teeth remained powerful. Though living bears have plantigrade feet, this condition has been secondarily acquired from digitigrade ancestors.

One large section of the carnivora, the Pinnipedia, which includes the seals and sea-lions, remains. These will be dealt with along with other mammals adapted for an aquatic habit.

A General History of the Hoofed Mammals.—The evolution of the carnivorous mammals was but an indication of the existence of a larger and more numerous race, upon which they preyed, and which fed, often in herds, upon the vegetation. In these herbivorous animals each digit bore a horny structure, called the hoof, which corresponds with the claw and nail of other animals, but differs from these in that it almost completely envelopes the last phalanx. Such hoof-bearing mammals are classed together in the largest of mammalian orders, the *Ungulata*. As with the carnivores, the history of this order falls into two great periods. An earlier, which lasted until the Middle Eocene, during which Archaic Ungulates predominated ; and a later, lasting from that date until the present day, during which modernized mammals have held the field. The passage from the one type to the other cannot always be traced, for some modern types evolved in regions as yet unexplored, and considered by some to lie between the northern portions of Europe and North America. From such regions these mammals migrated southwards, mingling with their smaller-brained and less adaptable relatives, and competing with them so successfully that by the opening of the Upper Eocene they had almost completely displaced them.

In Europe and North America the next great event was a considerable influx of yet more modernized mammals during the lower Oligocene. In the Oligocene period the rainfall sufficed to support extensive open woodlands and forests, and the ungulates were for the most part types which cropped the soft leaves of the trees and browsed upon the succulent undergrowth. Under these conditions fleet running was out of the question, and therefore animals with primitive sturdy limbs and unspecialized feet predominated. With the opening of the Miocene there appears to have come a decrease of the rainfall, and a shrinkage of the sylvan areas ; carpet vegetation, grasses and flowers, were left in possession of the plains, and thus extensive grazing grounds came into being. This drier food required prolonged chewing, and brachydont teeth passed into hypsodont. Respite from the attack of carnivores could now be secured chiefly by fleet running, and limbs became slim, and feet longer and more specialized for speed.

Throughout the Pliocene a gradual lowering of temperature took place, and the northern vegetation belts migrated slowly southwards. First came the temperate woodlands, bringing a comparatively rich fauna similar in adaptational characters to that of the Oligocene but belonging to a later evolutionary stage. After that came the steppes and the tundras with scanty faunas. During the Pleistocene the movements of these belts were oscillatory, corresponding to the oscillations of climate of the period, from genial to frigid and back again. In total effect this glacial period left the northern portions of this hemisphere greatly impoverished in animal life and consequently subsequent history has consisted in a repeopling of these regions by migrations from Asia and the South.

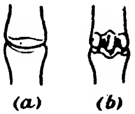

(a) (b)

FIG. 335.—Diagram of typical Joint in : (a) an Archaic Ungulate with rounded surfaces ; (b) a modernized Ungulate in which the Joint is strengthened by a tongue and groove.

Archaic Ungulates.—The Archaic Ungulates differ from the modern in the small size of their brains, in the presence of all or nearly all their digits in a primitive or only slightly modified state, and in the simple rounded character (Fig. 335*a*) of the articular surfaces of the joints in their limbs and feet. It is this last feature which suggested the name for the first of the two great orders into which they are divided: viz. *Condylarthra* and *Amblypoda*.

The Condylarthra (Fig. 336*a*) are small-bodied light-limbed animals with feet of only moderate length. The Amblypoda (Fig. 336*b*) were heavy-bodied creatures with short stout limbs resembling those of the elephant. *Phenacodus* (L. Eoc., Amer.), the best known of the Condylarthra, was about the size of a sheep. It walked upon its three middle digits, which were distinctly larger than the laterals and bore small hoofs. In other respects it resembled the creodonts. Thus its fore-limbs were short and consequently its shoulders were lower than its withers, its tail was long, its brain small, its premolars were sharp and piercing; and its lateral digits bore claws. The more primitive *Tetraclænodon* (Fig. 337), (Bas. Eoc., Amer.) was even more like a creodont, and both its knees and elbows bent slightly outwards. These two genera differ from the carnivores in that their molars had attained to the sextuberculate crushing condition.

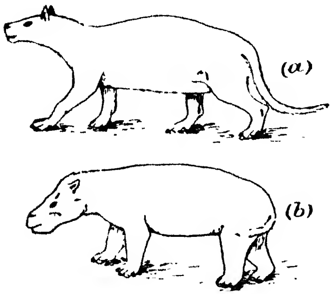


Fig. 336.—Outline Restorations of Archaic Ungulates.

(*a*) *Phenacodus* (light limbed). (*b*) *Coryphodon* (heavy limbed). (Both after Scott.)

Among the Amblypoda, *Pantolambda* (Bas. Eoc., N. Amer.) was in its general organization more primitive than *Tetraclænodon* and approached even more closely to the Creodonta. Its limbs bent outwards at the elbow, and its front paws were everted and almost plantigrade. Its molars, though they retained marked traces of their trituberculate origin, had their cusps already modified in a selenoid manner. Starting from this genus, which was no larger than a pig, the Amblypoda underwent a progressive increase in size through *Coryphodon* (L. Eoc., Amer.) to the forms like the gigantic *Dinoceras* (cp. Fig. 338) and *Uintatherium* (M. Eoc.). The limbs increased in thickness correspondingly (Figs. 336*b*, 337*b*). Meanwhile, the upper incisors disappeared, and the upper canines became long and trenchant (Fig. 338). The cusps passed through a partly selenoid, partly

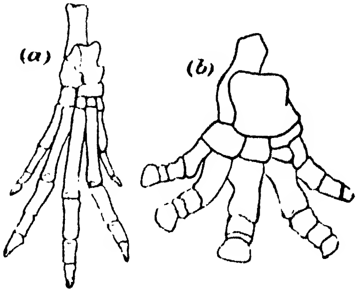


Fig. 337.—Skeleton of the Hind Feet of two Archaic Ungulates.

(*a*) *Tetraclænodon*, light-limbed cursorial type (after Matthew). (*b*) *Coryphodon*, heavy-limbed amblypod type (after Osborn).

lophoid condition in *Coryphodon* and became completely lophoid in the later genera. Throughout all these changes the molars remained brachydont and tritubercular.

The Condylarthra became extinct at the close of the Lower Eocene, but the Amblypoda continued to evolve, and attained their maximum size and specialization in the Middle Eocene, and eventually disappeared in the Upper Eocene. Neither order furnished the starting point for any modernized stock of Ungulates.

In early Tertiary times South America became separated from the rest of the continent. Though at first the fauna resembled that living elsewhere it subsequently evolved along independent lines and produced an assemblage ot peculiar forms unknown in other parts of the world.

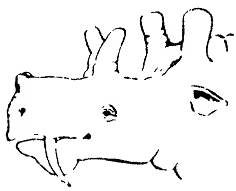


FIG. 338.—Outline Restoration of the Head of a Great Amblypod (*Eobasileus*), allied to *Dinoceras* (after Osborn).

Modernized Ungulates.—The three greatest orders into which living ungulates are divided are represented by the Horse (*Equus*), the Sheep (*Ovis*) and the Elephant (*Elephas*). With regard to the limbs it is seen that in the horse the middle line passes through the centre of a single hoof, in the sheep it passes between a pair of hoofs (Fig. 339). The former condition is characteristic of the *Perissodactyla* (odd-toed ungulates), which had their home primarily in North America. The latter characterizes the *Artiodactyla* (even-toed ungulates), which form the most numerous section of the ungulates to-day, and have always had the Old World for their headquarters. The Elephant, whose limbs are stout pillars bearing five digits (Fig. 340), of which the central ones are only a little larger than the lateral, represents the *Proboscidea* and originated in Africa.

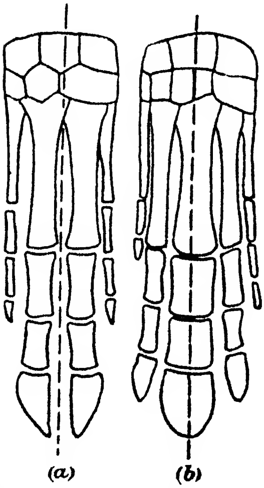


FIG. 339.—Diagrams illustrating the Plan of Structure of the Foot of (*a*) an Artiodactyle, (*b*) a Perissodactyle.

THE ARTIODACTYLES, OR EVEN-TOED UNGULATES.—Among living artiodactyles the Pig (*Sus*) and the Sheep exhibit respectively the lowest and the highest grades of evolution. This fact is reflected in the feet and the teeth.

In the Pig (Fig. 341*a*) both hands and feet have four digits.

The two middle ones (III and IV) are equal to one another, but are larger than the two laterals (II and V). The pig walks upon the end phalanges of all digits, that is to say it is *unguligrade*. In the Sheep (Fig. 341*b*) there are only two digits (III and IV), the metapodials of which have become greatly elongated and, to secure lightness and rigidity, have become fused together to form one bone, the "cannon bone." The dentition of the pig is complete $\left(\frac{3,1,4,3}{3,1,4,3}\right)$; that of the sheep is reduced $\left(\frac{0,0,3,3}{3,1,3,3}\right)$, and the continuity of the series is broken by a wide space, the *diastema*, in front of the premolars (Fig. 342). This feature is peculiarly characteristic of vegetable feeders. In the pig the molars exhibit the primitive brachydont and bunodont conditions. In the sheep they present the specialized hypsodont and selenodont conditions.

