THE ELEMENTS OF COMPARATIVE ANATOMY.

LECTURES

ON THE

ELEMENTS OF COMPARATIVE ANATOMY.

BY

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ON THE CLASSIFICATION OF ANIMALS

AND

ON THE VERTEBRATE SKULL.

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DEDICATION.

To GEORGE BUSK, Esq., F.R.S.

My dear Busk,

I beg leave to dedicate these Lectures of mine to you, partly as my old and staunch friend, and partly as a member of the Council of the Royal College of Surgeons, and therefore a representative of the body to which I am indebted for the opportunity of delivering them.

Ever

Yours very faithfully,

T. H. HUXLEY.

The Royal School of Mines, Jermyn Street.

March 7th, 1864.

PREFACE.

The present work contains, substantially, the Lectures which I delivered, in the spring of 1863, at the Royal College of Surgeons of England, in discharge of my duty as Hunterian Professor of Comparative Anatomy and Physiology to the College. I purpose, should I continue to hold that honourable office, to publish the substance of subsequent courses in a similar manner; and by that process to bring out, eventually, a comprehensive, though condensed, systematic work on Comparative Anatomy. In *intention*, therefore, the volume now before the reader is the first of a series, to be followed in due order by a second, "On Man and the other *Primates;*" a third, on the remaining *Mammalia,* and so on. Whether this intention will ever be fully carried out depends on so many contingencies, however, that I have thought it the better course to let each volume remain, in form, independent of the rest.

I have much pleasure in expressing my obligations to the President and Council of the Royal College of Surgeons for the unrestricted access which I have enjoyed to the abundant anatomical treasures contained in their Museum and its store-rooms, to which my Lectures are indebted for many of their most instructive illustrations.

Nor can I conclude without a word of thanks to the young artist, Mr. W. H. Wesley, to whose skill, painstaking, and thorough faithfulness, the excellence of most of those illustrations is due. It will be understood that, when the contrary is not expressly stated, the drawings are original.

The Lectures differ, by the omission of the inaugural Discourse, which would have been out of place in this volume of the work I contemplate; by additions to others; and by a change of arrangement, from those which were published in the "Medical Times and Gazette."

T. H. H.

LONDON, *March 7th*, 1864.

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LECTURES

ON THE

ELEMENTS OF COMPARATIVE ANATOMY.

LECTURE I.

ON THE CLASSIFICATION OF ANIMALS.

THE GREGARINIDA, RHIZOPODA, SPONGIDA, AND INFUSORIA.

By the classification of any series of objects, is meant the actual, or ideal, arrangement together of those which are like and the separation of those which are unlike; the purpose of this arrangement being to facilitate the operations of the mind in clearly conceiving and retaining in the memory, the characters of the objects in question.

Thus, there may be as many classifications of any series of natural, or of other, bodies, as they have properties or relations to one another, or to other things; or, again, as there are modes in which they may be regarded by the mind: so that, with respect to such classification as we are here concerned with, it might be more proper to speak of *a* classification than of *the* classification of the animal kingdom.

The preparations in the galleries of the Museum of this College are arranged upon the basis laid down by John Hunter, whose original collection was intended to illustrate the modifications which the great physiological apparatuses undergo in the animal series: the classification which he adopted is a classification by organs, and, as such, it is admirably adapted to the needs of the comparative physiologist.

But the student of the geographical distribution of animals, regarding animated creatures, not as diverse modifications of the great physiological mechanism, but in relation to one another, to plants and to telluric conditions, would, with equal propriety, dispose of the contents of a Zoological Museum in a totally different manner; basing his classification, not upon organs, but on distributional assemblages. And the pure palæontologist, looking at life from yet another distinct point of view, would associate animal remains together on neither of these principles, but would group them according to the order of their succession in Time.

Again, that classification which I propose to discuss in the present Lectures, is different from all of these: it is meant to subserve the comprehension and recollection of the facts of animal structure; and, as such, it is based upon purely structural considerations, and may be designated a Morphological Classification. I shall have to consider animals, not as physiological apparatuses merely; not as related to other forms of life and to climatal conditions; not as successive tenants of the earth; but as fabrics, each of which is built upon a certain plan.

It is possible and conceivable that every animal should have been constructed upon a plan of its own, having no resemblance whatsoever to the plan of any other animal. For any reason we can discover to the contrary, that combination of natural forces which we term Life might have resulted from, or been manifested by, a series of infinitely diverse structures: nor, indeed, would anything in the nature of the case lead us to suspect a community of organization between animals so different in habit and in appearance as a porpoise and a gazelle, an eagle and a crocodile, or a butterfly and a lobster. Had animals been thus independently organized, each working out its life by a mechanism peculiar to itself, such a classification as that which is now under contemplation would obviously be impossible; a morphological, or structural, classification plainly implying morphological, or structural, resemblances in the things classified.

As a matter of fact, however, no such mutual independence of animal forms exists in nature. On the contrary, the different members of the animal kingdom, from the highest to the lowest, are marvellously interconnected. Every animal has a something in common with all its fellows: much, with many of them; more, with a few; and, usually, so much with several, that it differs but little from them.

Now, a morphological classification is a statement of these gradations of likeness which are observable in animal structures, and its objects and uses are manifold. In the first place, it strives to throw our knowledge of the facts which underlie, and are the cause of, the similarities discerned into the fewest possible general propositions—subordinated to one another, according to their greater or less degree of generality; and in this way it answers the purpose of a *memoria technica*, without which the mind would be incompetent to grasp and retain the multifarious details of anatomical science.

But there is a second and even more important aspect of morphological classification. Every group in that classification is such in virtue of certain structural characters, which are not only common to the members of that group, but distinguish it from all others; and the statement of these constitutes the definition of the group.

Thus, among animals with vertebræ, the class *Mammalia* is definable as those which have two occipital condyles, with a well-ossified basi-occipital; which have each ramus of the mandible composed of a single piece of bone and articulated with the squamosal element of the skull; and which possess mammæ and non-nucleated red blood-corpuscles.

But this statement of the characters of the class *Mammalia* is something more than an arbitrary definition. It does not merely mean that naturalists agree to call such and such animals *Mammalia*: but it expresses, firstly, a generalization based upon, and constantly verified by, very wide experience; and, secondly, a belief arising out of that generalization. The generalization is that, in nature, the structures mentioned are always found associated together: the belief is, that they always have been, and always will be, found so associated. In other words, the definition of the class *Mammalia* is a statement of a law of correlation, or coexistence, of animal structures, from which the most important conclusions are deducible.

For example: if a fragmentary fossil be discovered, consisting of no more than a ramus of a mandible and that part of the skull with which it articulated, a knowledge of this law may enable the palæontologist to affirm, with great confidence, that the animal of which it formed a part suckled its young and had non-nucleated red blood-corpuscles; and to predict that should the back part of that skull be discovered, it will exhibit two occipital condyles and a well-ossified basi-occipital bone.

Deductions of this kind, such as that made by Cuvier in the famous case of the fossil opossum of Montmartre, have often been verified, and are well calculated to impress the vulgar imagination; so that they have taken rank as the triumphs of the anatomist. But it should carefully be borne in mind, that, like all merely empirical laws, which rest upon a comparatively narrow observational basis, the reasoning from them may at any time break down. If Cuvier, for example, had had to do with a fossil *Thylacinus* instead of a fossil Opossum, he would not have found the marsupial bones, though the inflected angle of the jaw would have been obvious enough. And so, though, practically, *any one who met with a characteristically mammalian jaw* would be justified in expecting to find the characteristically mammalian occiput associated with it; yet, he would be a bold man indeed, who should strictly assert the belief which is implied in this expectation, viz., that at no period of the world's history did animals exist which combined a mammalian occiput with a reptilian jaw, or *vice versâ*.

Not that it is to be supposed that the correlations of structure expressed by these empirical laws are in any sense accidental, or other than links in the general chain of causes and effects. Doubtless there is some very good reason why the characteristic occiput of a Mammal should be found in association with mammæ and non-nucleated blood-corpuscles; but it is one thing to admit the causal connexion of these phenomena with one another, or with some third; and another thing to affirm that we have any knowledge of that causal connexion, or that physiological science, in its present state, furnishes us with any means of reasoning from the one to the other.

Cuvier, the more servile of whose imitators are fond of citing his mistaken doctrines as to the nature of the methods of palæontology against the conclusions of logic and of common sense, has put this so strongly that I cannot refrain from quoting his words.*

"But I doubt if any one would have divined, if untaught by observation, that all ruminants have the foot cleft, and that they alone have it. I doubt if any one would have divined that there are frontal horns only in this class: that those among them which have sharp canines for the most part lack horns.

"However, since these relations are constant, they must have some sufficient cause; but since we are ignorant of it, we must make good the defect of the theory by means of observation: it enables us to establish empirical laws, which become almost as certain as rational laws when they rest on sufficiently repeated observations; so that now, whoso sees merely the print of a cleft foot may conclude that the animal which left this impression ruminated, and this conclusion is as certain as any other in physics or morals. This footprint alone, then, yields to him who observes it, the form of the teeth, the form of the jaws, the form of the vertebræ, the form of all the bones of the legs, of the thighs, of the shoulders, and of the pelvis of the animal which has passed by: it is a surer mark than all those of Zadig."

Morphological classification, then, acquires its highest importance as a statement of the empirical laws of the correlation of structures; and its value is in proportion to the precision and the comprehensiveness with which those laws, the definitions of the groups adopted in the classification, are stated. So that, in attempting to arrive at clear notions concerning classification, the first point is to ascertain whether any, and if so, what groups of animals can be established, the members of which shall be at once united together and separated from those of all other groups, by well-defined structural characters. And it will be most convenient to commence the inquiry with groups of that order which are commonly called CLASSES, and which are enume-

* 'Ossemens fossiles,' éd. 4me, tome 1r, p. 164.

rated in an order and arrangement, the purpose of which will appear more fully by and by, in the following table.

TABLE OF THE CLASSES OF THE ANIMAL KINGDOM.

The Limits of the Four Cuvierian Sub-Kingdoms are indicated by the Brackets and Dotted Line.

RADIATA.

Gregarinida. *Infusoria.*		*Scolecida* (?).	
Rhizopoda (?).		*Echinodermata.*	
Spongida.			
		Annelida.	ARTICULATA.
Hydrozoa.		*Crustacea.*	ARTICULATA.
Actinozoa.		*Arachnida.*	ARTICULATA.
		Myriapoda.	ARTICULATA.
Polyzoa.		*Insecta.*	ARTICULATA.
Brachiopoda.	MOLLUSCA.		
Ascidioida.	MOLLUSCA.		
		Pisces.	VERTEBRATA.
Lamellibranchiata.	MOLLUSCA.	*Amphibia.*	VERTEBRATA.
		Reptilia.	VERTEBRATA.
Branchiogasteropoda.	MOLLUSCA.	*Aves.*	VERTEBRATA.
Pulmogasteropoda.	MOLLUSCA.	*Mammalia.*	VERTEBRATA.
Pteropoda.	MOLLUSCA.		
Cephalopoda.	MOLLUSCA.		

It is not necessary for my purpose that the groups which are named on the preceding table should be absolutely and precisely equivalent one to another; it is sufficient that the sum of them is the whole of the Animal Kingdom, and that each of them embraces one of the principal types, or plans of modification, of animal form; so that, if we have a precise knowledge of that which constitutes the typical structure of each of these groups, we shall have, so far, an exhaustive knowledge of the Animal Kingdom.

I shall endeavour, then, to define—or, where definition is not yet possible, to describe a typical example of—these various groups. Subsequently, I shall take up some of those further classificatory questions which are open to discussion; inquiring how far we can group these classes into larger assemblages, with definite and constant characters; and, on the other hand, how far the existing subdivisions of the classes are well based or otherwise. But the essential matter, in the first place, is to be quite clear about the different classes, and to have a distinct knowledge of all the sharply-definable modifications of animal structure which are discernible in the animal kingdom.

The first class of which I shall speak is the group of the GREGARINIDA. These are among the simplest animal forms of which we have any knowledge. They are the inhabitants of the bodies for the most part of invertebrate, but also of vertebrate, animals; and they are commonly to be found in abundance in the alimentary canal of the common cockroach, and in earthworms. They are all microscopic, and any one of them, leaving minor modifications aside, may be said to consist of a sac, composed of a more or less structureless, not very well-defined membrane, containing a soft semi-fluid substance, in the midst, or at one end, of which lies a delicate vesicle; in the centre of the latter is a more solid particle. (Fig. 1, A.) No doubt many persons will be struck with the close resemblance of the structure of this body to that which is possessed by an ovum. You might take the more solid particle to be the representative of the germinal spot, and the vesicle to be that of the germinal vesicle; while the semi-fluid sarcodic contents might be regarded as the yelk, and the outer membrane as the vitelline membrane. I do not wish to strain the analogy too far, but it is, at any rate, interesting to observe this close morphological resemblance between one of the lowest of animals and that form in which all the higher animals commence their existence. It is a very remarkable characteristic of this group, that there is no separation of the body into distinct layers, or into cellular elements. The *Gregarinida* are devoid of mouths and of digestive apparatus, living entirely by imbibition of the juices

Fig. 1.

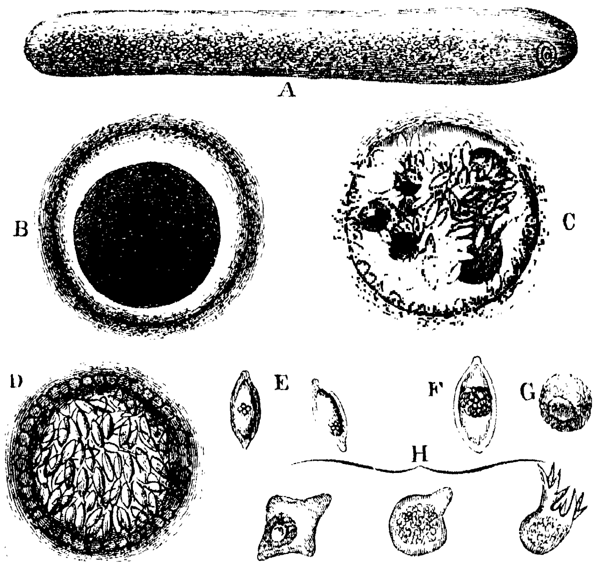


Fig. 1.—A, *Gregarina* of the earthworm (after Lieberkühn); B, encysted; C, D, with the contents divided into pseudo-navicellæ; E, F, free pseudo-navicellæ; G, H, free amœbiform contents of the latter.

of the animal in whose intestine, or body cavity, they are contained. The most conspicuous of those phenomena, which we ordinarily regard as signs of life, which they exhibit, is a certain contraction and expansion along different diameters, the body slowly narrowing, and then lengthening, in various directions. Under certain circumstances (though the conditions of the change are not thoroughly understood), it is observed that one of these *Gregarinida*, whatever its form may be, will convert itself into a well-rounded sac, the outer membrane ceasing to exhibit any longer those movements of which I spoke, and becoming coated by a structureless investment, or "cyst" (Fig. 1, B).

The substance of the body contained within the cyst next undergoes a singular change. The central nucleus and the vesicle disappear; after a time, the mass breaks up into a series of rounded portions and, then, each of those rounded portions elongates, and, becoming slightly pointed at each end, constitutes a little body which has been called a "*Pseudo-navicella*," from its resemblance to the Diatomaceous *Navicula* or *Navicella* (Fig. 1, C, D). Next, the capsule bursts and the *Pseudo-navicellæ* (Fig. 1, E, F) are scattered and passed out of the body of the animal which they inhabit. Though, of course, a great number of them are destroyed, some, at any rate, are devoured by other animals; and, when that is the case, the little particle of protein substance which is inclosed within the *Pseudo-navicella* is set free from its shell, and exhibits much more lively movements than before, thrusting out processes in various directions, and drawing them in again, and, in fact, closely resembling one of those animalcules which have been called *Amœbæ* (Fig. 1, H). The young Amœbiform *Gregarina* grows, increases in size, and at length assumes the structure which it had at first. That, in substance, is all that we know of this lowest division of animal life. But it will be observed, there is a hiatus in our knowledge. We cannot say that we know the whole nature and mode of existence of this, or any other animal, until we have traced it to its sexual state; but, at present, we know nothing whatever of this condition among the *Gregarinæ;* so that in reasoning about them we must always exercise a certain reticence, not knowing how far we may have to modify our opinions by the discovery of the sexual state hereafter.

The process of becoming encysted, preceded or accompanied very often by the mutual apposition of two *Gregarinæ,* was formerly imagined to correspond with what is termed among plants "conjugation,"—a process which in some cases, at any rate, appears to be of a sexual nature. But the discovery that a single *Gregarina* may become encysted and break up into *Pseudo-navicellæ* seems to negative this analogy.

But now, leaving this, I pass on to the next class—that which is indicated in the table as the RHIZOPODA. I have put a query against it, as I shall have to return to it as another of those respecting which our knowledge is incomplete. And at this moment I merely direct attention to the salient and characteristic features of the whole group (Fig. 2).

Fig. 2.

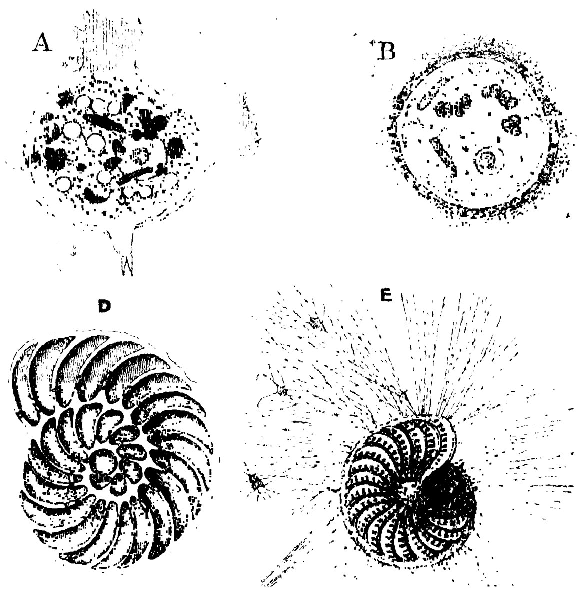


Fig. 2.—A, B, Free and encysted conditions of an *Amœba* (after Auerbach); E, a Foraminifer (*Rotalia*) with extended pseudopodia; D, its shell in section (after Schulze).

It seems difficult to imagine a stage of organization lower than that of *Gregarinida*, and yet many of the *Rhizopoda* are still simpler. Nor is there any group of the animal kingdom which more admirably illustrates a very well-founded doctrine, and one which was often advocated by Hunter himself, that life is the cause and not the consequence of organization; for, in these lowest forms of animal life, there is absolutely nothing worthy of the name of organization to be discovered by the microscopist, though assisted by the beautiful instruments that are now constructed. In the substance of many of these creatures, nothing is to be discerned but a mass of jelly, which might be represented by a little particle of thin glue. Not that it corresponds with the latter in composition, but it has that texture and sort of aspect; it is structureless and organless, and without definitely formed parts. Nevertheless, it possesses all the essential properties and characters of vitality; it is produced from a body like itself; it is capable of assimilating nourishment, and of exerting movements. Nay, more, it can produce a shell; a structure, in many cases, of extraordinary complexity and most singular beauty (Fig. 2, D).

That this particle of jelly is capable of combining physical forces in such a manner as to give rise to those exquisite and almost mathematically-arranged structures—being itself structureless and without permanent distinction or separation of parts—is, to my mind, a fact of the profoundest significance.

Though a Rhizopod is not permanently organized, however, it can hardly be said to be devoid of organs; for the name of the group is derived from the power which these animals possess of throwing out processes of their substance, which are called "pseudopodia," and are sometimes very slender and of great length (Fig. 2, E), sometimes broad and lobe-like (Fig. 2, A). These processes may flow into one another, so as to form a network, and they may, commonly, be thrust out from any part of the body and retracted into it again.

If you watch one of these animals alive, you see it thrusting out, first one and then another of its pseudopodia, exhibiting changes of form comparable to those which the colourless corpuscles of the human blood present. The movements of these Rhizopods are quite of the same character, only they are much more extensive and effect locomotion. The creature also feeds itself by means of its pseudopodia, which attach themselves to nutritive particles, and then draw them into the substance of the body. There is neither ingestive nor egestive aperture, neither special motor nor prehensile organs, but the pseudopodia perform each function as it may be required.

But here, again, we labour under an imperfection of knowledge. For, although it is quite certain that the *Rhizopoda* may multiply by division of their substance—in a way somewhat analogous to that which I detailed when speaking of the *Gregarinida*—yet, as in that case, we have no knowledge of any true sexual process. It is a most remarkable circumstance that though these animals are abundant, and are constantly under observation, we are still in doubt upon that essential point,—still uncertain whether there may not be some phase in the cycle of vital phenomena of the *Rhizopoda* with which we are unacquainted; and, under these circumstances, a perfect definition of the class cannot even be attempted.

The next division is the group of the SPONGIDA, which exist under such multitudinous forms in both salt and fresh waters. Up to the last few years we were in the same case, with respect to this class, as with the *Gregarinida* and the *Rhizopoda*. Some zoologists even have been anxious to relegate the sponges to the vegetable kingdom; but the botanists, who understood their business, refused to have anything to do with the intruders. And the botanists were quite right; for the discoveries of late years have not left the slightest doubt that the sponges are animal organisms, and animal organisms, too, of a very considerable amount of complexity, if we may regard as complex a structure which results from the building up and massing together of a number of similar parts.

The great majority of the sponges form a skeleton, which is composed of fibres of a horny texture, strengthened by needles, or spicula, of silicious, or of calcareous, matter; and this framework is so connected together as to form a kind of fibrous skeleton. This, however, is not the essential part of the animal, which is to be sought in that gelatinous substance, which invests the fibres of the skeleton during life, and is traversed by canals which open upon the surface of the sponge, directly or indirectly, by many minute, and fewer large, apertures.

If I may reduce a sponge to its simplest expression—taking the common *Spongilla*, for example, of our fresh waters,—the structure—removing all complexities, and not troubling ourselves with the skeleton, because that has nothing to do with what we are now considering—may be represented by the diagram (A, Fig. 3). There is a thin superficial layer (*a*) formed entirely of a number of the so-called sponge particles, or ultimate components of the living substance of the sponge, each of which is similar to an *Amœba*, and contains a nucleus. These

Fig. 3.

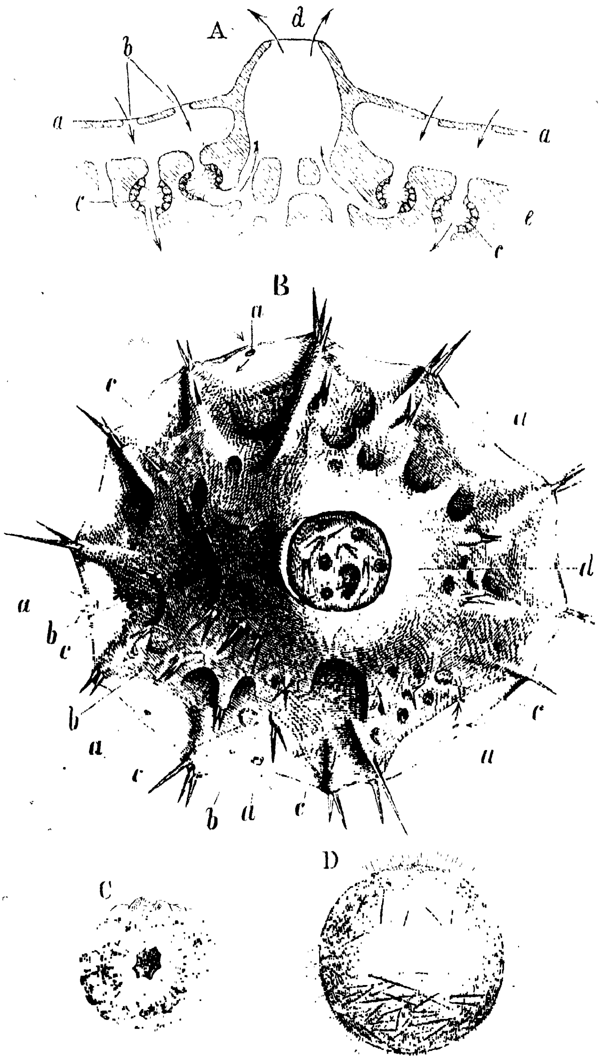


Fig. 3.—A, Hypothetical section of a *Spongilla;* *a*, superficial layer; *b*, inhalent apertures; *c*, ciliated chambers; *d*, an exhalent aperture; *e*, deeper substance of the sponge. The arrows indicate the direction of the currents. B, A small sponge with a single exhalent aperture, seen from above (after Lieberkühn); *a*, inhalent apertures; *c*, ciliated chambers; *d*, exhalent aperture. C, a ciliated chamber. D, a free-swimming ciliated embryo.

are all conjoined in a single layer, so as to form a continuous lamellar membrane, which constitutes the outer and superficial layer of the body. Beneath this is a wide cavity, communicating with the exterior by means of minute holes in the superficial layer (*b*), and, of course, filled with water. The cavity separates the superficial layer of the sponge from its deeper substance, which is of the same character as the superficial layer, being made up of a number of aggregated sponge particles, each of which has a nucleus and is competent to throw out numerous pseudopodial prolongations if detached. While the living sponge is contained in water, a great number of currents of water set in to the wide cavity beneath *a*, *a*, through the minute apertures (*b*), which have thence been termed "inhalent."

In the floor of the cavity, there are a number of apertures which lead into canals ramifying in the deep layer, and eventually ending in the floors of certain comparatively lofty funnels, or craters. The top of each of these presents one of those larger and less numerous apertures, which have been referred to as existing on the surface of the sponge, and which are fitly termed "exhalent" apertures. For, as Dr. Grant discovered, many years ago, strong, though minute, currents of water are constantly flowing out of these large apertures; being fed by the currents which as constantly set in, by the small apertures and through the superficial cavity, into the canals of the deeper substance. The cause of this very singular system of currents remained for a long time unknown. It was rendered intelligible by Dr. Bowerbank's discovery of the existence of vibratile cilia in the genus *Grantia*, but it is only quite recently that the precise nature of the arrangement of the apparatus which gives rise to these currents in ordinary sponges, has been made out by Lieberkühn and by Carter. The canals which enter the deep substance of the sponge become dilated into spheroidal chambers, lined with sponge particles (Fig. 3, A, *c*, C), each of which is provided with a vibratile cilium; and as all these cilia work in one direction—towards the crater—they sweep the water out in that direction, and its place is taken by fresh water, which flows in through the small apertures and through the superficial chamber. The currents of water carry along such matters as are suspended in them, and these are appropriated by the sponge particles lining the passages, in just the same way as any one of the *Rhizopoda* appropriates the particles of food it finds in the water about itself. So that we must not compare this system of apertures and canals to so many mouths and intestines; but the sponge represents a kind of subaqueous city, where the people are arranged about the streets and roads, in such a manner, that each can easily appropriate his food from the water as it passes along.

In the sponges two reproductive processes are known to occur: the one of them, asexual, corresponding with the encysting process of the *Gregarinida;* and the other, truly sexual, and answering to the congress of the male and female elements in the higher animals. In the common fresh-water *Spongilla*, towards the autumn, the deeper layer of the sponge becomes full of exceedingly small bodies, sometimes called "seeds" or "gemmules," which are spheroidal, and have, at one point, an opening. Every one of these bags—in the walls of which are arranged a great number of very singular spicula, each resembling two toothed wheels joined by an axle—is, in point of fact, a mass of sponge particles which has set itself apart—gone into winter quarters, so to speak—and becoming quite quiescent, encysts itself and remains still. The whole *Spongilla* dies down, and the seeds, inclosed in their case, remain uninjured through the winter. When the spring arrives, the encysted masses within the "seed," stimulated by the altered temperature of the water, creep out of their nests, and straightway grow up into *Spongillæ* like that from which they proceeded.

But there is, in addition, a true sexual process, which goes on during the summer months. Individual sponge particles become quiescent, and take on the character of ova; while, in other parts, particular sponge particles fill with granules, the latter eventually becoming converted into spermatozoa.