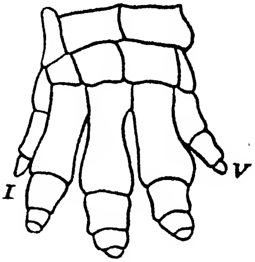


Fig. 340.—Diagram showing the Structure of the Foot of an Elephant.

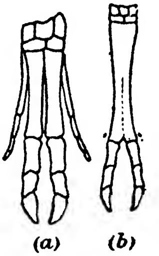

(*a*) (*b*)

Fig. 341.—Diagrams showing the Structure of the Left Fore Feet of (*a*) Pig and (*b*) Sheep.

In the Eocene there existed a number of primitive artiodactyles, *e.g. Homacodon* (America) and *Dichobune* (Europe). These were closely allied to, if not actually ancestral to, the pigs (*Suina*). True pigs evolved in Europe and were already represented in the upper Eocene by *Chæropotamus* (Europe), in the Miocene by *Hyotherium* (Europe), and in succeeding ages by a constant succession of forms. In America they were represented only during Oligocene times by a giant race, the *Entelodonts* (Fig. 343), in which the limbs were more slender, and had lost their lateral digits.

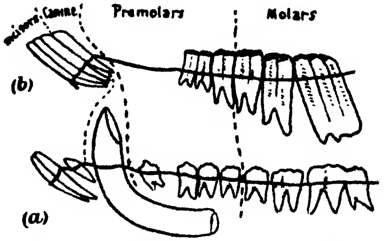


Fig. 342.—Diagram showing the Arrangement and General Character of the Teeth in (*a*) Pig, (*b*) Sheep.

From the close of the Eocene to the opening of the Miocene there existed a group of artiodactyles in an intermediate grade of evolution between the more primitive bunodonts and the more specialized selenodonts. In these the outer cusps of the molars were crescentic or selenoid, and the inner bunoid. Some of these forms resembled the pigs in the general clumsiness of their build, *e.g.* *Anthracotherium* (U. Eoc.–Olig.). Others approximated to the selenodonts, and like them were of more graceful build, *e.g.* *Cænotherium* (L. Mioc.), *Anoplotherium* (U. Eoc.).

All the remaining artiodactyles may be spoken of collectively as Ruminants because, like the sheep, they chew the cud. They appeared upon the scene in both the Old and New World during the Upper Eocene. The earlier forms, like primitive animals generally, were small, being no larger than a hare. Their teeth formed usually a closed series, and the molars were bunoselenodont. Though they may not be regarded as the ancestral stock of modern ruminants, they were undoubtedly closely allied to that stock. One family, the Oreodontidæ, flourished and disappeared during the Miocene, but developed many modifications.

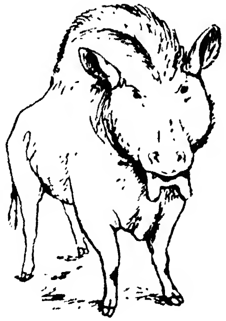


FIG. 343.—Outline Restoration of *Entelodon* or Giant Pig (adapted from Osborn).

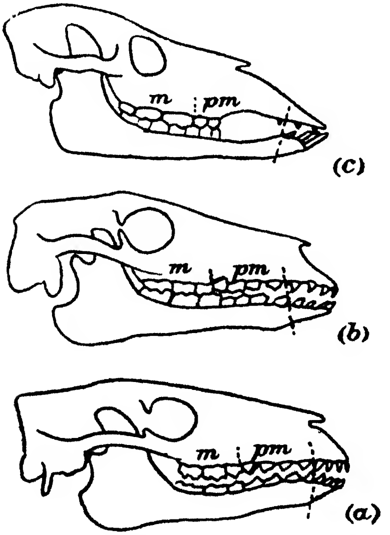


FIG. 344.—Diagrams of the Skulls of Dentition of Camels.
(*a*) *Protylopus* (after Scott) (*b*) *Pæbrotherium* (after Scott). (*c*) *Camelus*.
m, molars. *pm*, premolars.

Another family, the Camelidæ (Fig. 344), was represented at that early date by *Protylopus*. In this genus vestiges of the lateral digits were present and the metapodials were not united (Fig. 345*a*). Through stages testified by such a succession of genera as *Pœbrotherium* (Fig. 345*b*) (Oligo.) and *Procamelus* (345*c*) (Mio. and Plio.), it gave rise to the modern camels. In addition to numerous other changes there was a gradual elongation of metapodials, III and IV, accompanied by increasing closeness of union and final fusion to form a cannon bone. The dental series, which at first was complete and closed (Fig. 344*a*), gradually lost the upper incisors, and developed a wide diastema above and below.

A third family, the Tragulines, remained almost stationary, so that between its Eocene members, *e.g.* *Leptotragulus* (America) and

Lophiomeryx (Europe) and the present-day Mouse Deer (*Tragulus*) and Water Chevrotain (Fig. 346) (*Dorcatherium*), of Southern Asia there is little difference. Among living artiodactyles these little creatures supply the most correct pictures of the primeval ruminant. They still retain the two lateral digits, and in *Dorcatherium* the metapodials of the fore-limbs are not united to form a cannon bone. This condition is found also in some of the Eocene and Oligocene Tragulines, *e.g.*, *Gelocus*. In others again the dental formula was $\frac{3,1,4,3}{3,1,4,3}$.

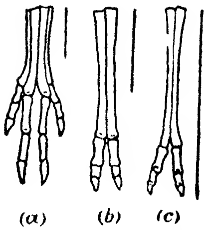


FIG. 345.—Diagrammatic Representation of the Skeleton of the feet of Camels (after Cope).

(*a*) *Protylopus*. (*b*) *Pœbrotherium*. (*b*) *Procamelus*. Note the progressive elongation of the metapodials and their closer union to form cannon bone. Straight lines show true relative sizes of these feet.

From some such diminutive and primitive stock there evolved in Middle Oligocene times the ancestors of all the true Ruminants, all of which have selenodont and hypsodont molars. The majority belong to one or other of two families, *Bovidæ* and *Cervidæ*, of which the former have horns and the latter have antlers. Both these structures have a bony core which is attached to the frontal bones. In the horns this is a simple cone with a hard horny covering which lasts throughout life. In antlers there is no horn, the core is branched, and after each breeding season it is shed. Every year, from the third onwards, a fresh antler is grown. The first has only two branches or *tines*; the second has three; and in each succeeding year the number is increased by one until the full number for the species is obtained. This process is paralleled during evolution. Thus the Oligocene deer (*Cervidæ*), *e.g.* *Amphitragulus* (Eur.), were hornless. The lower Miocene ones, *e.g.*, *Dicrocerus*, like the living *Cervulus* (Fig. 347*a*) had a simple forked antler borne upon a tall pedicel. The Upper Miocene and Lower Pliocene deer had three tines (Fig. 347*b*), as in the present day Roedeer, *Capreolus*. From the Middle Pliocene onwards the antlers attained various degrees of complex branching (Fig. 347*c*). Thus the study of antlers illustrates three complementary methods of working out the evolution of structures of animals, namely, the development

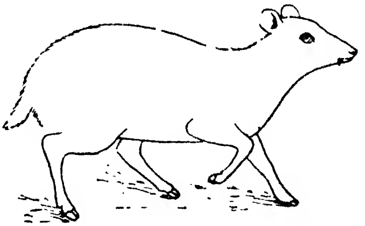


FIG. 346.—Outline Figure of the Water Chevrotain (*Dorcatherium*) to show the probable appearance of the earliest modernized Ungulates (adapted from Flower).

in the individual, the comparison of living forms, and the study of fossils.

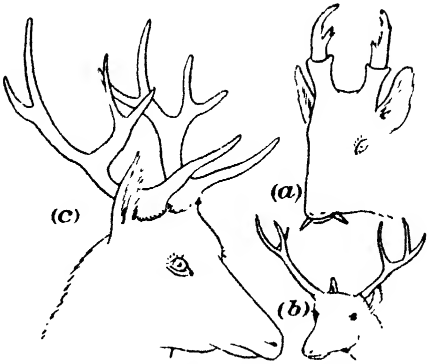


FIG. 347.—Head and Antlers of Cervidæ.
(*a*) *Cervulus* (Present). (*b*) *Merycodus* (Miocene), (after Scott). (*c*) *Cervus* (Present).

Both living and fossil deer which are without, or have only bifurcated antlers, are armed with long trenchant upper canines (cp. Figs. 346, 347*a*). With the further evolution of the antlers the teeth disappear and their function is performed by the antlers. This furnishes an illustration of the phenomenon of the functional substitution of organs. In primitive and early Bovidæ the horns were slender and straight, and arose close together (cp. Fig. 348) almost between the eyes. This condition is still seen among living antelopes. One line of specialization was the elongation and widening of the frontal bones, which naturally led to a separation and a backward shifting of the horns. This serial change reaches its maximum in the oxen (Fig. 348*b*). Antelopes and sheep appear as early as the Upper Miocene, but oxen and goats are not known until the Pliocene.

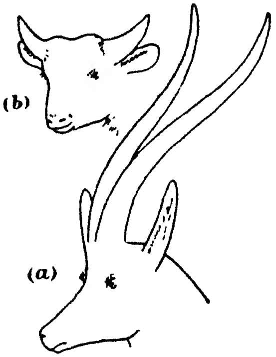


FIG. 348.—Heads of Bovidæ.
(*a*) Antelope. (*b*) *Bos* (ox).