These sacs burst and some of the spermatozoa, coming into contact with the ova, impregnate them. The ova develop and grow into ciliated germs (D, fig. 3), which make their way out, and, after swimming about for a while, settle themselves down and grow up into *Spongillæ*.

Now that we know the whole cycle of the life of the sponges, and the characters which may be demonstrated to be common to the whole of this important and remarkable class, I do not think any one who is acquainted with the organization or the functions of plants, will be inclined to admit that the *Spongida* have the slightest real affinity with any division of the vegetable kingdom.

The next group to be considered is the division of the INFUSORIA; and here, again, within the last few years, prodigious strides have been made in our knowledge of the subject. Although the *Infusoria* have been favourite studies for many years, still it is only quite recently that the cycle of life of these animals has been made almost completely known, and that we have become acquainted with the true sexual process as it occurs in them.

Fig. 4.

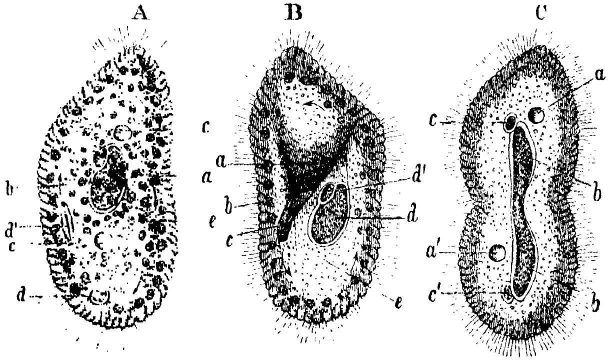


Fig. 4.—*Paramœcium bursaria* (after Stein): A, The animal viewed from the dorsal side; *a*, cortical layer of the body; *b*, "nucleus;" *c*, contractile chamber; *d d'*, matters taken in as food; *c*, chlorophyll granules.

B, The animal viewed from the ventral side; *a*, depression leading to *b*, mouth; *c*, gullet; *d*, "nucleus;" *d'*, "nucleolus;" *e*, central sarcode. In both these figures the arrows indicate the direction of the circulation of the sarcode.

C, *Paramœcium* dividing transversely; *a a'*, contractile spaces; *b b'*, "nucleus" dividing; *c c'*, "nucleoli."

The different species of the genus *Paramœcium* are very common among the microscopic inhabitants of our fresh waters, swimming about by means of the vibratile cilia with which the whole surface of their bodies is covered; and the structure which essentially characterises these animals is probably that which is common to the whole of the *Infusoria*, so that an account of the leading structural features of *Paramœcium* is, in effect, a definition of those of the group.

Imagine a delicate, slipper-shaped body inclosed within a structureless membrane, or *cuticula*, which is formed as an excretion upon its outer surface. At one point (Fig. 4, B *a*) the body exhibits a slight depression, leading into a sort of little funnel (*b c*) coated by a continuation of the same cuticular investment, which stops short at the bottom of the funnel. The whole of the bag formed by the cuticula is lined by a soft layer of gelatinous matter, or "sarcode," which is called the "cortical" layer (Fig. 4, A *a*); while inside that, and passing into it quite gradually, there being no sharp line of demarcation between the two, is a semi-fluid substance, which occupies the whole of the central region of the body. Neither in the cuticle, the cortical layer, nor the central substance, has any anatomist yet discovered a differentiation into cellular layers, nor any trace of that histological composition which we meet with in the tissues of the higher animals; so that here is another case of complex vital phenomena proceeding from a substance which, in a histological sense, is structureless.

At two points of the body (Fig. 4, A *c c*) the substance of the cortical layer exhibits a remarkable power of contraction and dilatation. If you watch one of those points, the sarcode suddenly seems to open like a window and, for a while, a clear space is visible, which then, quite suddenly, shuts again. After a little time the same diastole and systole are repeated. As the systole takes place, it is possible, occasionally, to discern certain radiating canals, which extend from the cavities into the surrounding sarcode, and disappear again before diastole occurs. There is no doubt that the clear space is a chamber filled with fluid in the cortical layer, and since good observers maintain that there is an aperture of communication, through the cuticula, between the 'contractile chamber' and the exterior, this fluid can be little more than water. Perhaps the whole should be regarded as a respiratory or secretory mechanism: in one shape or another, it is eminently characteristic of the *Infusoria*. Besides this singular apparatus, there lies embedded in another part of the cortical layer a solid mass, of an elongated oval shape (Fig. 4, A B *d*), which has been called the "nucleus," though it must be carefully distinguished from the "nucleus" of a cell. Upon one side of this, and, as it were, stuck on to it, is a little rounded body (Fig. 4, B *d'*), which has received the name of the "nucleolus." The animal swims about, driven by the vibration of its cilia, and whatever nutriment may be floating in the water is appropriated by means of the current which is caused to set continually into the short gullet by the cilia which line that tube.

But it is a singular circumstance that these animals have an alimentary canal consisting of a mere gullet, open at the bottom, and leading into no stomach or intestine, but opening directly into the soft central mass of sarcode. The nutritious matters passing down the gullet, and then into the central more fluid substance, become surrounded by spheroids of clear liquid (Fig. 4, A *d*), consisting apparently of the water swallowed with them, so that a well-fed *Paramœcium* exhibits a number of cavities, each containing a little mass of nutritious particles. Hence formerly arose the notion that these animals possess a number of stomachs. It was not unnaturally imagined that each of the cavities in question was a distinct stomach; but it has since been discovered that the outer layer of the sarcode is, by means of some unknown mechanism, kept in a state of constant rotation; so that the supposed stomachs may be seen to undergo a regular circulation up one side of the body and down the other. And this circumstance, if there were no other arguments on the same side, is sufficient to negative the supposition that the food-containing spaces are stomachs; for it is impossible to imagine any kind of anatomical arrangement which shall permit true dilatations of an alimentary canal to rotate in any such manner. Fæcal matters are extruded from an anus, which is situated not far from the mouth, but is invisible when not in use. It is an interesting and important character of the *Infusoria*, in general, that, under some circumstances, they become quiescent and throw out a structureless cyst around their bodies. The *Infusorium* then not unfrequently divides and subdivides, and, the cyst bursting, gives rise to a number of separate *Infusoria*.

The remarkable powers of multiplication by fission and gemmation which many of the group exhibit are well known; but within the last few years the investigations of Müller, Balbiani, Stein, and others, have shown that these minute creatures possess a true process of sexual multiplication, and that the sexual organs are those which have been denominated "nucleus" and "nucleolus." The nucleus is the true ovary—the nucleolus, the testis, in *Paramœcium*. At particular times, the latter increases very much in size, and its substance is broken up into rod-like bodies, which represent spermatozoa. Two *Infusoria*, in this condition, become conjoined, and the nucleolus (now converted into a spermatic capsule) of each passes into the body of the other. The spermatic filaments are said to enter the nucleus, which then enlarges, and either divides into, or gives off, a number of rounded germs, which become oval ciliated bodies provided with long processes. These make their way out of the body, and, it is believed, are metamorphosed directly into young *Paramœcia*. But, perhaps, further information is required before we can be quite certain on this point.

LECTURE II.

ON THE CLASSIFICATION OF ANIMALS.

THE HYDROZOA, ACTINOZOA, POLYZOA, BRACHIOPODA, ASCIDIOIDA, LAMELLIBRANCHIATA, BRANCHIOGASTEROPODA, PULMOGASTEROPODA, PTEROPODA, AND CEPHALOPODA.

In giving an account of the lowest forms of animal life in the preceding Lecture, I have substituted for a definition of each class, a description of the structure of some particular member of that class, or of the organic features which are most obviously characteristic of the class; because, in hardly any of those groups has the structure of many, and widely different, members been thoroughly and exhaustively worked out.

I entertain little doubt, however, that the main features of the description of *Spongilla* might substantially be taken as a definition of the *Spongida*, and those of the description of *Paramæcium*, as a definition of the *Infusoria*. On the other hand, we possess no such complete knowledge of the vital cycle of any *Gregarina* or *Rhizopod;* and neither description nor definition of the corresponding classes, of a thoroughly satisfactory kind, is attainable.

No such difficulties beset us in studying the next class, the Hydrozoa (comprising the Hydroid polypes and the *Medusæ*), which may be defined with as much precision as any group in the Animal Kingdom.

All the *Hydrozoa* exhibit a definite histological structure, their tissues primarily presenting that kind of organization which has been called cellular. Again, the body always exhibits a separation into at least two distinct layers of tissue—

an outer and an inner—which have been termed, respectively, *ectoderm* and *endoderm.* The endoderm is that layer which lines the inner cavities of the body, from the mouth inwards; the ectoderm is that which forms its external covering.

These two layers are shown in the accompanying diagram-

Fig. 5.

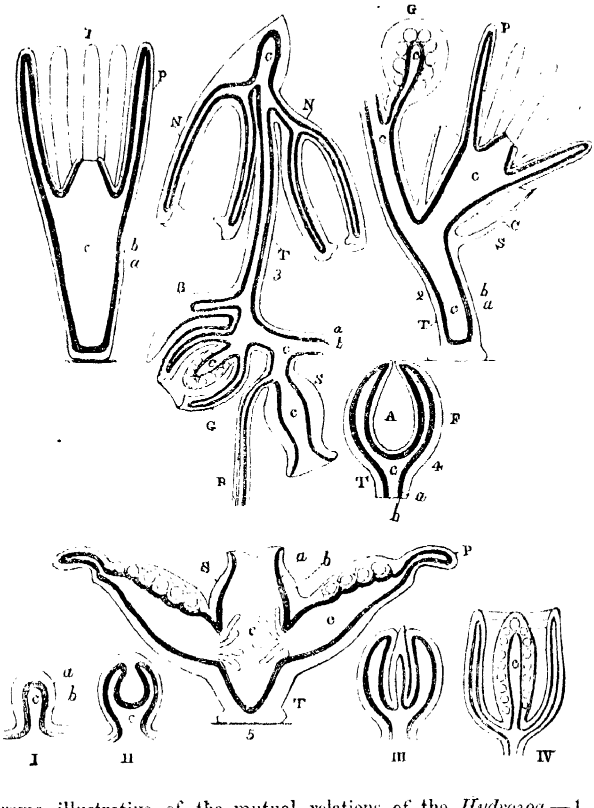


Fig. 5.—Diagrams illustrative of the mutual relations of the *Hydrozoa.*—1. *Hydra.* 2. Sertularian. 3. Diphyes. 4. Physophorid. 5. *Lucernaria.* *a.* Ectocyst. *b.* Endocyst. *c.* Their enclosed cavity.

P. Tentacles. N. Natatorial organ. T. Cœnosarc. B. Bract. C. Cell. S. Polypite or digestive cavity. G. Reproductive organ. A. Air vesicle. F. Float.

I., II., III., IV. represent the successive stages of development of a Medusiform zooid or reproductive organ.

matic sections of the leading forms of *Hydrozoa,* the ectoderm being represented by the thin line with the adjacent clear space, the endoderm by the thick dark line.

A third distinctive character of the *Hydrozoa* is, that the digestive cavity communicates directly, by a wide aperture, with the general cavity of the body; the one, in fact, passing by direct continuity into the other. Furthermore, the digestive sac is not in any way included in the substance of the rest of the body, but stands out independently, so that the outer wall of the digestive cavity is in direct contact with the water in which the animal lives, and there is no perivisceral chamber. The like is true of the reproductive organs, which may vary very much in form, but have the common peculiarity of being developed as outward processes of the body wall, so that their external surfaces are directly in contact with the surrounding medium.

No nervous system has yet been discovered in any of these animals. The majority of them seize their prey by means of tentacula developed either around the mouth, or from the walls of the digestive cavity, or from the body wall; and these tentacles, as well as other parts of the body, are provided with those peculiar weapons of offence which have been termed "thread-cells."

The class of the ACTINOZOA contains those animals which are familiar to us as Sea-anemones and Coral-polypes, by the latter of which, in many parts of the world, those huge reefs, which are so well known to navigators, are constructed. It embraces the Sea-pens and the Red coral, and those creatures which are known to us under the names of *Beröe*, *Cydippe*, *Pleurobrachia*, &c., transparent, beautifully symmetrical, free-swimming animals, provided with eight rows of longitudinally-disposed large cilia. In all these animals we find a great uniformity of structure, and their plan of construction is quite as readily definable as that of the preceding class, with which they exhibit a close affinity. Like the majority of the *Hydrozoa*, most *Actinozoa* have their mouths surrounded by tentacles; and there is the same primary distinction of the body into two cellular layers—the ectoderm and the endoderm—though, in the adult forms of the more highly organized *Actinozoa*, these primitive layers become further differentiated into bundles of definitely disposed muscular fibres, and even into nerves and ganglia.

As in the *Hydrozoa*, again, the alimentary canal communicates freely, and by a wide aperture, with the general cavity of the body; but the whole of the *Actinozoa*, polype-like as they are in external appearance, differ from the *Hydrozoa* by a very important further progress towards complexity. We found that in the *Hydrozoa* the digestive cavity was completely outside the general cavity of the body, the digestive portion of the organism being continued into, and not in any way contained within, the part which contains the general cavity. But if you make a vertical section of a sea anemone (Fig. 6), you will find that the alimentary cavity—as freely open at the bottom as in the *Hydrozoa*—is enclosed within a part of the body which contains a prolongation of the general cavity. If you could suppose the stomach of a *Hydrozoon* thrust into that part of the body with which it is continuous, so that the walls of the body should rise round it and form a sort of outside case, containing a prolongation of the general cavity, the *Hydrozoon* would be converted into an *Actinozoon*.

Fig. 6.

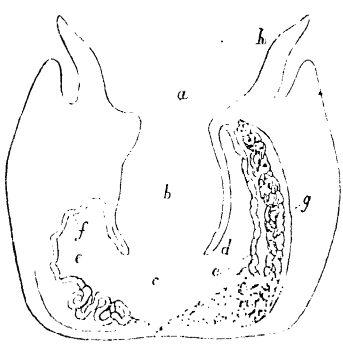


Fig. 6.—Perpendicular section of *Actinia holsatica* (after Frey and Leuckart); *a*, mouth; *b*, alimentary cavity; *c*, common cavity; *d*, intermesenteric chambers; *e*, cord containing thread-cells at the edge; *f*, the mesentery; *g*, reproductive organ; *h*, tentacle.

The prolongation of the general cavity thus produced, which, as it surrounds the chief viscus, may be termed the "perivisceral cavity" (*d*), receives the products of digestion mixed with much sea-water; and the nutritive fluid, which fills the perivisceral cavity and its ramifications, plays the same part as the blood of the more highly organized animals. The gastric chamber of the *Actinozoa* does not lie free in the interior of the body, but is connected to the sides of it by means of membranous partitions, the so-called "mesenteries" (*f*), which pass radially from the stomach to the side walls of the body, and so divide the "perivisceral cavity" into a number of chambers, which communicate with the bases of the tentacles. In the whole of the *Hydrozoa* the reproductive organs were attached to the exterior of the body, and projected from it. In the whole of the *Actinozoa*, on the other hand, the reproductive organs (of which both sexes are frequently combined in the same individual) are internal, inasmuch as they are situated in the substance of the mesenteries (*g*).

These are the universal and distinctive characters of the *Actinozoa*. That some are simple and some are compound organisms; that some are fixed and some free swimmers; that many are soft, while a great number are provided with very dense skeletons; that some possess a rudimentary nervous system, while the majority have as yet afforded no trace of any such structure, are secondary circumstances in no way affecting the problem before us, which is, to find a diagnostic definition of the group.

Notwithstanding the invariably minute size of the organisms which constitute the next class on the list—the POLYZOA—they exhibit a very great advance in complexity of structure. In such a compound *Polyzoon* as the Sea-mat, or *Flustra*, the entire surface of the foliaceous expansion, on being examined by the microscope, will be found to be beset with an infinitude of minute apertures leading into little chambers, out of each of which, when the animal was living and active, multitudes of little creatures might be seen protruding the oral extremities of their bodies. The ends of the branches of the freshwater genus *Plumatella*, represented in Fig. 6, present a similar spectacle. Each mouth is surrounded by a circlet of tentacles; and, as every tentacle is fringed with long and active vibratile cilia, lashing the water towards the mouth, hundreds and thousands of little Maelströms are created, each tending to suck down such nutritious bodies, living or dead, as come within its range.

The mouth (Fig. 8) leads into a long and wide pharyngeal and œsophageal tube, which opens, below, into a definite stomach. From this is continued a distinct intestine, which bends upon

Fig. 7.

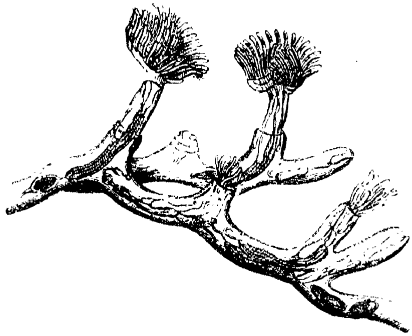


Fig. 7.—*Plumatella repens*, a freshwater Polyzoon, magnified (after Allman).

itself towards the oral end of the body, so as to form a sharp angle, and then terminates upon the outer surface near the mouth; so that we have here, for the first time in our ascending survey of the Animal Kingdom, an animal possessing a complete intestine, not only structurally separated from the general substance of the body, and provided with permanent apertures, as in the *Hydrozoa* and *Actinozoa*, but completely shut off from the perivisceral cavity, and in *direct* communication only with the external medium. All the *Polyzoa* possess a nervous system, the characters and position of which are very well defined. It consists of a single ganglion (Fig. 8, *w*), placed between the oral and the anal apertures, and sending off nerves in various directions. It has been affirmed that, in some *Polyzoa*, there is a more extended system of nerves by which the various zooids of the compound organism are placed in communication; but of that we want further evidence. In these animals no heart has been discovered as yet, the matters which result from digestion percolating through the walls of the intestine, and becoming mixed with the perivisceral fluid. One of the structural characters which I have mentioned is exceedingly important. As I have said, the intestine is not straight, but is bent upon itself (Fig. 8), and the direction of flexure is such that the nervous ganglion, which corresponds with those called "pedal" in *Lamellibranchiata,* is placed in the re-entering angle between the gullet and the rectum. In order to express

Fig. 8.

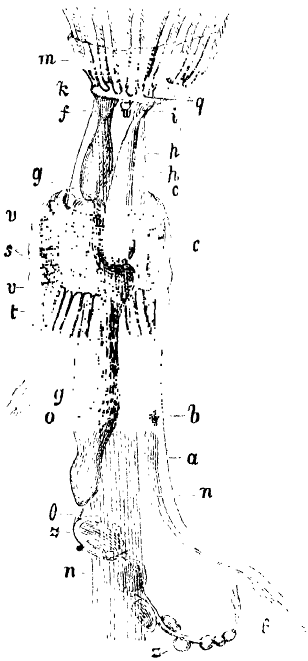


Fig. 8.—*Plumatella repens,* a single cell more magnified; *m,* calyx at the base of the ciliated tentacula borne by the disk or lophophore; *k,* gullet; *g g,* stomach; *h,* intestine; *i,* anus; *v,* nervous ganglion (after Allman).

this relation of the nervous system to the alimentary canal, the flexure of the latter has been called "neural"—the side of the body on which the principal ganglion is placed, and towards which the intestine is bent, being the "neural" side. Whatever our terminology, however, the great point is to remember that the structural relation which it expresses is constant throughout the *Polyzoa.*

In the next division, the BRACHIOPODA, which are animals differing very much in external appearance from the *Polyzoa,* we shall find, nevertheless, a singular fundamental resemblance of internal structure to the latter. All known *Polyzoa* are compound animals, that is to say, the product of every ovum gives rise, by gemmation, to great assemblages of partially independent organisms, or zooids. The *Brachiopoda*, on the contrary, are all simple, the product of each ovum not giving rise to others by gemmation. All the *Brachiopoda* possess a bivalve shell—a shell composed of two, more or less horny, or calcified, pieces, which are capable of a certain range of motion on one another, and are very commonly articulated together by teeth and sockets. The proper body, which is small when compared with the size of the shell, has its dorsal integument produced into broad membranous expansions, which line the interior of the valves of the shell, and are called the lobes of the mantle, or "pallium." The aperture of the mouth is situated in the middle line, between the pallial lobes, and, on each side of it, is a longer or shorter prolongation of the body, provided with ciliated tentacula. It is from the presence of these "arms" that the class has received its name. The tentaculate oral disk of a *Plumatella* is already horse-shoe shaped (Figs. 7 and 8); suppose each crus of the horse-shoe to be pulled out to a much greater length, and tentaculated "arms" would be produced, closely resembling those of the *Brachiopoda*.

The mouth leads into a gullet which is directed towards, or lies along, that side of the body from which one lobe of the mantle, the anterior, is continued; the gullet opens into a stomach, provided with a well-developed liver; and from the stomach, an intestine proceeds, which is directed towards, or along, that side of the body from which the other lobe of the mantle proceeds; and then either, as I pointed out some years ago,* ends, blindly, in the middle line (Fig. 9), or else terminates in a distinct anus between the pallial lobes.

* Professor Owen, in the second edition of his lectures on the "Comparative Anatomy and Physiology of the Invertebrate Animals," published in 1855, thought it not unbecoming to sneer at this discovery. "There may be blindness somewhere, but I think not at the termination of the intestine of *Terebratula*."—L. c., p. 403. As my statements have subsequently been fully borne out by Mr. Albany Hancock and by M. Lacaze Duthiers—two of the best minute anatomists of the day—I trust Mr. Owen is now fully satisfied as to where the "blindness" really was, in 1855.

The principal ganglionic mass is situated behind and below the mouth, in the re-entering angle between the gullet and the rectum; in other words, the intestine has, as in the *Polyzoa*, a neural flexure (Fig. 9). In all *Brachiopoda* which have been

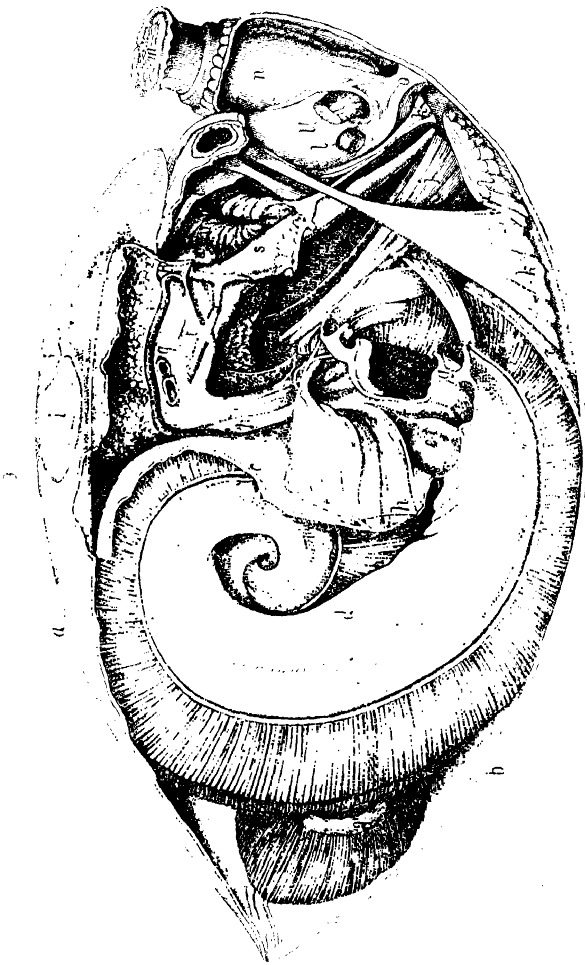


Fig. 9.—Lateral view of the viscera of *Waldheimia australis* (after Hancock). *a*, anterior layer of mantle: *b*, posterior layer; *c*, anterior walls of the body between the mantle lobes; *d*, arms; *p*, gullet; *q*, stomach, with cut biliary ducts of the left side; *r*, right hepatic mass; *s*, intestine ending cæcally between *j* and *k*: *v*, so-called "auricle" of the right "pseudo-heart," the left being almost wholly removed; *w*, pyriform vesicle fixed at the back of the stomach, and probably performing the function of a true heart; *z*, œsophageal ganglia.

carefully dissected, a singular system of cavities and canals situated in the interior of the body, but in free communication with the surrounding medium, has been discovered. This, which I shall term the "atrial" system, from its close correspondence with the system of cavities, which has received the same name in the Ascidians, has been wrongfully regarded as a part of the true vascular system, and the organs by which it is placed in communication with the exterior have been described as "hearts." There are sometimes two and sometimes four of these "pseudo-hearts" situated in that part of the body wall which helps to bound the pallial chamber. Each pseudo-heart is divided into a narrow, elongated, external portion (the so-called "ventricle"), which communicates, as Mr. Hancock has proved, by a small apical aperture with the pallial cavity; and a broad, funnel-shaped inner division (the so-called "auricle"), communicating, on the one hand, by a constricted neck with the so-called "ventricle;" and, on the other, by a wide, patent mouth, with a chamber which occupies most of the cavity of the body proper, and sends more or less branched diverticula into the pallial lobes. These have been described as parts of the blood vascular system; and arterial trunks, which have no existence, have been imagined to connect the apices of the ventricles with vascular networks of a similarly mythical character, supposed to open into the branched diverticula.

In fact, as Mr. Hancock has so well shown in his splendid and exhaustive memoir, published in the *Philosophical Transactions* for 1857, the true vascular system is completely distinct from this remarkable series of "atrial" chambers and canals, the function of which would appear to be to convey away excretory matters and the products of the reproductive organs, which are developed in various parts of the walls of the atrial system.

The precise characters of the true vascular system of the *Brachiopoda* probably require still further elaboration than they have yet received; and the same may be said, notwithstanding the valuable contributions of F. Müller and of Lacaze Duthiers, of their development; but the shell, the pallial lobes, the intestine, and the nervous and the atrial systems, afford characters amply sufficient to define the class.

The next great division is that of the ASCIDIOIDA, which, like the *Brachiopoda*, are marine animals, and are very common all over the world; the more ordinary forms of them being always easily recognisable by the circumstance that their external integument is provided with two prominent, adjacent apertures, so that they look very much like double-necked jars (Fig. 10). At first sight you might hardly suspect the animal nature of one of these singular organisms, when freshly taken from the sea; but if you touch it, the stream of water which it squirts out of each aperture reveals the existence of a great contractile power within; and dissection proves that this power is exerted by an organism of a very considerable degree of complexity. Of the two apertures, the one which serves as a mouth is often — but not always — surrounded by a circlet of tentacles (Fig. 11, *e*). It invariably leads into an exceedingly dilated pharynx, the sides of which are, more or less extensively, perforated. The gullet comes off from the end of the pharynx, and then dilates into the stomach, from which an intestine, usually of considerable length, is continued to the anal aperture. The latter is almost always situated within a chamber, which opens, externally, by that second aperture upon the exterior of the test, to which I referred just now. Furthermore, in all Ascidians which I have examined, the first bend of the intestine takes place in such a manner that, if the intestine continued to preserve the same direction, it would end on the opposite side of the mouth to the nervous ganglion (Fig. 11); in other words, the nervous ganglion would not be situated in the re-entering angle between the gullet and the rectum, but on the opposite side of the gullet to that angle. Therefore, the flexure of the intestine is not neural, as in the *Polyzoa;* but as, on the contrary, the intestine is primarily bent towards the heart side of the body, its flexure may be termed "hæmal." And this hæmal flexure of the intestine in the Ascidians thus constitutes an important element in the definition of the class.

Fig. 10.

Fig. 10.—*Phallusia mentula; a*, oral; *b*, atrial aperture; *c*, base of attachment.

In these animals there is an atrial system, the development of which is even more extraordinary than in the *Polyzoa.* The second aperture to which I have referred (*b*, Figs. 10 and 11) is continued into a large cavity, lined by a membrane, which is reflected, like a serous sac, on the viscera, and constitutes what is called the "third tunic," or "peritoneum." From the chamber which lies immediately within the second aperture (*k*, Fig. 11) it is reflected over both sides of the pharynx, extending, towards its dorsal part, very nearly as far as that structure which has been termed the "endostyle" (*m*, Fig. 11). It then passes from the sides of the pharynx to the body walls, on which the right and left lamellæ become continuous, so as to form the lining of the chamber (*k*), into which the second aperture (*b*) leads, or the "atrial chamber." Posteriorly, or at the opposite end of the atrial chamber to its aperture, its lining membrane (the "atrial tunic") is reflected to a greater or less extent over the intestine and circulatory organs, sometimes inclosing each of their parts in distinct plications (as in the genus *Phallusia*), sometimes merely passing over them, and limiting the blood sinus in which they are contained (as in *Clavelina*, &c.). Where the atrial tunic is reflected over the sides of the pharynx, the two enter into more or less close union, and the surfaces of contact become perforated by larger or smaller, more or less numerous, apertures. Thus the cavity of the pharynx acquires a free communication with that of the atrium; and,

Fig. 11.