At the time of the first separation of the *Cervidæ* and *Bovidæ* there arose from the same stock a peculiar offshoot which ultimately produced the giraffes (*e.g. Helladotherium*, L.-Plio., Eur.) and showed a tendency towards the elongation of the neck and fore-limbs, a stage still seen in the forest-loving *Okapi*. This line of change finds its fullest expression in true giraffes.

PERISSODACTYLES OR ODD-TOED UNGULATES.—Unlike the artiodactyles, which were never more numerous and varied than they are to-day, the perissodactyles attained their hey-day in the late Eocene and early Oligocene, a period which may be aptly called the "Age of Perissodactyles." During that time every family was represented and there were many genera. Half of these died out before the end of the Oligocene, and each of the three surviving families is now represented by only one genus, namely *Tapirus*, *Rhinoceros*, and *Equus*.

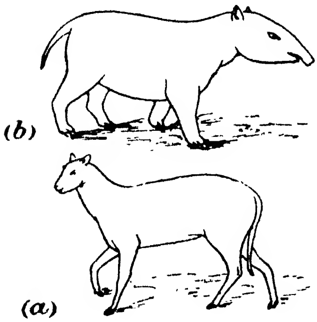


FIG. 349.—Outline Restorations of Primitive Perissodactyles.

(*a*) *Eohippus* (after Osborn), light-limbed form, earliest ancestor of the Horse. (*b*) *Palæotherium* (after Lydekker), heavy-limbed form.

During the Early Eocene there existed both in Europe and America a number of primitive perissodactyles which so closely resembled one another that they might be classed as one family, were it not for the fact that they are the most primitive members of families which in later times diverged widely from one another. They were, *e.g.* *Eohippus* (Fig. 349*a*), *Hyracotherium*, *Systemodon*, *Lophiodon*, *Hyrachyus* and *Propachynolophus*. The first two were swift-footed slender forms no larger than a small-sized dog. The remainder were equally primitive but were of clumsier build (cp. Fig. 349*b*).

Eohippus (Amer.) and *Hyracotherium* (Eur.) represent the earliest-known ancestors of the horses. Their molars were brachydont with bunodont crowns bearing six cusps. The hand had four fingers (Fig. 350*a*), the first being reduced to little more than a splint bone. The foot had only three toes. In both cases digit III was the largest, digits II and IV were slightly smaller and equal. In *Orohippus* (Fig. 350*b*) (M. Eoc., Amer.), a larger animal, the splint-like vestige of digit I had disappeared. In *Mesohippus* (Fig. 350*c*) (L. Olig., Amer.), the size of a small sheep had been attained. In it digit V was reduced to a splint, so that the hand as well as the foot was practically tridactyle, with digit III distinctly larger than II and IV. The

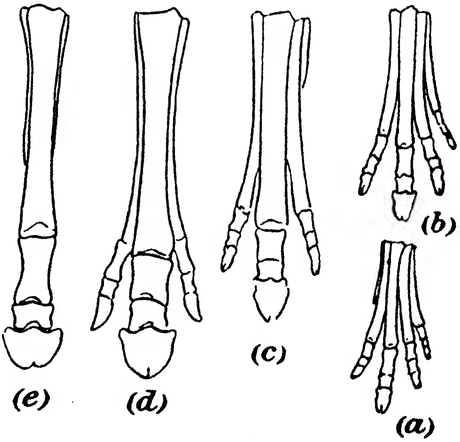


FIG. 350.—Diagrams illustrating the Evolution of the Horse's Foot from that of a Four-toed Ancestor.

(*a*) *Eohippus* (L. Eoc.). (*b*) *Orohippus* (M. Eoc.). (*c*) *Mesohippus* (L. Oligo.). (*d*) *Hypohippus* (Miocene). (*e*) *Equus* (Pliocene to Present). (After Cope.)

molar teeth were still brachydont. The grade of structure exhibited by this genus was retained by a conservative series of woodland and riverside forms until the Miocene (*Anchitherium*, Eur., *Hypohippus*, Amer. Fig. 350*d*.). Meanwhile, others evolved to a further stage on the open plains. In *Protohippus* (L. Plio., Amer.) the molars were as complex as in modern horses, but not so deeply crowned, and the hollows between their elevated cusps were partly filled with cement. Digits II and IV were now too small to reach the ground, and only digit III was functional. In *Pliohippus* (L. Plio., Amer.) the lateral digits had lost their phalanges. By Upper Pliocene times true horses existed (Equus, Fig. 350*e*). In them the modification of the mammalian plan of structure for progression upon land reached its climax. Every superfluous bone has gone, and those which remain have been correspondingly strengthened. Digit III alone is present in all four feet whilst II and IV are mere splints of bone. The dental series is complete $\frac{3, 1, 4, 3}{3, 1, 4, 3}$. The molars have very deep and complex crowns (Fig. 325) with all crevices between the cusps filled with cement. Specialization has also affected premolars 2, 3, 4, which now rival the molars in size.

Of the other primitive Lower Eocene perissodactyles referred to above, the *Lophiodon* type rose to abundance, and then disappeared during the late Eocene. *Propachynolophus* gave rise to an important old-world family which in a clumsier way evolved parallel to the Equidæ, and in the genus *Palæotherium* (Fig. 349) (U. Eoc., L. Oligo., Eur.) it attained a stage equivalent to *Mesohippus* (cp. Fig. 350*c*) and then became extinct. *Systemodon* gave rise to a conservative stock which exists to-day, slightly altered, in the Tapir of South America and Asia. *Hyrachyus*, on the other hand, was the earliest member of a much more virile race which gave origin to several branches of which one survives in the living Rhinoceroses. These were all characterized by the presence of horns on the middle line of the snout, which had no bony core but were produced entirely from the skin.

From Middle Eocene to Lower Oligocene there existed in North America a group of perissodactyles, the Titanotheres, having a bunolophodont type of dentition. For the short period of their existence they were a very vigorous race. The type genus, *Titanotherium* (L. Oligocene), was of elephantine proportions. It had a pair of abnormally placed horn cores upon the naso-frontal border. The evolution of these horns has been proved by careful measurement of ample material to have proceeded not by leaps, but slowly and gradually (Fig. 351). Its foot had three digits of perissodactyle

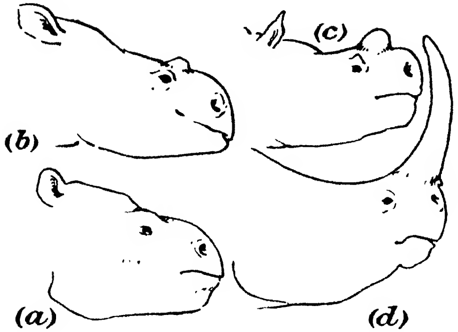


FIG. 351.—Outline Restorations of the Heads of a Series of Titanotheres showing the gradual Evolution of the Horns.

(*a*) *Palæosyops* (Lower M. Eoc.). (*b*) *Manteoceras* (M. Eoc.). (*c*) *Diplacodon* (U. Eocene). (*d*) *Titanotherium* (L. Oligocene). (All after Scott.)

pattern, but the hand had four digits arranged upon the artiodactyle plan.

PROBOSCIDEA. — The most specialized features of the Elephants lie in the head. The limbs, apart from the massiveness of the bones, retain a primitive arrangement of the parts. The oldest and most primitive proboscidean genus, *Mœritherium* (Fig. 352*a*) (U. Eoc., L. Olig., Africa), was about the size of a pig. It had a normally-shaped skull elongated from back to front. The series of teeth was almost complete, $\frac{3, 1, 3, 3}{2, 0, 3, 3}$. The second upper and lower incisors were enlarged and sloped forwards, and the molars were brachydont and bunodont. The prenasal region of the snout, and the front (symphysial) portions of the lower jaw were lengthened. In *Palæomastodon* (Fig. 352*b*) (Oligo.) the elongation of the prenasal and symphysial regions was more marked, and the postnasal portion of the skull was shortened and elevated as in the Elephant. The large incisors of the upper jaw were long and tusk-like, but still had a downward curvature.

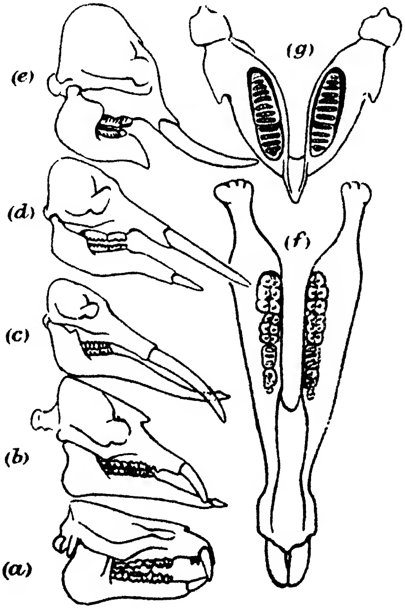


FIG. 352.—Skulls and Lower Jaws of Proboscidea.

(*a*) *Mœritherium*. (*b*) *Palæomastodon*. (*c*) *Tetrabelodon*. (*d*) *Mastodon*. (*e*) *Elephas*. (*f*) Lower jaw at maximum elongation (*Palæomastodon*). (*g*) Lower jaw at minimum shortening (*Elephas*) (after Andrews).