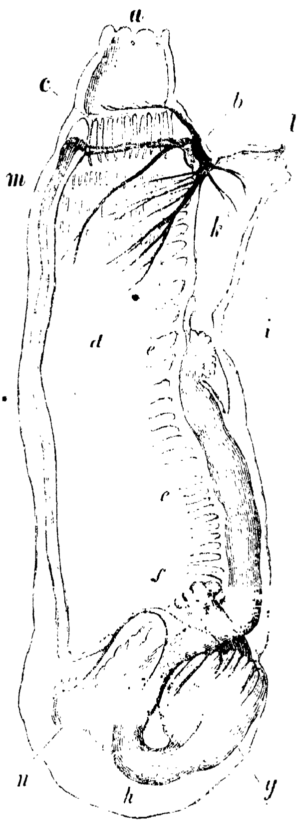


Fig. 11.—*Phallusia mentula*; the test removed, and hardly more of the animal drawn than would be seen in a longitudinal section. *a*, oral aperture; *b*, atrial aperture; *c*, circlet of tentacles; *d*, pharyngeal, or branchial, sac: the three rows of apertures in its upper part indicate, but do not represent, the pharyngo-atrial apertures; *e*, the languets: a series of tongue-shaped processes which project into the branchial sac; *f*, œsophageal opening; *g*, stomach; *h*, intestine performing its hæmal flexure; *i*, anus; *k*, atrium; *l*, ganglion; *m*, endostyle; *n*, heart.

as the margins of the pharyngo-atrial apertures are fringed with cilia, working towards the interior of the body, a current is produced, which sets in at the oral aperture, and out by the atrial opening, and may be readily observed in a living Ascidian.

The Ascidians possess a distinct heart, but of a very simple construction, seeing that it is merely an incomplete muscular tube, open at each end, and devoid of valves. Functionally, it is not less remarkable than structurally; for, in the great majority of Ascidians, if not in all, it exhibits a regular alternation in the order of the peristaltic contractions of its muscular substance, which has no parallel in the Animal Kingdom. The result of this reversal in the direction of the contractions of the heart is a corresponding periodical reversal of the course of the circulation of the blood, so that the two ends of the heart are alternately arterial and venous.

The perforated pharynx performs the function of a branchial apparatus, the blood contained in its sieve-like walls being subjected to the action of constant currents of aërated water. All Ascidians possess a single nervous ganglion placed upon one side of the oral aperture (*l*, Fig. 11), and, in all known genera but *Appendicularia*, it is situated between the oral and atrial apertures, and, indeed, between the oral and anal apertures; for, in all genera but that mentioned, the intestine, after it has made its hæmal bend, curves down towards the neural side of the body, and opens into the atrium on that side of the body, and behind the nervous ganglion.

The outer integument of the Ascidians secretes upon its surface, not a calcareous shell, but a case or "test," which may vary in consistence from jelly to hard leather or horn. And it is not one of the least remarkable characteristics of the group that this test is rendered solid, by impregnation with a substance identical in all respects with that "cellulose" which is the proximate principle of woody fibre, and forms the chief part of the skeleton of plants. Before the discoveries of late years had made us familiar with the production of vegetable proximate principles by the metamorphosis of animal tissues, this circumstance was justly regarded as one of the most remarkable facts of comparative physiology.

The last common and distinctive peculiarity of the Ascidians which I have to mention, is one which acquires importance only from its constancy. The middle of the hæmal wall of the pharynx, from near the oral to the œsophageal end, in all these animals, is pushed out into a longitudinal fold, the bottom of which projects into a blood sinus, and has a much thickened epithelial lining. Viewed from one side, the bottom of the fold consequently appears like a hollow rod, and has been termed the "endostyle" (*m*, Fig. 11). The functions of this structure are unknown, but it has been noticed in all genera of Ascidians hitherto examined.

In the next group, that of the LAMELLIBRANCHIATA, which comprises those creatures which we know as mussels, cockles, and scollops, and all the fabricators of what are commonly known as bivalve shells (except the *Brachiopoda*), we meet with

Fig. 12.

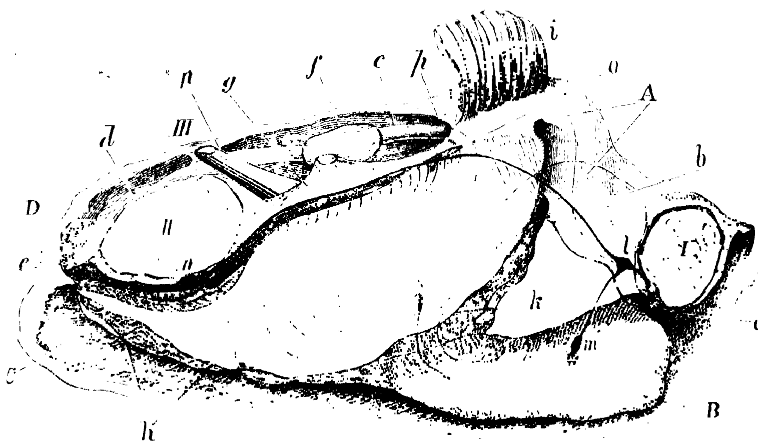


Fig. 12.—Sectional diagram of a freshwater mussel (*Anodon*). *A A*, mantle, the right lobe of which is cut away; *B*, foot; *C*, branchial chamber of the mantle cavity; *D*, anal chamber; *I*, anterior adductor muscle; *II*, posterior adductor muscle; *a*, mouth; *b*, stomach; *c*, intestine, the turns of which are supposed to be seen through the side walls of the foot; *d*, rectum; *e*, anus; *f*, ventricle; *g*, auricle; *h*, gills, except *i*, right external gill, largely cut away and turned back; *k*, labial palpi; *l*, cerebral; *m*, pedal; *n*, parieto-splanchnic ganglia; *o*, aperture of the organ of Bojanus, *p*, pericardium.

an important advance in organization. In all these animals, the body, as is exemplified by the diagram (Fig. 12) of a freshwater mussel (*Anodon*), is included within a mantle or "pallium," which is formed by a prolongation of the dorsal integument,—a structure in principle quite similar to that which we met with in the *Brachiopoda.* But there is this essential difference between the two,—that whereas, in the *Brachiopoda,* the mantle lobes corresponded with the anterior and posterior regions of the body, in the *Lamellibranchiata* they answer to the right and left halves of the body. The intestine, which always terminates by a definite anus between the mantle lobes, at the posterior end of the body, has its first flexure neural. There is always a well-developed heart, which is much more complex than that of the Ascidians or Brachiopods, being divided into distinct auricular and ventricular chambers. Commonly, there are two auricles and one ventricle, as in *Anodon;* but in other *Lamellibranchiata,* such as the oyster, there is a single auricle and a single ventricle, and in some exceptional cases there are two auricles and two ventricles, forming two distinct hearts. Distinct respiratory organs, which usually have the form of lamellæ (as the name of the class

Fig. 13.

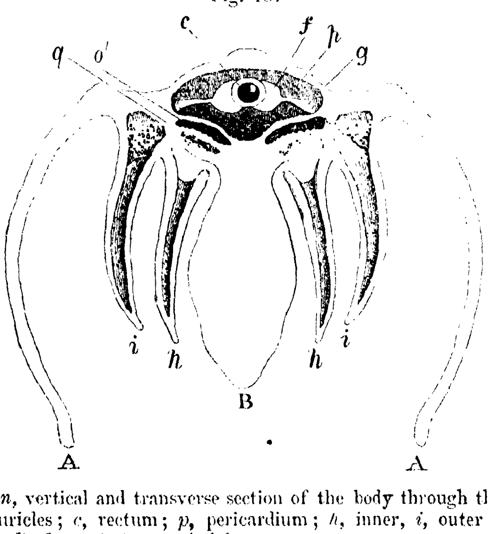


Fig. 13.—*Anodon,* vertical and transverse section of the body through the heart; *f,* ventricle; *g,* auricles; *c,* rectum; *p,* pericardium; *h,* inner, *i,* outer gill; *o'q,* organ of Bojanus; B, foot; A A, mantle lobes.

implies), are found in all *Lamellibranchiata,* and are situated upon each side of the body, in a chamber which extends between the foot and the mantle lobes in front, and between the mantle lobes posteriorly (Fig. 13). The branchial organs may consist of distinct filaments, or of plates composed of tubular rods supporting a network of blood-vessels, and covered with cilia, by the action of which they are constantly bathed by currents of water.

The nervous system presents a no less distinct advance than the other organs. All Lamellibranchs possess at least three pairs of principal ganglia—a cerebral pair at the sides of the mouth, a pedal pair in the foot, and a third pair on the under surface of the posterior adductor muscle, which are commonly called "branchial," but which, as they supply not only branchial, but visceral and pallial filaments, may more properly be termed "parieto-splanchnic." Three sets of commissural filaments connect the cerebral ganglia with one another, with the pedal, and with the parieto-splanchnic ganglia. The inter-cerebral commissures surround the mouth, and the other two pairs of cords extend respectively, from the cerebral to the pedal, and from the cerebral to the parieto-splanchnic ganglia.

Finally, there is always, in these animals, an external shell, which is formed as an excretion from the surface of the lobes of the mantle, and is composed of layers of animal matter hardened by deposit of carbonate of lime, which may or may not take a definite form, and so give rise to "prismatic" and "nacreous" substance. As the lobes are right and left, so the valves of the shell are right and left, and differ altogether from the valves of the shell of the *Brachiopoda*, which are anterior and posterior. The valves of the shell can be brought together by adductor muscles. Of these one (Fig. 12, *II*) always exists, posteriorly, on the neural side of the intestine. A second (Fig. 12, *I*) is commonly found anteriorly to the mouth, on the hæmal side of the intestine.

The hiatus between the next class, which is termed BRANCHIOGASTEROPODA in the table, and that just defined, is considerable, though not quite so well marked as that between the Ascidians and the *Lamellibranchiata*. This group, which contains the whelks, periwinkles, sea-slugs, and the *Heteropoda* of Cuvier, consists of animals which, like the Lamellibranchs, possess (in their young state, at any rate) a mantle; a foot, which is the chief organ of locomotion; and three principal pairs of ganglia—cerebral, pedal, and parieto-splanchnic. When they are provided with a heart, which is usually the case, it is divided into auricular and ventricular chambers; but the mantle, instead of being divided into two lateral lobes, is continuous round the body, and when it secretes a shell from its surface, that shell is either in a single piece, or the pieces are repeated from before backwards, and not on each side of the median line. The shell of a Branchiogasteropod may, therefore, be univalve, or composed of a single conical piece, straight or coiled; or it may be multivalve—formed of a number of segments succeeding one another antero-posteriorly; but it is never bivalve.

Sometimes a shelly, horny, or fibrous secretion takes place from the foot, giving rise to a structure resembling the byssus of some Lamellibranchs; it is the so-called "*operculum*," which serves to protect the animal when retracted into its shell; but as the operculum is developed from the foot and not from the mantle, it can obviously have no homology with the valves of either a Brachiopod or a Lamellibranch. The *Branchiogasteropoda* (Fig. 14) commonly possess a distinct head, provided with a pair of tentacles and a single pair of eyes, both of which are supplied with nerves from the cerebral ganglia. Cephalic eyes of this kind are not known in the *Lamellibranchiata*. But the characters which most definitely distinguish the *Branchiogasteropoda* are to be found in the alimentary canal. The cavity of the mouth is invariably provided with an organ which is usually, though not very properly, called the tongue, and which might more appropriately be denominated the "odontophore." It consists essentially of a cartilaginous cushion, supporting, as on a pulley, an elastic strap, which bears a long series of transversely disposed teeth. The ends of the strap are connected with muscles attached to the upper and lower surface of the hinder extremities of the cartilaginous cushions; and these muscles, by their alternate contractions, cause the toothed strap to work, backwards and forwards, over the end of the pulley formed by its anterior end. The strap consequently acts, after the fashion of a chain-saw, upon any substance to which it is applied, and the resulting wear and tear of its anterior teeth are made good by the incessant development of new teeth in the secreting sac in which the hinder end of the strap is lodged. Besides the chain-saw-like motion of the strap, the odontophore may be capable of a licking or scraping action as a whole.

Fig. 14.

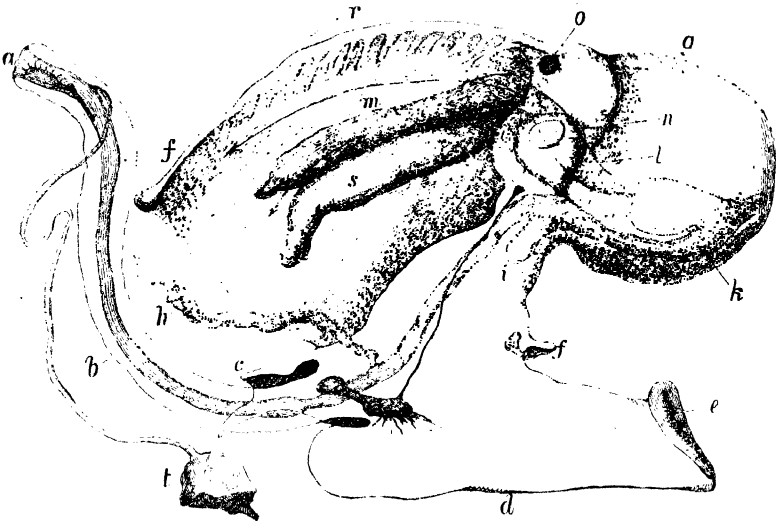


Fig. 14.—Section of a female whelk (*Buccinum*). The organs marked *t* and *h* are removed from their proper places; the others are seen *in situ*. *a*, mouth; *b*, gullet; *c*, head; *d*, foot; *e*, operculum; *f*, free part of the mantle; *g*, that part which invests the visceral mass lodged within the shell; *h*, a gland of unknown function connected with the gullet; *i*, crop; *k*, stomach; *l*, intestine; *m*, rectum; *n*, heart; *o*, aperture of the renal organ; *r*, mucous gland developed from the wall of the mantle cavity; *s*, oviduct; *t*, salivary gland. The arrows indicate the position of the branchiæ. The cerebral, pedal, and parieto-splanchnic ganglia closely surround the gullet, and the latter send off a long ganglionated cord towards the heart and branchiæ.