The next evolutionary stage is represented by *Tetrabelodon* (Fig. 352*c*). In the earlier members of this genus (M., Mio. L. Plio.) the symphysial region of the lower jaw was so long that its tusk-like incisors could touch the ground. The prenasal portion of the skull had remained little altered, but the upper incisors were greatly elongated, and still retained traces of the downward curvature. Meanwhile the prehensile nose must also have greatly lengthened, and formed the trunk so characteristic of the order. In later species the symphysial region underwent a rapid shortening, but the upper tusks remained, and were now straight. On the molars the cusps united in transverse rows to form transverse ridges.

It was during this *Tetrabelodon* stage in evolution that the Proboscidea, hitherto confined in Africa, escaped and migrated into Europe and Asia. By the middle of the Miocene they had even reached North America, probably by a land bridge across the Behring Straits.

The Proboscidea now divided into two branches. In the one, to which *Dinotherium* belonged, the lower tusks remained, taking, in the case of this genus, a marked downward curvature. This branch became extinct during the Pleistocene. In the other branch the lower tusks disappeared and the upper alone persisted. The symphysial region of the lower jaw was now reduced to a small spout-like process, a condition seen in *Elephas* (Fig. 352*e*) and *Stegodon*. The molars of the former had only three transverse ridges, those of the latter developed as many as six (Fig. 353). In *Elephas* (true elephant) those ridges underwent a progressive increase both in height and number, and the spaces between them were filled with cement. The maximum number 27 was attained in the Mammoth, *Elephas primigenius*.

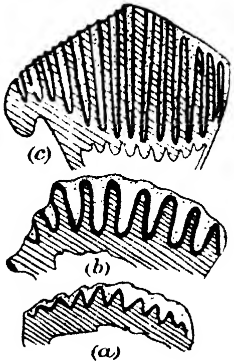


FIG. 353.—Diagrammatic section of the Teeth of Elephants showing the Progressive Increase in Height and Multiplication of Ridges.

Dentine (lined); enamel (black); cement (dotted). (*a*) *Stegodon*. (*b*) *Loxodon*. (*c*) *Elephas*.

Other Mammals.

In this chapter several orders of Mammalia may be briefly dealt with which never occupied such a prominent position in the fauna as the ungulates and carnivores.

The Edentata.—This order includes a mixed assemblage of forms rendered familiar, less by frequency of occurrence, than by anomaly of form and habit. The Armadillo has a flexible bony armour and burrows in the ground; the Sloth hangs body downwards from the branches of the trees; the Anteater tears open termite nests and feeds upon their inhabitants. To-day the Edentates are limited mainly to South America. During the Pliocene and Pleistocene periods the fossil allies of these forms made up a more conspicuous portion of the fauna of the same region. Most prominent of all was *Megatherium* (Plio. and Pleist., Fig. 354). This Giant Ground Sloth, like many dinosaurs, had a heavy tail and massive hind-quarters. The lighter fore part of the body was lifted off the ground to enable the creature to feed upon the leaves of trees, the branches of which it pulled down with its great hook-like claws. It walked awkwardly on all fours, upon the outer edges of its feet.

FIG. 354.—Restoration of the Giant Ground Sloth (*Megatherium*). (After Scott.)

Mylodon (Pleist.) was smaller, and less specialized. It was closely allied to *Glossotherium*, a portion of the skin of which has been found in the dust on the floor of a very dry cave. This specimen proved that these animals were clothed with coarse fur, and had numerous little round bones imbedded in the skin. The Armadillo also is a diminutive representative of an extinct giant race, of which *Glyptodon* (Plio.) was the type (Fig. 355). In form it presented a striking parallel adaptation to that of the tortoises. Its head and trunk were enclosed in a casing composed of a mosaic of polygonal bony plates. Its tail was also protected by a series of thick bony rings. With such armour *Glyptodon* was safe from the attacks of the great carnivores with which it was contemporaneous.

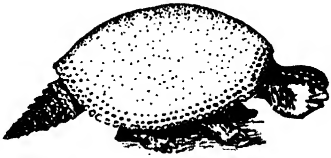


FIG. 355.—Restoration of *Glyptodon*. (After Brit. Mus. Cat.)

The affinities of the *Edentates* with other mammals is an unsolved problem.

The Rodentia or Gnawing Mammals.—Unlike the edentates, the rodents are in their prime at the present time. They have numerous representatives on all continents, except Australia, but even there a few species are found. It is only necessary to mention rats, rabbits, squirrels, beavers and porcupines to call up pictures of their wide range of adaptation to very diverse habitats. The earliest rodents known occur in the Lower Eocene of North America. But even then they differed in no essential respect from existing forms. At that early date they were forest folk; it was not until the Oligocene that plain dwellers arrived. *Paramys* (Eoc.) was like a squirrel; *Ceratogaulus* (L. Plio.) had a pair of horns on its snout.

Here again the affinities of rodents with other mammals is still a mystery.

The Insectivores.—Among living mammals these approximate most closely to the condition of the primitive Mesozoic *Eutheria*. Because of the simplicity of their brains, their plantigrade or semiplantigrade feet with five clawed digits, the nourishment of the fœtus upon abundant yolk, and many like characters they have long been regarded as belonging to a lowly race.

The modern representatives, *e.g.* Hedgehog and Shrew, are but decadent relics of that race which have survived by reason of their small size, and peculiar habits and food. These have kept them apart from competition with larger mammals. Insectivores, *e.g.*, *Deltatheridium* (Fig. 322), appear first in the Cretaceous, but in the Lower and Middle Eocene they were more abundant. In the Bridger Basin (M. Eoc., N. Amer.) they formed such an important section of the fauna that their remains make up no less than one third of all the specimens collected. The fauna of that basin was that of a thickly forested river plain. It is not surprising that there arboreal and aquatic, as well as terrestrial, insectivores lived. *Hyopsodus* in its teeth and skull exhibits features in common with the lemurs and the Condylarthra. *Pantolestes*, an aquatic form, shows similar affinities with the creodonts. *Leptictis* (M. Oligo., Amer.) was like the hedgehog, but had more typically tritubercular molars. Modern forms like shrews and moles appeared in the late Eocene and Oligocene, and hedgehogs were present in the Miocene. The insectivores, in spite of their insignificance, are an interesting central group whose early members were linked in affinity with the primitive members of such diverse orders as the *Ungulata*, the *Carnivora* and the *Primates*.

The Chiroptera. Bats.—The bats supply among mammals an adaptive parallel to the Pterosauria among reptiles, but in this case four of the digits are greatly elongated for the support of the membranous wings. They are closely allied to the insectivores, and must have originated from them at a very early date for already true bats existed in the Upper Eocene.

Aquatic Mammals.—With mammals as with reptiles there was a constant tendency for individual members of the various groups to resort to an amphibious mode of existence. In such the limbs generally tended to become shortened, *e.g. Patriofelis*, a creodont; *Teleoceras*, a rhinoceros.

The seals, however, represent a division of the Carnivora, viz. the Pinnipedia, in which all the members lead an aquatic life. Nothing is known about their origin and evolution. Modern whales (cetacea) are as perfectly adapted to a life in the open sea as were the ichthyosaurs. *Agorophius* (U. Eoc.) exhibits slightly more primitive features but does not furnish any clue to the affinities of the whales with any known terrestrial mammalian order. The Eocene of Egypt and North America has yielded remains of forms like *Protocetus* and *Zeuglodon* which are just as perfectly equipped in their adaptation to aquatic conditions. Their teeth, however, retain traces which point to a creodont ancestry. They cannot, however, be regarded as ancestral Whales. The Sea Cows or Sirenians occur as fossils as early as the Eocene (Egypt), but no connecting links with typical terrestrial mammals are known. Their general structure points to an ungulate, possibly a proboscidean ancestry.

The Primates.—The order Primates includes the Lemurs, the Monkeys and the Apes. Though they do not at any time form a prominent section of the fossil faunas, they are especially interesting because they furnished the stock from which man himself has been derived. At the present time the Primates are confined to the tropical regions of the world, and for the most part lead an arboreal life. Their skeleton on the whole is primitive and non-progressive, the feet and hands are plantigrade or semi-plantigrade (Fig. 356), and each has five digits; the lower limb bones are equal and separate from one another. Adaptation to arboreal life is shown in the ability to move the lower end of the radius over the ulna and thus rotate the hand into any position the angle of a bough may demand; and, again, in the ability to place

FIG. 356.—Picture of a Gorilla (after Flower).

Note the prominent eyebrow ridges, sloping forehead, long forelimb, prehensile first toe and plantigrade hands and feet.

the first digit over against the others for purposes of grasping (Fig 356).

The chief structural changes have taken place in the head skeleton (Fig. 358), for the outstanding characteristic of the Primates is the progressive enlargement and increasing complexity of the brain. This factor dominates the modifications which the skull undergoes. Chief among these is the swelling up of the brain case, and the shortening of the face. Minor changes are the shifting of the orbits from facing sideways to facing forwards ; the closing in of the orbits by a rim of bone round the margin, and by a plate of bone between it and the temporal fossa. The shortening of the face entails the shortening of the tooth margin and a reduction in the number of teeth from 44 $\left(\frac{3,1,4,3}{3,1,4,3}\right)$ in the lowliest primates to 32 $\left(\frac{2,1,2,3}{2,1,2,3}\right)$ in Man (Fig. 357).

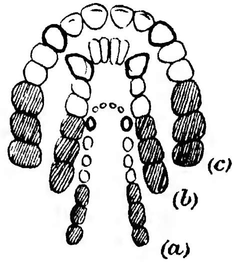


FIG. 357.—Diagram showing the Teeth and their Arrangement in (*a*) The extinct Lemur, *Homunculus* : (*b*) The extinct ape, *Pliopithecus* ; (*c*) Man, *Homo*.

Canine teeth (black outline). Molars (lined).

The earliest phases of these changes are preserved to-day in the lemurs. These are for the most part small animals which have their headquarters in Madagascar. The first fossil remains of Primates which have been found belong to lemurs, and come from the Lower Eocene of both Europe and America. These approximate so closely to the insectivores that it is often difficult to decide to which order they should be referred. The genera *Pelycodus* and *Notharctus* (L.–U. Eoc., Amer.) are undoubtedly lemurs. Their teeth exhibit the transition from a trituberculate to the quadrituberculate type of molar usually found in Primates. The Old World *Adapis* (U. Eoc.) shows an early stage in the enlargement of the brain case. Its face also is slightly shortened, but no reduction in the number of teeth has taken place. *Anaptomorphus* (L.–U. Eoc., Amer.), and the closely similar *Necrolemur* (U. Eoc., Eur.), exhibit, in the larger brain case and more shortened face, a condition transitional to that of the monkeys.

Monkeys and Apes are classed together with Man in the order *Anthropoidea*. In them there are usually only two incisors and three molars. Moreover, the orbits face forwards and are shut off posteriorly from the temporal fossæ by a thin bony plate. The Old World monkeys (*Catarrhini*) have features in common with man which point to a community of ancestry. Thus the nostrils are separated by only a thin partition, and the dental formula is $\frac{2,1,2,3}{2,1,2,3}$. *Oreopithecus* (Mio.) and *Mesopithecus* (Fig. 358*c*) (Plio.) are the best known. The man-like apes, *e.g.* Gorilla (Fig. 356) and Orang Outang, have a small prehensile first toe, projecting brow ridges over the eyes, and marked crests for the attachment of muscles on the roof of the skull. They are represented by *Dryopithecus* (Mio.).

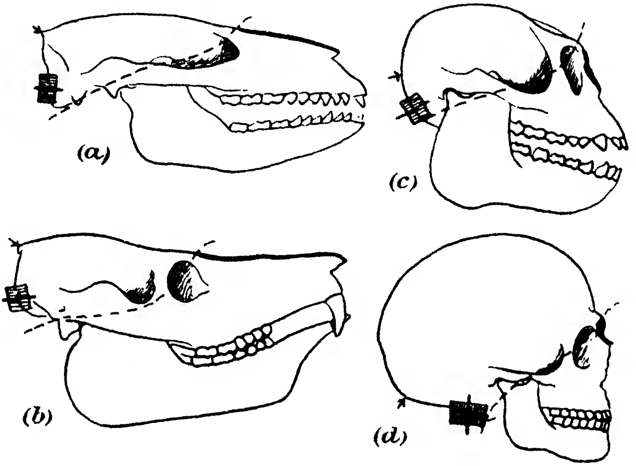


FIG. 358.—Diagrams illustrating some of the more obvious Changes which take place in the Head Skeleton of the Primates.

(*a*) An Eocene Insectivore allied to Lemurs. (*b*) An Extinct Lemur, *Megaladapis*. (*c*) An Extinct Old World Monkey, *Mesopithecus*. (*d*) Man.

The broken line marks the boundary between the brain case and face. Note the enlargement of the former and shortening of the latter and of the tooth margin. The lined area marks the position of the foramen magnum—which changes with the gradual assumption of an erect attitude of body. The arrow marks the Lambdoid crest which lies along the upper border of the occipital region, and provides attachment for the muscles of the neck. The thickened portion of the outline indicates the progressive shortening of the region between nares and brow.

The Gibbon differs in having no such ridges and crests, so that the brain case is smooth as in man. *Pliopithecus* and *Proliopithecus* from the Miocene and Oligocene respectively carry the gibbon-type back beyond the first appearance of men and the other apes to a stock which fulfils the requirements of common ancestor for all three.

Mankind.—Fossil remains of early man are rare. No doubt his great intelligence and alertness enabled him to anticipate and avoid those natural catastrophes which would otherwise have led to his entombment. That same intelligence, however, found expression in the handiwork of weapons and tools. Before the discovery of metals, which was a comparatively recent event in his history, stone (especially flint) was the chief material used by him. Being of such a durable nature these stone implements have been preserved and found in comparative abundance in the ground by the rivers where man encamped, and in the rubbish which accumulated on the floor of the caves where he dwelt. This long period in his development is called the Stone Age.

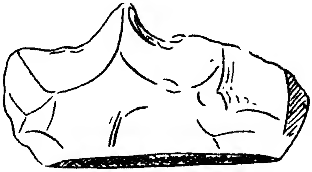


FIG. 359.—Eolith from Piltdown Gravels (after Dawson and Woodward).

With one flint for material and another for hammer he knocked off chips and flakes until the stone was of suitable shape for his purpose. In his first attempts he would choose a stone as near in shape to what he wanted as he could find, and this he would improve by knocking off a few flakes. Such an implement would be difficult to distinguish from a stone which had been chipped naturally. Many such stones have been found in the oldest gravels and are called Eoliths (Fig. 359).

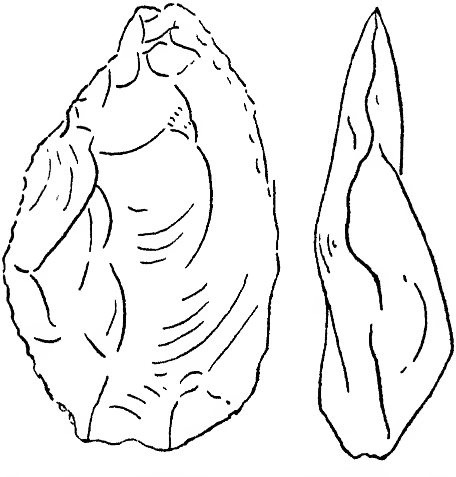


FIG. 360.—Early Form of Palæolith from Piltdown Gravels (after Dawson and Woodward).

In later gravels stones have been found which have undoubtedly been shaped systematically to certain favourite forms. These are called Palæoliths, and the period during which they were made is the Palæolithic or Old Stone Age. At first the chipping was coarse and crude and the edge of the implement was rough and irregular (Fig. 360), but with advancing skill the edge was straightened by re-chipping and trimming. A very great advance was made when it was discovered how to knock off long flakes with sharp knife-like edges with which pieces of bone could be cut to useful shapes. Some of the flakes were trimmed at the ends into sharp points for boring holes or into sharp edges for carving. By this time man had become an artist and sculptor of no mean merit (Fig. 361). These differences mark off the Lower Palæolithic which lasted until the climax of the last glacial stage from the Upper Palæolithic which lasted during the final recession of glaciation.

Later still the art of smoothing the surface of the implements by rubbing them on stones was discovered. This ushered in the Neolithic or New Stone Age. Man had by this time attained some degree of civilization, for he was now an agriculturist, and had tamed many of the domesticated animals. He knew something also of the arts of weaving and of pottery making, but nothing of metallurgy. His surroundings—climate, vegetation, wild beasts, distribution of land and sea—were practically the same as ours to-day, for he lived just before and at the dawn of history. The circumstances of palæolithic man were quite different. He was contemporary with the mammoth, the woolly rhinoceros, the cave bear and cave lion—all long since extinct. In Western and Central Europe he hunted the reindeer and musk ox, animals which to-day live within the Arctic Circle. Only portions of the Palæolithic races experienced the rigours of the Ice Age. During this time much more genial conditions prevailed in other regions, and it was there that early man had his headquarters.

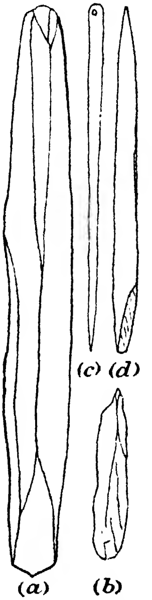


FIG. 361.—Late Palæolithic Instruments.

(*a*) Flint Scraper (after Girod). (*b*) Flint Borer. (*c*) Bone Needle. (*d*) Bone Arrowhead (*c* and *d* after Breuil).

Fragmentary remains of man himself have been found. The oldest come from two widely separated situations. The first to be discovered, called *Pithecanthropus* (Fig. 362), was found in Java. The other, called *Eoanthropus* (Fig. 363), was found in ancient gravels at Piltdown in Sussex. The cranium of the former has a capacity of 850–900 c.c. or about 250–300 c.c. greater than that of the largest ape and only slightly smaller than that of the smallest known human brain. It exhibited ape-like brow ridges, and a receding forehead which was pinched in at the sides behind the orbits. *Eoanthropus* had a brain capacity of 1,100 c.c., though according to some authorities it was rather larger. As in modern man the brow ridges are not prominent, the forehead is smooth and rounded, and is not markedly pinched in at the sides. Combined with these modernized features it has an ape-like chin, prominent canines and a projecting face. More recently similar remains of a third type called *Sinanthropus* have been found near Pekin. All three lived about the beginning of the Ice Age.