The other peculiarity of the alimentary canal of the *Branchiogasteropoda* is that it is always bent upon itself, at first, not to the neural, but to the hæmal, or heart side of the body—the rectum very commonly opening into the mantle cavity, above the cephalic portion of the body.

In most *Branchiogasteropoda* the foot is a broad, flat, muscular body, without any distinct division of parts; but in some forms, such as the *Heteropoda* of Cuvier, it is divided into three very well-marked portions—an anterior, a middle, and a posterior, which are termed respectively the *propodium*, *mesopo-*

dium, and *metapodium*;* while the *Aplysiæ*, in which the foot proper has the ordinary composition, exhibit processes from the lateral and upper surfaces of that organ, having the form of great muscular lobes, which serve as a sort of aquatic wings to some species, and are termed *epipodia*.

The *Branchiogasteropoda* are such of the *Gasteropoda* of Cuvier as breathe water either by means of the thin wall of the mantle cavity (*Atlanta*, *e.g.*), or by special pallial branchiæ (*Pectinibranchiata*, *Tectibranchiata*, &c.), or by certain parts of the integument of the body (*Nudibranchiata*) more or less

Fig. 15.

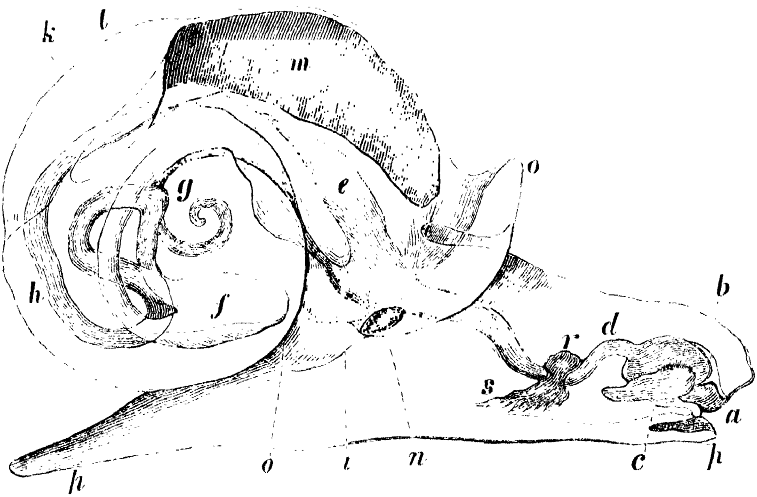


Fig. 15.—Diagram exhibiting the disposition of the intestine, nervous system, &c., in a common snail (*Helix*). *a*, mouth; *b*, tooth; *c*, odontophore; *d*, gullet; *e*, its dilatation into a sort of crop; *f*, stomach; *g*, coiled termination of the visceral mass; the letter is also close to the commencement of the intestine, which will be seen to lie *under* the œsophagus, and not over it as in the whelk; *h*, rectum; *i*, anus; *k*, renal sac; *l*, heart; *m*, lung, or modified pallial chamber; *n*, its external aperture; *o*, thick edge of the mantle united with the sides of the body; *p*, foot; *r*, cerebral, pedal, and parieto-splanchnic ganglia aggregated round the gullet.

specially modified. The next class, the PULMOGASTEROPODA,† on the other hand, are the Pulmonate *Gasteropoda* of Cuvier,

* I proposed these terms in a Memoir in the "Morphology of the Cephalous Mollusca," published in the *Philosophical Transactions* for 1853.

† I adopt these convenient names at the suggestion of my friend Professor Greene, of Queen's College, Cork.

the snails and slugs, which agree with the *Branchiogasteropoda* in the general characters of their body, mantle, nervous and respiratory systems, and in possessing an odontophore; but differ from them, not only in breathing air by means of the thin lining of the pallial chamber, but, as I believe, by the direction of the flexure of their intestine. A careful dissection of a common snail, for example (Fig. 15), will prove that, though the anus is situated in the same way as in the *Branchiogasteropoda*, on the dorsal or hæmal side of the body, the primary bend of the intestine is not to the hæmal, but to the neural, side, the eventual termination of the intestine on the hæmal side being the result of a second change in its direction.

How far this neural flexure of the intestine really prevails among the Pulmo-gasteropods is a question which must be decided by more extensive investigations than I have as yet been enabled to carry out.

The members of the class PTEROPODA are small, or even minute, molluscs; all marine in habit, and for the most part pelagic, or swimmers at the surface of deep seas. Like the two preceding groups, they possess three principal pairs of ganglia, an odontophore, a mantle, which is not divided into two lobes, and which secretes a univalve shell, if any. But the propodium, mesopodium, and metapodium are usually rudimentary, and locomotion is almost wholly effected by the epipodia, which are enormously developed, and, in most of the genera, perform the office of aquatic wings still more efficiently than those of the *Aplysiæ*. Furthermore, the intestine is flexed towards the neural side of the body; and the head, with the organs of sight, are usually quite rudimentary. I include in this group not only *Criseis*, *Cleodora*, *Hyalæa*, *Pneumodermon*, &c., but also the aberrant genus *Dentalium*.*

The last class of this series is that of the CEPHALOPODA—comprising the Poulpes, the Cuttle-fishes, the Squids, and the pearly Nautilus; a group definable by most marked and distinct characters from all the preceding, though it resembles them in

* *Dentalium* resembles the *Pteropoda* in its rudimentary head, the neural flexure of its intestine, its epipodial lobes, and the character of its larva.

fundamental characters. Thus, the mantle is related to the body, as in *Pteropoda* and *Gasteropoda;* when an external shell exists it is composed of a single piece, and the Cephalopods have

Fig. 16.

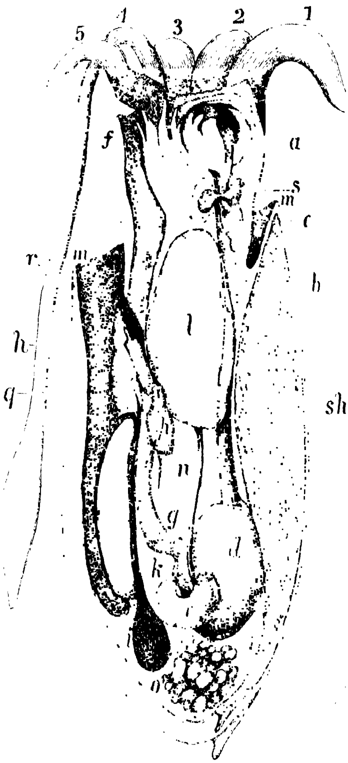


Fig. 16.—Diagrammatic section of a female Cephalopod (*Sepia officinalis*). *a*, Buccal mass surrounded by the lips, and showing the horny jaws and tongue; *b*, œsophagus; *c*, salivary gland; *d*, stomach; *e*, pyloric cæcum; *f*, the funnel; *g*, the intestine; *h*, the anus; *i*, the ink-bag; *k*, the place of the systemic heart; *l*, the liver; *n*, the hepatic duct of the left side; *o*, the ovary; *p*, the oviduct; *q*, one of the apertures by which the atrial system, or water-chambers, are placed in communication with the exterior; *r*, one of the branchiæ; *s*, the principal ganglia aggregated round the œsophagus; *m*, the mantle; *sh*, the internal shell, or cuttle-bone. 1, 2, 3, 4, 5, the produced and modified margins of the foot, constituting the so-called "arms" of the *Sepia*.

an odontophore constructed upon just the same principle as that of the other classes. The nervous system, the foot, and the epipodia exhibit the same primary relations as in these groups, and there is a distinct head, with ordinarily well-developed optic and olfactory organs. That which essentially characterises the *Cephalopoda*, in fact, is simply the manner in which, in the course of development (as Kölliker long since proved), the margins of the foot proper and the epipodia become modified and change their relations. The margins of the foot are produced into more or less numerous tentacular appendages, often provided with singularly constructed suckers or acetabula; and the antero-lateral parts of each side of the foot extend forwards beyond the head, uniting with it and with one another; so that, at length, the mouth, from having been situated, as usual, above the anterior margin of the foot, comes to be placed in the midst of it. The two epipodia, on the other hand, unite posteriorly above the foot, and where they coalesce, give rise either to a folded muscular expansion, the edges of which are simply in apposition, as in *Nautilus*; or to an elongated flexible tube, the apex of which projects beyond the margin of the mantle (Fig. 16, *f*), called the "funnel" or "infundibulum," as in the dibranchiate *Cephalopoda*.

The *Cephalopoda* present a vast number of the most interesting features, to which it would be necessary to devote much attention if we were studying all the organic peculiarities manifested by the class; but it is in the characters of foot and of the epipodium that the definition of the class must be chiefly sought. In addition, the flexure of the intestine is, in all Cephalopods, neural; and the mouth is always provided with a horny or more or less calcified beak, like that of a parrot, composed of two curved pieces, which move in the median antero-posterior plane of the body; and one of which, that on the neural side, is always longer than the other.

LECTURE III.

ON THE CLASSIFICATION OF ANIMALS.

THE ECHINODERMATA, SCOLECIDA, ANNELIDA, CRUSTACEA, ARACHNIDA, MYRIAPODA, AND INSECTA.

HITHERTO, it has not been a matter of very great difficulty to discover the characters in which the members of the various classes, which have passed under our notice, agree with one another and differ from the members of all other classes. But to-day we shall be met, at the outset of our studies, by a large series of organisms which present us with much greater obstacles,—the result, in a great measure, of imperfect knowledge.

The first group on the list—the ECHINODERMATA—comprises the star-fishes, sea-urchins, sea-cucumbers, trepangs, and feather-stars—known technically as *Asteridea, Echinidea, Holothuridea, Ophiuridea, Crinoidea,* &c.,—marine animals which differ vastly in external appearance, though they all, in the adult state, present a more or less definitely radiate arrangement of some parts of their organization.

That which most remarkably distinguishes the *Echinodermata* is the nature of the embryo, and the strange character of the process by which the adult form is originated by a secondary development within that embryo.

In the great majority* of the *Echinodermata,* the develop-

* In *Ophiolepis squamata* and *Echinaster sepositus,* the larva appears to attain only a very imperfect state of development before the appearance of the echinoderm body; and careful re-examination is required to decide how far the larvæ of these animals are truly bilaterally symmetrical.

ment of which has been examined, the impregnated egg gives rise to a free-swimming, ovoid, ciliated embryo, the cilia of which soon become restricted to, and, at the same time, largely developed upon, one, two, or more bands, which are disposed either transversely, or more or less obliquely to the longitudinal axis of the body, but which are, in any case, bilaterally symmetrical (Fig. 17).

Fig. 17.

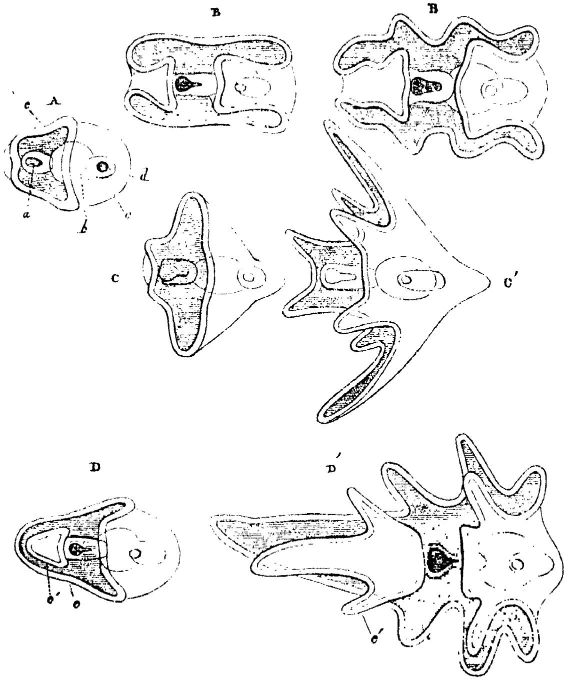


Fig. 17.—Diagram exhibiting the general plan of the development of the *Echinoderms* (after Müller).—A. Common form whence the Holothurid (B, B′) and Ophiurid or Echinid (C, C′) larvæ are derived. D, D′. Younger and more advanced stages of the Asterid (*Bipinnaria*) larvæ. *a′*. Mouth. *b*. Stomach. *c*, Intestine. *d*. Anus. *e*. Ciliated band. *c′*. Second or anterior ciliated circlet.

The parts of the body which carry the ciliated band, or bands, often become developed into processes, which correspond upon each side of the body, and thus render its bilateral symmetry more marked (Fig. 17, C′, D′). And, in the larvæ of some *Echinidea* and *Ophiuridea*, other bilaterally symmetrical processes are developed from parts of the body which do not lie in the course of the ciliated bands.

The larvæ of *Asteridea* and *Holothuridea* are devoid of any continuous skeleton, but those of *Ophiuridea* and *Echinidea* possess a very remarkable bilaterally symmetrical, continuous, calcareous skeleton, which extends into, and supports the processes of the body (Fig. 20).

A distinctly defined alimentary canal early makes its appearance in these Echinoderm larvæ. It is divided into a well-marked oral and œsophageal portion, a globular stomach, and a short intestine terminating in an anal aperture (Figs. 17 and 18). All the parts of the alimentary canal are disposed in a longitudinal and vertical plane, dividing the larval body into two symmetrical halves; but the œsophageal and intestinal portions are so disposed as to make an angle, open towards the ventral side, with one another. No nervous, or other organs, besides those indicated, have as yet been discovered in these larvæ.

Fig. 18.