More numerous remains have been found associated with the later phases of Lower Palæolithic culture. These have certain common characteristics which distinguish them from all later men

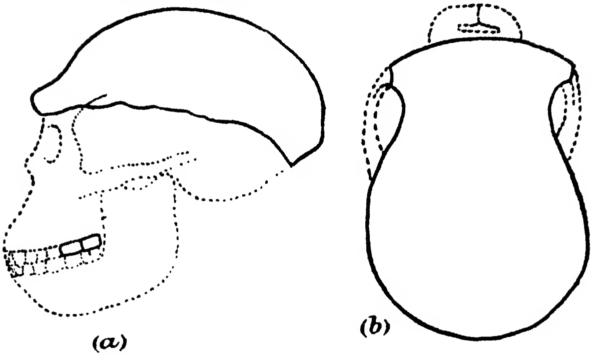


FIG. 362.—Cranium and Molar Teeth of *Pithecanthropus* with other Part restored in broken line (after MacGregor).
(*a*) Side view. (*b*) View from above.

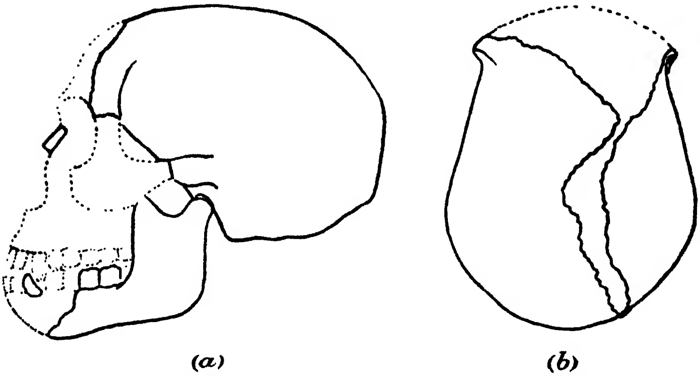


FIG. 363.—Portions of the Head Skeleton of *Eoanthropus*, with Missing Parts restored in broken line (after Woodward).
(*a*) Side view. (*b*) View from above.

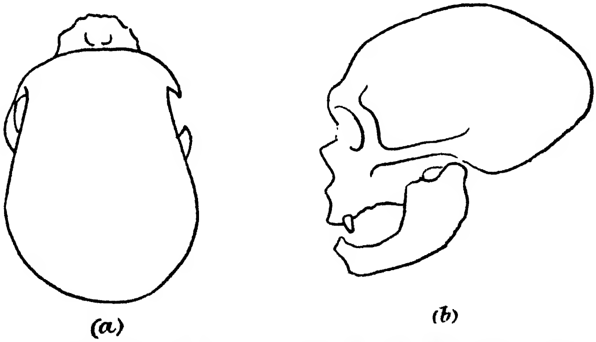


FIG. 364.—Head Skeleton of Neanderthal Man (after Boule).
(*a*) View from above. (*b*) Side view.

and are referred to as Neanderthal Man (Fig. 364), after the name of one of the sites where remains have been found. This man was of uniformly small stature. He had prominent brow ridges and sloping forehead pinched in behind the orbits. He exhibited a cranial capacity ranging from 1,100 c.c. in the earliest to 1,600 in some of the latest members of the race. The face projected as in the apes. The eyes were far apart, and the narial openings very large.

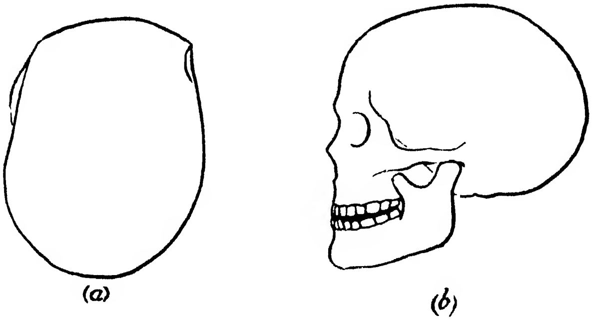


Fig. 365.—Head Skeleton of Cro-Magnon Man (after Verneau).
(*a*) View from above. (*b*) Side view.

Several races of Upper Palæolithic man are known from actual remains. Chief among these is the Cro-Magnon type (Fig. 365). This very tall race differed from the Neanderthal man in the same way as did *Eoanthropus* from *Pithecanthropus*, in having inconspicuous brow ridges and rounded unconstricted forehead. Whilst the lower Palæolithic man evolved along lines in some respects parallel to that of the apes and became quite extinct, Upper Palæolithic man was more modernized, and may quite easily have been closely allied to the stock whence modern men have arisen.

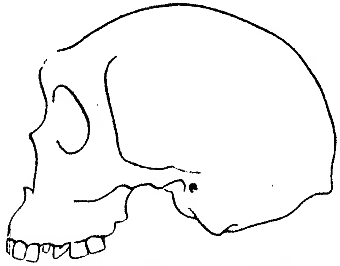


Fig. 366.—Skull of Rhodesian Man (after Brit. Mus. Guide).

The skull and fragments of other parts of the skeleton of an extinct type of man have been recently found in a cave in Northern Rhodesia (Fig. 366). The age of these remains is uncertain, for they have not undergone that change which usually has taken place in the remains of prehistoric man which have been found in Europe. Moreover, the bones of other animals associated with them point to a fauna little if at all different from that which exists in the same part of the world to-day. On the other hand the skull is that of a very primitive type of man. The brain case is typically human and has a capacity of 1,280 c.c. Its occipital region is flat and extensive and indicates a stout and powerful neck. The position of the foramen magnum agrees more with that of modern than of Lower Palæolithic or earlier man, and indicates an erect attitude. The face is remarkably large and in superficial aspect recalls that of the Gorilla. This resemblance is, however, due to the same type of parallel development as that already referred to above, whilst the detailed proportions and shape of parts are typical or even ultrahuman.

SECTION XIII

THE PRINCIPLES OF STRUCTURAL CHANGE

Our survey of the field of animal palæontology is now ended. It may not be out of place therefore, at this stage, to gather together those general principles, clues to which seem to have been suggested by the facts studied in the previous pages.

Racial Stocks.—The attention at the outset is drawn to the individual organism whence it passes quickly to all those other organisms with which that individual is connected ; to those on the one hand which preceded it, and are called its parents and ancestors ; and to those on the other hand which followed it, its offspring and descendants. These terms imply the principle that no generation arises spontaneously, but descends from a previous generation. The existence of this principle is supported by all known facts, is universally accepted, and underlies all modern palæontological and biological thought.

In thinking of these ancestors and descendants it is easy to slip into the practice of visualizing these genetically related individuals as lying in lineal series which run parallel to one another, especially as the terms " line of descent " and " lineage " are in common use. Reflection will, however, soon lead to the realization that such parallel lines of individuals do not exist, for each individual is a point upon which many lines of ancestors converge, and from which many lines of descendants diverge. Moreover, in normal circumstances each individual arises from two parents, and therefore represents the coming together and intertwining of two lines. All closely related individuals, past, present and future, or more correctly the threads of germplasm of which they are the outward and visible manifestation, form a network or plexus of descent. The terms " lineage " and " line of descent " may, however, be usefully retained provided that they are understood to refer only to a series of individuals selected as representing the main phases of change exhibited in the plexus of descent.

When parents and offspring, ancestors, contemporaries and descendants are compared carefully two important phenomena emerge. Firstly, there is a striking resemblance between all these organisms. This is because they have a common heritage, which is but another way of saying that the general constitution of the germplasm remains remarkably constant from generation to generation. Secondly, notwithstanding this close resemblance no two individuals are exactly alike in every detail, for differences, sometimes slight, sometimes quite striking, distinguish both contemporary and successive individuals from one another. This fact proves that the germplasm is not absolutely constant in constitution, but undergoes change. These two phenomena are referred to respectively as Heredity and Variation.[1] The former is a conservative tendency which makes for the retention of that which has been tried and proved. The latter implies plasticity and leads to either progression or retrogression. In the course of many successive generations the differences mentioned above tend to accumulate, with the result that the later members in a plexus of descent come to differ to a marked degree from the earlier members. The stock as a whole is then said to have evolved. The sequence of differences which mark the path of this evolution is described as Phylogeny, or the course of evolution of the stock.

The phenomena described above must not be thought of only in terms of the adult. Every individual has a history of its own in the course of which it passes from the condition of a single cell, through a rapidly changing series of stages, leading gradually up to the adult condition. This series of changes is described as Ontogeny or the development of the individual. The hereditary resemblances already noted between adults also extend to many of the features in development. In this case, however, the resemblances are not merely to the young of other individuals, but in a more or less marked degree to the adults at the various stages in the evolution of the stock to which the individual belongs. There is in fact a tendency for the development of the various individuals to reproduce to a lesser or greater extent features manifested by the various adults belonging to the ancestral stock. The expression " the development of the individual recapitulates the history of the race " expresses the truth as it appears in a lineage, but it is inadequate when the whole plexus is taken into account. It is impossible for one young individual to reproduce the wide range of variations exhibited by adults in an ancestral community. Nevertheless, a comparable range of variations may be reproduced in the youthful stages of a number of descendant individuals. This phenomenon is referred to as *Palingenesis*.

In addition to the evolution of the adult there is an evolution of the young so that there are features in development which have no counterpart in either the adults or the young of past generations. These features are often associated with the special conditions under which the creature exists during early life. This phenomenon is referred to as *Cœnogenesis*. Palingenetic characters are those which

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[1] Variation here includes both fluctuations and saltations (Mutations of De Vries).

have a phylogenetic significance, Cœnogenetic characters those which have not. Nevertheless these new characters may, with the passage of generations, persist in later development and ultimately be manifested even in adult life. This phenomenon is known as *Proterogenesis*. It seems probable, however, that in some cases this invasion of the later developmental stages did not take place gradually through a long succession of generations, but almost if not quite simultaneously within a very brief period of time. This was followed by the progressive elimination of those varieties in which the invasion was less complete.

Biocharacters and Bioseries.—The individual organism, by reason of its compactness and the harmony with which its parts work together, is usually taken as the unit in evolution and classification. This unit is, however, one of great complexity, and consists of a number of simpler units of colour and form, structure and function. These are generally referred to as characters, and are used as the terms by means of which the organism is described, and the species to which it belongs is defined. They also furnish the only true starting point from which to set out on the study of general principles.

Many of these characters have been the subjects of Mendelian experimentation. This has proved them to have such a marked degree of independence of one another that it is possible to interchange a given character in one breed with a comparable character in another breed without disturbing the other characters in either stock. Through successive crossings and intercrossings this character is found to remain stable and distinct, and therefore the terms Unit Character and *Biocharacter* have been suggested for it. In the following pages the latter term will be adopted.

When a biocharacter is examined in a number of individuals belonging to the same species and to the same horizon, it is found that differences or fluctuations in degree can be detected. Thus the septum of a coral varies in length, the cusp of a mammalian tooth varies in size, the shell of a cephalopod varies in the closeness of its coiling. Such variations in a single character are not uniformly distributed among the members of a species. Thus whilst in a large proportion of individuals the character differs but slightly and approximates closely to an average type, in the remainder it differs from this in varying and often very marked degrees. Generally the number of individuals diminishes as the difference increases. When these facts are plotted graphically the resultant curve conforms to the normal curve of dispersion or of error. Since the frequency distribution of these variations can be thus represented by a simple curve they evidently belong to a continuous and linear series.

A similar study of the same character in a number of very young individuals shows that the frequency distribution of its variations also conforms to a normal curve of dispersion, but that the most frequent variation or the mode of the curve is separated by some distance from that for the adult. For the adolescent young the mode occupies an intermediate position between the other two. It follows therefore that the mode shifts during development, that it shifts in a definite direction, and that variations which are common in youth become rarer in the adult.

Between the development of a character, as just described, and its evolution there is a close parallelism. Thus if collections of numerous specimens of the same or genetically related species are made, and the variations of some one character closely studied it is found that the frequency distribution curve for each horizon in the rocks again conforms to a normal curve of dispersion, and that the mode for successive horizons shifts gradually in a definite direction. Each appreciable stage in the shifting of the mode is called a mutation. In no case where such careful study of the evolution of a biocharacter has been conducted has any indication of saltation [1] been detected. Between the stages in the development of a character and the mutations in its evolution there is a close correspondence. This is true for the other characters also and consequently there is manifested the phenomenon of palingenesis in the organism as a whole.

Such facts as these show that each biocharacter has a history of its own, made up of a continuous series of changes moving in a definite direction, from an almost imperceptible or incipient first appearance to a full and extreme expression. For many characters only one direction of change is conceivable. Thus, for example, to coiling and uncoiling, to shortening and lengthening, to widening and narrowing there can be no other alternatives. It is also characteristic of such series of changes that each is limited in range. Thus beyond the extremes of straightness and complete involution there is nothing. A bone never grows to infinite length, and on the other hand it can do no more than disappear.

In at least some cases, possibly in all, a simple biocharacter is not something which stands by itself, but it is one step in a series. Its presence in an animal implies the possession by the stock to which it belongs of the potentiality for passing through a corresponding series of changes. This potentiality, and not merely the

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[1] Saltation is here used as a substitute for the term mutation used in the sense of De Vries by most Biologists. It implies the idea of discontinuity or of a break in the continuity of Variation. Those who believe in saltations hold that they may be minute or great.

isolated biocharacter, is passed on from generation to generation and finds its expression in the developmental stages as well as in the adult. It will be convenient, therefore, to refer to such series as *bioseries*, and to conceive of each as an independently heritable unit.

For some bioseries the attainment of the final term puts an end to all further change. For others the series of changes may be re-expressed in the reverse order. It is possible, therefore, to distinguish reversible and irreversible bioseries, the history of coiling in the cephalopods illustrates the former, whilst the evolution of antlers in deer serves to illustrate the latter. In a reversible series movement in the positive direction is spoken of as progression or anagenesis; that in the negative direction, as retrogression or catagenesis. Since the expression of a bioseries is definite in direction and limited in extent, it may be represented conventionally by the figures 0–100, and the steps in the series by percentages of the whole. As already seen an organism consists of numerous biocharacters representing equally numerous bioseries. If each heritable unit be represented by a letter, *e.g.* A, B, C, etc., then the corresponding bioseries will be A, 0–100; B, 0–100; C, 0–100, etc. If in any individual A has attained to the expression stage, 15, B to stage 30 and C to the stage 25, then the organism can be described by the formula A15, B30, C25. This will illustrate the fact that an organism is better regarded as a combination of stages in the expression of a number of bioseries, than as a congeries of characters.

Rate of Change in Bioseries.—Associated with the serial change described above is the equally important phenomenon of rate of change. The rate of expression of a single bioseries is by no means constant. During ontogeny it varies, for it may be slow, rapid, or even stationary. When, however, the expression of corresponding series is followed from one geological age to another in individuals of the same racial stock a progressive change of velocity is found to take place. Most frequently this change is an acceleration. Thus, for example, in any given sequence of individuals of successive periods there is a speeding up of the development, which leads to the expression in the adult of later and yet later steps in the bioseries. This acceleration continues even when catagenesis has set in and, as a consequence, the return to the lower terms in the series is usually very rapid. Such hastening of development is known as *Tachygenesis*. It results in a progressive shifting of the mode of the frequency curve of variation during geological time, and is therefore a phenomenon of fundamental importance in evolution. As yet nothing is known of the causes which produce this acceleration.

Intimately associated with tachygenesis is the phenomenon of

Lipo-palingenesis, or the non-expression, during the development of a certain character, of some of the stages passed through in its evolution. These omitted stages may be the earliest or some of the later. Omission in the latter case frequently tends to take place when there has been a reversal of the direction of change during evolution. The development is then often short-circuited between the corresponding stages in the positive and negative portions of the series. Thus suppose the evolutionary sequence to be 25, 26, 27, 28, 29, 28, 27, 26, 25; then in development it may be short-circuited to 25, 26, 27, 28, 28, 27, 26, 25; or even to 25, 26, 26, 25.

Retardation in development (*Bradygenesis*) is a less frequent phenomenon. In a few cases it seems to affect the positive portion of a short-circuited series, so that the early stages in development are passed through more slowly and appear to persist to a later time in the life of the individual than they did in previous generations.

The rate of change in the expression of a certain bioseries is not necessarily the same for all members of an evolving racial stock. Sometimes it becomes more rapid in one portion of the stock than in another. The mode for that stock consequently splits, that is to say the variations of maximum frequency for its two portions become separated; and may continue to separate more widely, until the differences in the corresponding adult characters become sufficiently great to justify the classification of the two groups of organisms as distinct varieties, or even species. Changing velocity in the expression of a bioseries is therefore a differentiating influence of considerable importance in evolution.

Rate of Change in Clusters of Bioseries.—It has been already noticed that in the development of a single organism not one but many bioseries are represented. Notwithstanding the apparent unity of the organism as a whole these series are not all expressed at the same rate; on the contrary each unfolds to a very great extent independently of the others; one more rapidly, one less; one uniformly, another with fluctuating velocity. This is true also for the unfolding of bioseries in the evolution of any stock.[1]

This independence in the rate of expression of two or more bioseries is likewise a differentiating influence of first importance, for though two stocks may be endowed with precisely the same cluster of heritable units, *e.g.* A, B, C, derived from a common ancestor whose formula is perhaps A14, B23, C10, these units attain to different degrees of expression in each stock, so that the formula for one may become A15, B30, C26, and for the other A45, B25,

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[1] For a full treatment of the phenomena referred to in this paragraph see Thompson, "On Growth and Form," and Huxley, "Problems of Relative Growth."

C12. These two sets of organisms are now sufficiently distinct to be treated as belonging to different species or even genera, which owe their existence to differences of the velocity of expressional change not only within one bioseries, but also between several such series.

In the first stages of this differentiation of an ancestral stock into two, the differences between these in the actual biocharacters are very slight, and can be referred to one or other of two categories. There are differences of the type dealt with above and usually classed as " fluctuating variations " in which only one bioseries is concerned. The other differences are associated with the existence of a cluster of bioseries, and are due to the relationships of the velocities of change of all the bioseries to one another in one cluster, being different from those in the other cluster.

Whatever the rates of expression may be, sooner or later the members of one stock endowed with a slowly changing series will exhibit the same biocharacters as have been already manifested by those of another stock, in which the corresponding bioseries has been expressed more rapidly. If these biocharacters happen to be ones which strike the eye, then the two sets of organisms are said to be remarkably alike, and are described as homœomorphs one of the other. Inasmuch as each bioseries is of limited range the attainment of the final term by one or several series is merely a matter of time, as well for the organism in which the movement is slow as for the one in which it is rapid. In these circumstances homœomorphy is the only goal, and extinction the only reward, unless a reversal of the direction of movement takes place, or the appearance of a new bioseries introduces fresh possibilities of progress. In the former case the final term at the other end is not far away.