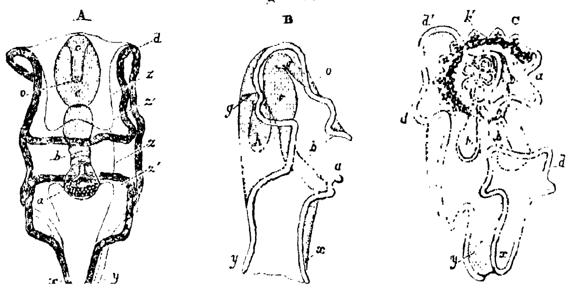
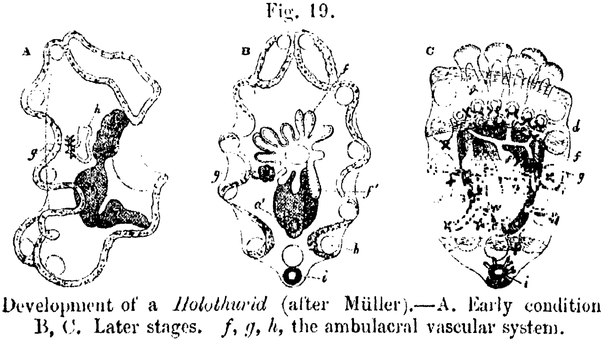


Fig. 18.—A young *Asterid* larva (after Müller).—A. Ventral. B. Lateral views of the larva. C. Commencing rudiment of the starfish. *a*. Mouth. *b*. Œsophagus. *c*. Stomach. *c'*. Intestine. *o*. Anus. *x*. Anterior, and *y*, principal ciliated band. *h*. Cæcal diverticulum, forming the rudiment of the ambulacral vascular system, and opening externally by the pore, *g*. *k*. Perisoma of the starfish.

Fig. 19.



19.—Development of a *Holothurid* (after Müller).—A. Early condition of larva. B, C. Later stages. *f*, *g*, *h*, the ambulacral vascular system.

Fig. 20.

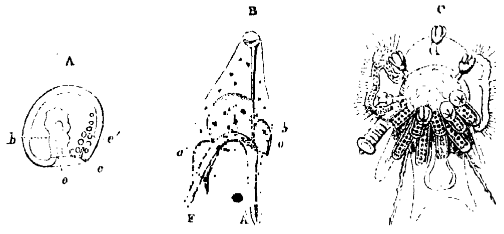


Fig. 20.—Development of an *Echinid* larva (after Müller).—A. earliest, and B, later condition of larva. C. The Echinid imago developed within and nearly obliterating the larva.

After swimming about in this condition for a while, the larva begins to show the first signs of those changes by which it is converted into the adult Echinoderm. An involution of the integument takes place upon one side of the dorsal region of the body, so as to give rise to a cæcal tube, which gradually elongates inwards, and eventually reaches a mass of formative matter, or blastema, aggregated upon one side of the stomach. Within this, the end of the tube becomes converted into a circular vessel, from which trunks pass off, radially, through the enlarging blastema. The latter, gradually expanding, gives rise in the *Echinidea,* the *Asteridea,* the *Ophiuridea,* and the *Crinoidea,* to the body-wall of the adult; the larval body and skeleton (when the latter exists), with more or less of the primitive intestine, being either cast off as a whole, or disappearing, or becoming incorporated with the secondary development, while a new mouth is developed in the centre of the ring formed by the circular vessel. The vessels which radiate from the latter give off diverticula to communicate with the cavities of numerous processes of the body—the so-called feet—which are the chief locomotive organs of the adult. The radiating and circular vessels, with all their appendages, constitute what is known as the "ambulacral system;" and, in Asterids and Echinids, this remarkable system of vessels remains in communication with the exterior of the body by canals, connected with perforated portions of the external skeleton—the so-called "madreporic canals" and "tubercles." In Ophiurids the persistence of any such communication of the ambulacral system with the exterior is doubtful, and still more so in Crinoids. In Holothurids no such communication obtains, the madreporic canals and their tubercles depending freely from the circular canal into the perivisceral cavity.

Whether the larva possessed a skeleton or not, the adult Echinoderm presents a calcareous framework which is developed quite independently of that of the larva. This skeleton may be composed of mere detached spicula, or plates, as in the Holothurids; or of definitely disposed ossicula, or regular plates, as in other Echinoderms. In the latter case its parts are always disposed with a certain reference to the disposition of the ambulacral system, and hence have a more or less distinctly radiate arrangement. It might be expected, in fact, that the arrangement of the organs of support should follow more or less closely that of the chief organs of movement of the adult Echinoderm, and it is not surprising to find the nervous system similarly related. It is, in all adult Echinoderms, a ring-like, or polygonal, ganglionated cord, situated superficially to that part of the ambulacral system which surrounds the mouth, and sending prolongations parallel with, and superficial to, the radiating ambulacral trunks.

The reproductive organs of the Echinoderms, which usually open upon, or between, parts of the radially disposed skeleton, commonly partake of the radial symmetry of that skeleton; but they have no such radial symmetry in the *Holothuridea.*

The alimentary canal of the adult Echinoderm is still less dependent upon the skeleton, and only in one group, the *Asteridea,* exhibits anything approaching a radiate disposition. Where skeletal elements are developed around the mouth or gullet, however, they have a radial disposition; as, *e. g.*, the parts of the so-called "lantern of Aristotle."

The vascular system which exists in many, if not all, adult Echinoderms, but the true nature of which is by no means understood at present, is closely related both to the alimentary and to the ambulacral systems, and partakes of the disposition of both.

No Echinoderm whatsoever has its organs, internal or external, disposed with that absolute and perfect radial symmetry which is exhibited by a *Medusa*, the tendency towards that kind of symmetry being always disturbed, either by the disposition of the alimentary canal, or by that of some part of the ambulacral apparatus. Very often, as in the Spatangoid sea-urchins, and in many *Holothuridea*, the ambulacral and nervous systems alone exhibit traces of a radial arrangement; and in the larval state, as we have seen, radial symmetry is totally absent, the young Echinoderm exhibiting as complete a bilateral symmetry as Annelids, or Insects.

Nothing can be more definite, it appears to me, than the class *Echinodermata*, the leading characteristics of which have just been enumerated; but it is a very difficult matter to say whether the seven groups, some of considerable extent, which are massed under the next head, that of SCOLECIDA, are rightly associated into one class, or should be divided into several. The seven groups to which I refer are the *Rotifera* (or Wheel-animalcules), the *Turbellaria*, the *Trematoda* (or flukes), the *Tæniada* (or tapeworms), the *Nematoidea* (or threadworms), the *Acanthocephala*, and the *Gordiacea*. Of these, five are composed of animals parasitic upon others; and exhibiting the anomalies of structure and of development which might be expected from creatures living under such exceptional conditions.

There is one peculiarity of organic structure which the first four of these groups certainly have in common; they all present what is termed the "water-vascular system,"—a remarkable set of vessels which communicate with the exterior by means of one, or more, apertures situated upon the surface of the body, and branch out, more or less extensively, into its substance.

In the *Rotifera* the external aperture of the water-vascular system is single, and situated at the hinder end of the body; it communicates with a large, rhythmically contractile, sac, whence two trunks proceed, which usually give off short lateral branches, and terminate in the ciliated "trochal disk" of the Rotifer, in the middle of which its mouth is placed. Both the lateral offshoots and the terminal branches contain vibratile cilia. The Trematode and Tænioid worms have a similar, but usually much more ramified apparatus; and it is interesting to observe that, in these animals, as in the *Aspidogaster conchicola*

(Fig. 21), the water-vascular system becomes divided into two distinct portions, one with contractile and non-ciliated walls, the other with non-contractile and ciliated walls. In some

Fig. 21.

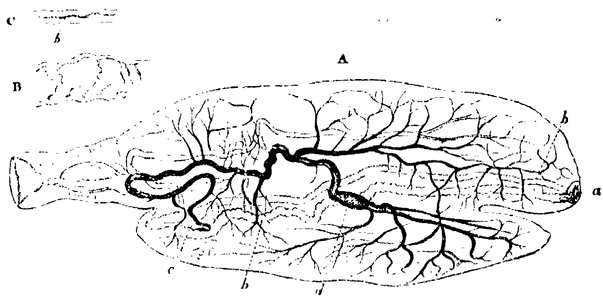


Fig 21.—A. Water-vascular system of *Aspidogaster conchicola*; *a*, terminal pore: *b*, lateral contractile vessels; *c*, lateral ciliated trunks, that of the left side shaded; *d*, dilatation of this trunk; B, one of the larger, and C, one of the smaller, ciliated vessels.

Turbellaria the apertures of the water-vascular apparatus are multiple; while it would seem that in others, as the *Nemertidæ*, the apparatus becomes shut externally in the adult state, and consists mainly, if not exclusively, of contractile vessels. The difficulties of observation are here, however, very great, and I would be understood to express this opinion with all due caution.

In none of these animals has any other set of vessels than those which appertain to the water-vascular system (if I am right in my view of the vessels of the *Nemertidæ*) been observed, nor has any trace of a true heart been noticed. The nervous system consists of one, or two, closely approximated ganglia.

This sum of common characters appears to me to demand the union of the *Rotifera*, *Turbellaria*, *Trematoda*, and *Tæniada* into one great assemblage. Ought the Nematoid worms to be grouped with them? If the system of canals, in some cases contractile, which open externally near the anterior part of the body (Fig. 22), and were originally observed by Von Siebold; and since by myself and others, are to be regarded as homologous with the water-vessels of the *Trematoda*, this question must, I think, be answered in the affirmative. It is almost the only system of organs in the *Nematoidea* which gives us a definite zoological criterion, the condition of the nervous system in these animals being still, notwithstanding the many inquiries which have been made into the subject, a matter of great doubt.

Fig. 22.

Fig. 22.—*Oxyuris*.—*a*. Mouth. *b*. Pharynx. *c*. Commencement of intestine, and *d* its termination; the intermediate portion is not figured. *e*. Genital aperture. *f*. Opening of vessels. *g*. Their receptacle. *h*. One of the vessels. *i*. Cellular matter enveloping them. A portion of one of the contractile vessels is represented above, more highly magnified.

In habit and feature, the *Gordiacea*, filiform parasites which inhabit the bodies of insects, and leave their hosts only to breed, resemble the *Nematoidea* so much that I can hardly doubt that their systematic place must be close to that of the latter; but positive evidence is almost wanting on this head, the extant accounts of the minute anatomy of these animals not having received that kind of confirmation which is desirable.

The structure of the *Acanthocephala*, comprising the formidable *Echinorhynchus* (Fig. 23) and its allies, is, on the other hand, pretty clearly made out. They are vermiform parasites, like the *Tæniada*, devoid of any mouth or alimentary canal, but provided with a proboscis armed with recurved hooks. The proboscis is supported within by a sort of rod-like handle, whence a cord is continued, to which the reproductive organs are attached. A single ganglion is seated in the "handle" of the proboscis. Immediately beneath the integument lies a series of reticulated canals containing a clear fluid, and it is difficult to see with what these can correspond if not with some modification of the water-vascular system.*

Fig. 23.

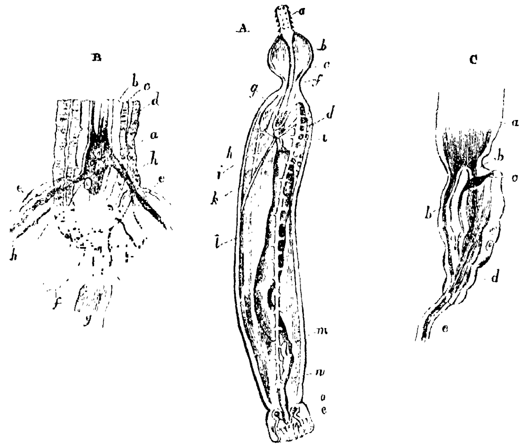


Fig. 23.—The *Echinorhynchus* of the Flounder.—A. Diagram exhibiting the relative position of the organs. *a.* Proboscis. *b.* Its stem. *c.* Anterior enlargement. *d.* Body. *e.* Posterior "funnel." *f.* Neck. *g.* Meniscus. *h.* Superior oblique tubular bands. *k.* Inferior muscles of the proboscis. *l, m.* Genitalia. *o.* Penis, or vulva. B. Lower extremity of the stem of the proboscis. *a.* Ganglion. *b.* Interspace. *d.* Outer coat. *c.* Inner wall. *e.* Tubular band, with the nerve *h.* *f.* Muscular bands. *g.* Suspensorium of the genitalia. C. Part of the female genitalia. *a.* Ovary. *b b.* Ducts leading from ovary to uterus (sperniducts?). *c.* Open mouth of oviduct. *d, e.* Uterus and vagina.

Leaving the division provisionally termed *Scolecida* in this confessedly unsatisfactory state, I pass on to the ANNELIDA, a class of large extent, containing the leech, the earthworm, the *Sipunculus*, the lobworm, the seamouse and *Polynöe* (Fig. 24), the *Serpula*, and the *Spirorbis*.

All the members of this class possess a nervous system, which consists of a longitudinal series of ganglia, situated along one side of the body, and is traversed anteriorly by the œsophagus, the præ-œsophageal, or so-called "cerebral," ganglia

* The recently published investigations of Leuckart, while they demonstrate still more clearly the close affinity which exists between the *Acanthocephala* and the *Tæniada*—by proving the adult worm to arise by secondary growth within a hooked embryo, in the former case as in the latter—leave some doubt upon the nature of the reticulated canals. According to Leuckart, they are the remains of the cavity which primitively lies between the wall of the embryo and the contained rudiment of the adult Acanthocephalan body.

being connected by lateral commissural cords with the post-œsophageal ganglia.

In many of these animals the body is divided into segments, each of which corresponds with a single pair of ganglia of the chain, and each of these segments may be provided with a pair of lateral appendages; but the appendages are never articulated; and are never so modified, as to be converted into masticatory organs, in the cephalic region of the body.

No Annelid ever possesses a heart comparable to the heart of a Crustacean, or Insect; but a system of vessels, with more or less extensively contractile walls, containing a clear fluid, usually red or green in colour, and, in some rare cases only, corpusculated, is very generally developed, and sends prolongations into the respiratory organs, where such exist. This has been termed the "pseudo-hæmal" system; and I have

Fig. 24.