A special type of homœomorphy termed transversal homœomorphy is exhibited when a reversal in the direction of change has taken place, for then the same stage may be reached in the course of this negative movement in one stock as that attained in another in which the movement is positive.

The Origin of Bioseries.—Up to this point the history of established bioseries has alone been considered. Such series must, however, have had a time and place of origin. In discussing this problem several considerations must be remembered. As each series is a heritable unit it evidently has either a material or dynamic representation in the germplasm that is capable of being reproduced indefinitely, so that every unit is represented in each of a vast multitude of germs. These units find expression in the soma; and it is this expression which alone lies open to examination, and alone furnishes a clue to the changes which have taken place in the germplasm in past ages.

The differences between one stock and another that are due to the appearance of new bioseries must be rarer phenomena than those which are due to the varying rates of change, and which have been already considered above. Moreover they provide a type of " variation " totally different from any that has been noticed previously.

Wherever the history of a bioseries is at all completely known it exhibits a progression from, or a retrogression towards, a low or incipient condition. This fact suggests that at its first appearance it was in all probability incipient in degree of expression. When, therefore, the earliest stage of expression known is an advanced one, it is probably quite unsafe to quote it as an example of the sudden appearance of a bioseries in an advanced stage of development, and as a proof that the evolution of a bioseries proceeds by saltation.

Many cases are on record, however, in which the earliest known stages of a series lie at or very close to the lowest possible term of expression of that series, such as the horns of titanotheres, the hinge teeth of pelecypods, etc. These cases supply some information concerning the method of origin of new bioseries. In the first place such usually find their first expression as local modifications of pre-existing features, *e.g.* a horn is a local modification of a nasal or a frontal bone, the pelecypod tooth is a local modification of the shell margin, the segments of a metamerically segmented animal are modifications of the tissue between the oral and anal regions of the body, the coral septum is due to a local modification of the general secretory activity of the aboral surface of the polype.

Further, these incipient expressions may appear singly and in a very definite relation to the function that the fully developed series will serve, *e.g.* horns ; or they may occur in considerable numbers, having only an indefinite relation to a specialized function (compare for example the actinodont and heterodont teeth of Pelecypoda) ; or again they may be repeated to the utmost capacity of the pre-forming tissue and apparently without any relation to a specialized function (*e.g.* placoid scales, and metameric and radial segments). In the light of these facts it is unwise to point to either external influences, or to inherent tendencies, as the sole originating cause of all new series. Whilst functional need is almost immediately met in some cases, in others the functional need does not appear to exist, except in the imagination of the observer ; and the new feature seems to arise spontaneously as the outcome of inherent tendencies.

The Establishment of a Bioseries.—The coming into existence of a bioseries is not necessarily followed by its full expression in either development or evolution. This is especially true for those cases in which the incipient expressions are great in number, and wide in distribution, in each organism of the stock. Thus, for example, of all the placoid scales which covered the body of the primeval vertebrate only a few reached the extreme expression found in the mammalian tooth.

More advanced expression seems to be evoked only in those regions of the body where they can satisfy a functional need. This they do either by a change in proportions, or by a concentration in numbers, or by a combination of both these processes (compare, for example, the canine tooth of a dog with the dental plate of Cochliodus). In those regions where no such functional need exists the incipient expression may disappear. In the former case the heritable unit is, as it were, reinforced dynamically, and its possible changes in expression rapidly sifted. In the latter case the heritable unit loses energy and may be ultimately lost, never to be again restored. As the total energy of the germ and of the soma is limited, the disappearance of ineffective incipients is generally a necessary accompaniment of specialization, that is of prolonged serial change on the part of a few.

The Co-ordination of Bioseries.—The influence of the appearance of a new bioseries upon those which already exist is probably far reaching. It requires investigation and cannot yet be discussed profitably. Whilst each bioseries has a history of its own, and is separable from its fellows in heredity, nevertheless the velocities of change of all are so closely co-ordinated with one another that functional efficiency is maintained throughout all the stages of development of the individual organism as a whole. This does not mean that the series all unfold with uniform velocities. On the contrary, both in ontogeny and phylogeny, the velocities of expression of the individual bioseries are constantly changing in close relationship with one another; thus, for example, whilst one series speeds up, another slows down, and a third comes actually to a standstill (Figs. 367, 368). Were this not the case then one series in its development might use up all the limited supply of developmental energy which is at the disposal of the organism, and thus tend to produce a strange monstrosity quite incapable of functioning in a normal environment.

Though many individuals attain a functionally efficient maturity, their number is very small compared with the number of those that have died at the various stages from the moment following the fertilization of the germ onwards. Great as that number may be, still greater is the possible number of combinations of bioseries, and of biocharacters, or rather of bioserial developmental velocities. It is conceivable that in no two individual organisms are the velocities of change in each and all the bioseries precisely the same. Here then is ample opportunity for the coming into existence of combinations of misfitting velocities, the which if they could proceed to mature development under the conditions presented by nature, would flood the world with strange monstrosities. The curious products of breeding under artificial conditions, *e.g.* megacephaly, dwarfed limbs, and waltzing mice, show that such formation of monstrous combinations can take place. The survival under natural conditions of only those individuals in which the combination of velocities is suitable tends to the establishment of harmonically balanced combinations.

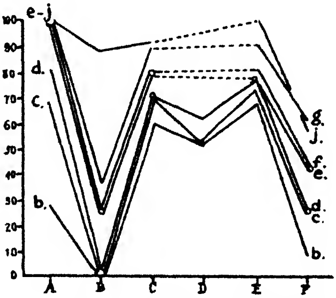

FIG. 367.—Graphs representing Stages in the Development of *Caninia cornucopiæ* (*vide* Fig. 45).

b–j = seven stages in development. *A–F* = six bioseries. Note the stationary character of *B* while *A* develops rapidly, and *vice versa*.

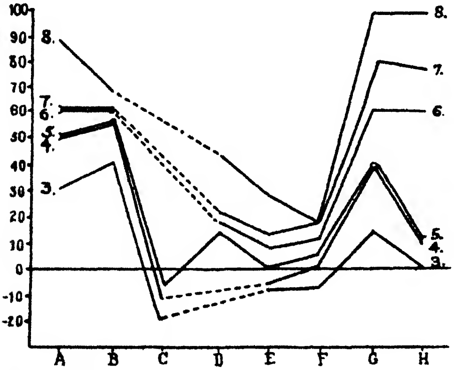

FIG. 368.—Graphs representing Stages in the Evolution of *Zaphrentis delanouei* (*vide* Table III).

3–8 = six stages in evolution. *A–H* = eight bioseries. Those which come below the zero line have experienced a reversal of direction. The reversal takes place during stages 4 and 5. During this time all the other bioseries experience a halt.

Two racial stocks in which such a counterpoising of velocities has been established may still be sufficiently closely related to allow of successful interbreeding. Mendelian experimentation has proved that, in such cases, biocharacters belonging to corresponding bioseries may be interchanged between the two stocks, so that a bioseries which has reached an advanced expression in one stock may replace the corresponding much less advanced series in the other. In this way a new type of organism, exhibiting a striking new character, may be suddenly produced. Herein there may possibly lie some explanation of such saltations as occur in nature. Saltation in the evolution of a combination of bioseries cannot, however, be taken as evidence of saltation in the evolution of the character itself. All the evidence available tends to show that it does not matter how a biocharacter is shuffled about by breeding from one section of a stock to another, its own evolution has proceeded within the whole plexus of descent by a series of imperceptible changes from an incipient beginning.

The satisfactory elucidation of the numerous problems touched upon above, as well as of many others that are at present only dimly perceived, awaits the yet closer co-operation of the students of rocks, of fossils and of living forms.

BIBLIOGRAPHY

Usually only more recent references are given. Earlier literature will be found mentioned in these.

ABBREVIATIONS :—

A.J.S.—American Journal of Science.
Amer. Nat.—American Naturalist.
Ann. Mag. Nat. Hist.—Annals and Magazine of Natural History.
Biol. Rev.—Biological Reviews.
B.M.G.—British Museum Guides.
Bull. Soc. Geol. France.—Bulletine Société Geologique de France.
Geo. Mag.—Geological Magazine.
Mem. Geo. Sur.—Memoirs of the Geological Survey of Great Britain.
Mem. Bos. Soc. Nat. Hist.—Memoirs of the Boston Society of Natural History.
Mem. Man. Lit. Phil.—Memoirs and Proceedings of The Manchester Literary and Philosophical Society.
Mon. Pal. Soc.—Monographs of the Palæontographical Society.
Proc. U.S.M.—Proceedings of the United States National Museum.
P.G.A.—Proceedings of the Geologists Association.
P.Z.S.—Proceedings of the Zoological Society of London.
Phil. Trans. Roy. Soc.—Philosophical Transactions of the Royal Society.
P.R.S.—Proceedings of the Royal Society.
Proc. Roy. Soc. Qd.—Proceeding of the Royal Society of Queensland.
Q.J.G.S.—Quarterly Journal of the Geological Society.
Rep. B.A.—Report of the British Association.
Smith. Misc. Coll.—Smithsonian Miscellaneous Collections.
T.N.Z. Inst.—Transactions of the New Zealand Institute.
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