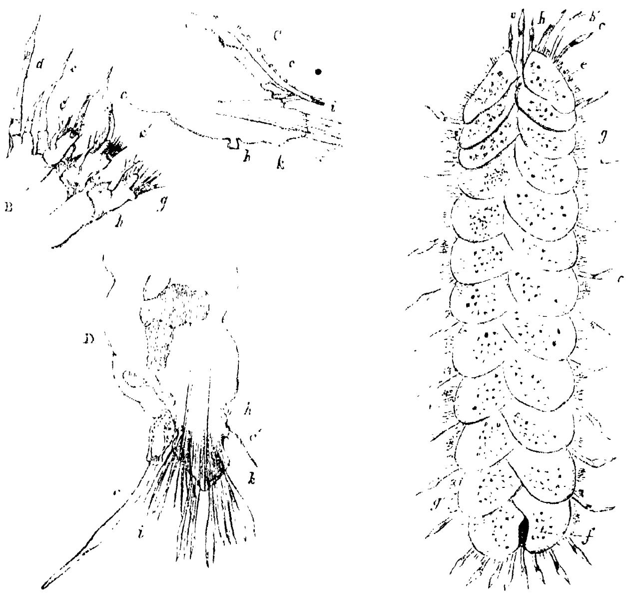


Fig. 24.—*Polynöe squamata*.

A. Viewed from above and enlarged. *a*, *b*. Feelers. *c*, *d*. Cirri. *e*. Elytra. *f*. Space left between the two posterior elytra. *g*. Setæ and fimbriæ of the elytra.

B. Posterior extremity, inferior view, the appendages of the left side being omitted. *h*. Inferior tubercle.

C. Section of half a somite with elytron. *i*. Notopodium. *k*. Neuropodium.

D. Section of half a somite with cirrus.

thought it probable that these "pseudo-hæmal" vessels are extreme modifications of organs homologous with the water-vessels of the *Scolecida*. As M. de Quatrefages has clearly shown, it is the perivisceral cavity with its contents that, in these animals, answers to the true blood-system of the Crustacea and Insects.

The embryos of Annelids are very generally ciliated, and vibratile cilia are commonly, if not universally, developed in some part or other of their organization. In both these respects they present a most marked contrast to the succeeding classes.

Fig. 25.

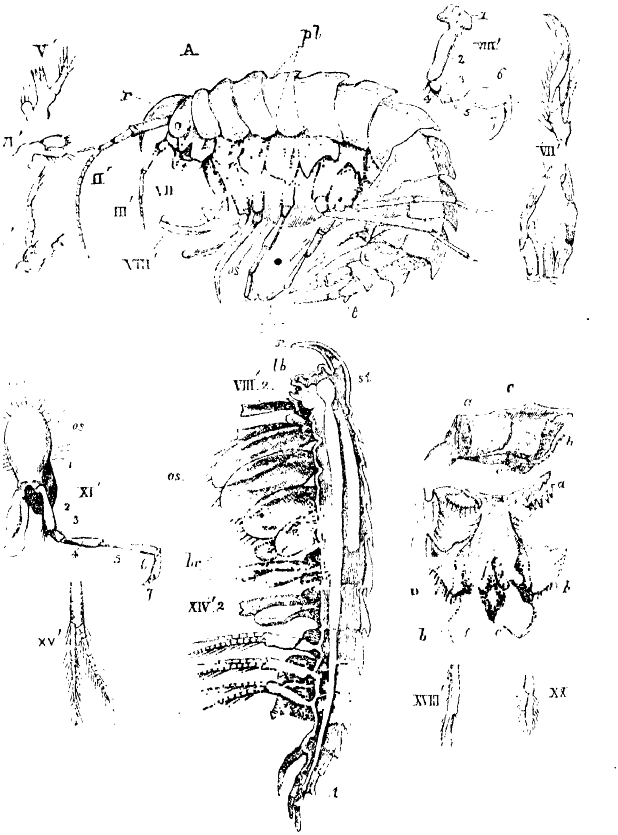


Fig. 25.—*Amphithoë*, an amphipodous Crustacean.—Lateral view (A), longitudinal and vertical section, detached appendages and stomach (C, D). The numbers I′ to XX′ indicate the appendages of the corresponding somites. *r*. Rostrum. *t*. Telson. *lb*. Labrum. *st*. Roof of the head, or cephalostegite. *os*. Oostegite. *Br*. Branchiæ. Stomach opened from above (D), and viewed laterally (C). *a*, *b*, *c*. Different parts of the armature.

In the CRUSTACEA (Fig. 25), the body is distinguishable into a variable number of "somites," or definite segments, each of which may be, and some of which always are, provided with a single pair of articulated appendages. The latter proposition is true of all existing *Crustacea:* whether it also held good of the long extinct *Trilobites*, is a question which we have no means of deciding. In most *Crustacea*, and, probably in all, one or more pairs of appendages are so modified as to subserve manducation. A pair of ganglia is primitively developed in each somite, and the gullet passes between two successive pairs of ganglia, as in the *Annelida.*

No trace of a water-vascular system, nor of any vascular system similar to that of the *Annelida*, is to be found in any Crustacean. All *Crustacea* which possess definite respiratory organs have branchiæ, or outward processes of the wall of the body, adapted for respiring air by means of water; the terrestrial *Isopoda*, some of which exhibit a curious rudimentary representation of a tracheal system, forming no real exception to this rule. When they are provided with a circulatory organ, it is situated on the opposite side of the alimentary canal to the principal chain of ganglia of the nervous system; and communicates, by valvular apertures, with the surrounding venous sinus—the so-called "pericardium."

The *Crustacea* vary through such a wide range of organization that I doubt if any other anatomical proposition, in addition to those which I have mentioned, except the presence of a chitinous integument and the absence of cilia, can be enunciated, which shall be true of all the members of the group.

It is this extreme elasticity, if I may so speak, of the crustacean type which renders the construction of any definition of the *Crustacea*, which shall include all its members and exclude the next class, the ARACHNIDA, so difficult. For the Spiders, Scorpions, Mites, and Ticks, which constitute this class, possess all the characters which have been just stated to be common to the *Crustacea* save one; when they are provided with distinct respiratory organs, in fact, these are not external branchiæ, adapted for breathing aërated water, but are a sort of involution of the integument in the form of tracheal tubes, or pulmonary sacs, fitted for the breathing of air directly. But then many of the lower *Arachnida*, like the lower *Crustacea*, are devoid of special respiratory organs, and so the diagnostic character fails to be of service.

Fig. 26.

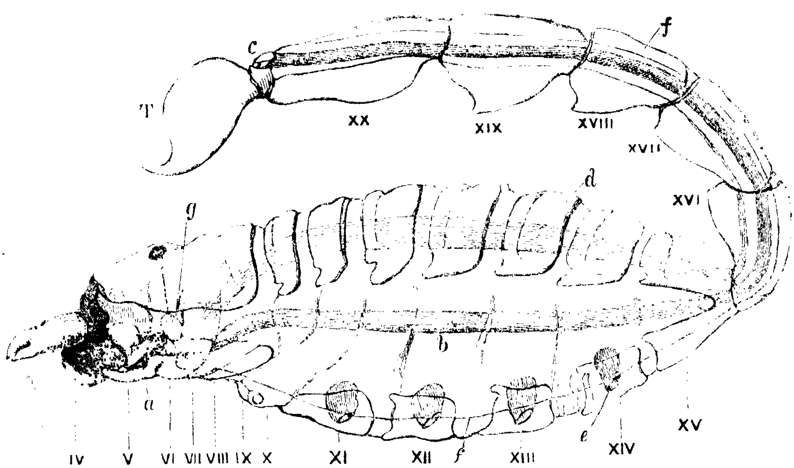


Fig. 26.—Diagrammatic section of a Scorpion, the locomotive members being cut away. *a*, Mouth leading into the pharyngeal pump. The large labrum lies above the mouth, and at the side of it are the bases of the large chelæ, or mandibles, IV., and above them the chelicerae, or antennæ. VI. to XX. Somites of the body. T, Telson; *b*, intestine; *c*, anus; *d*, indicates the position of the heart; *e*, the pulmonary sacs; *f*, a line indicating the position of the ganglionic chain; *g*, the cerebral ganglia.

The following common characters of the *Arachnida*, however, help out our diagnosis in practice. They never possess more than four pairs of locomotive limbs, and the somites of the abdomen, even when the latter is well developed, are not provided with limbs. Again, in the higher *Arachnida* (Fig. 26), as in the higher *Crustacea*, the body is composed of twenty somites, six of which are allotted to the head; but, in the former class, one of the two normal pairs of antennæ is never developed, and the eyes are always sessile, while, in the highest *Crustacea*, the eyes are mounted upon moveable peduncles, and both pairs of antennæ are developed.

Fig. 27.

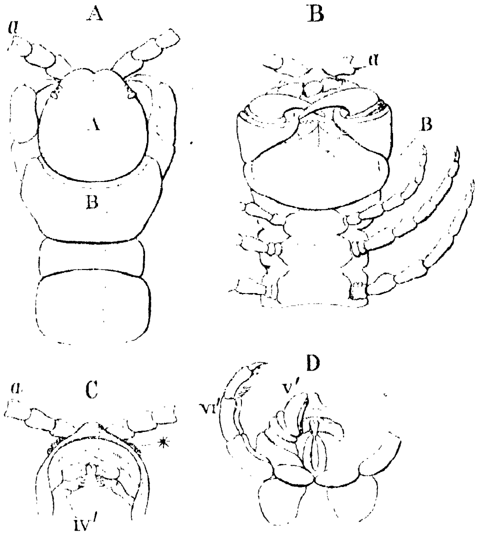


Fig. 27.—Anterior part of the body of *Scolopendra Hopei* (after Newport).—A, Anterior part of the body from above; B, from below; A, head proper; B, anterior thoracic somites; *a*, antennæ; C, antennæ, labrum, and mandibles (IV′) from below; D, under view of head, with the two pairs of maxillæ (V′ VI′) covering the foregoing.

The Myriapoda (Fig. 27) have the chitinous integument; the body divided into somites, provided with articulated appendages; and nervous and circulatory organs constructed upon a similar plan to those of the former groups. The body consists of more than twenty somites, and those which correspond with the abdomen of *Arachnida* are provided with locomotive limbs.

The head consists of at least five, and probably of six, coalescent and modified somites, and some of the anterior segments of the body are, in many genera, coalescent, and have their appendages specially modified to subserve prehension. The respiratory organs are tracheæ, which open by stigmata upon the surface of the body, and the walls of which are strengthened by chitin, so disposed as readily to pull out into a spirally coiled filament.

The Insecta, lastly, have respiratory organs like those of the *Myriapoda*, with a nervous and a circulatory system disposed essentially as in this and the two preceding classes. But the total number of somites of the body never exceeds twenty.

Fig. 28.

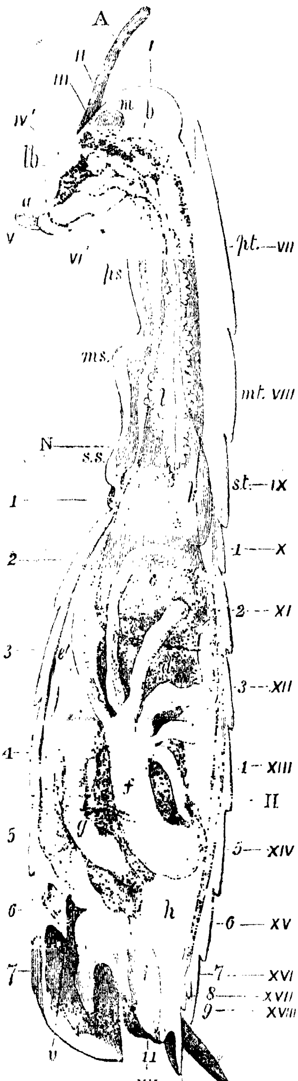


Fig. 28.—Longitudinal and vertical section of a female Cockroach (*Blatta*).—I. to XX., Somites of the body; 1 to 11, somites of the abdomen; A, antenna; *lb*, labrum; *a*, mouth; *b*, œsophagus; *c*, crop; *d*, stomach; *e*, pyloric cæca; *f*, *g*, *h*, intestine; *i*, rectum; *v*, vulva; *k*, *l*, salivary gland and receptacle; H, position of heart; *m*, cerebral ganglia; N, thoracic ganglia; *x*, palp-like appendage.

Fig. 29.

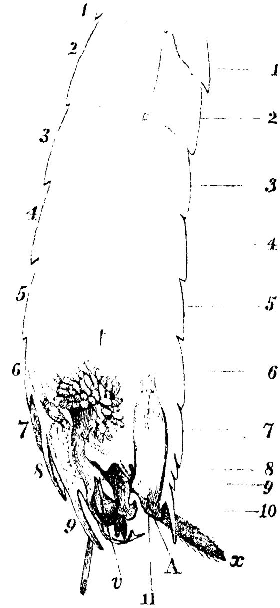


Fig. 29.—Longitudinal and vertical section of the abdomen of a male Cockroach (*Blatta*).—1, 2, 3, 4, &c., terga and sterna of the abdomen; *t*, testis; *v*, aperture of the vas deferens; A, anus.

Of these five certainly, and six probably, constitute the head, which possesses a pair of antennæ, a pair of mandibles, and two pairs of maxillæ; the hinder pair of which are coalescent, and form the organ called the "labium."

Three, or perhaps, in some cases, more, somites unite and become specially modified to form the thorax, to which the three pairs of locomotive limbs, characteristic of perfect insects,* are attached.

Two additional pairs of locomotive organs—the wings—are developed, in most insects, from the tergal walls of the second and third thoracic somites. No locomotive limbs are ever developed from the abdomen of the adult insect, but the ventral portions of the abdominal somites, from the eighth backwards, are often metamorphosed into apparatuses ancillary to the generative function (Figs. 28 and 29).

* The female *Stylops* is stated to possess no thoracic limbs.

LECTURE IV.

ON THE CLASSIFICATION OF ANIMALS.

THE VERTEBRATA: OR PISCES, AMPHIBIA, REPTILIA, AVES, AND MAMMALIA.

In the rapid survey of the animal kingdom with which we have been occupied in the preceding lectures, I have, for reasons which will be obvious by and by, taken group by group, and considered each separately upon its own merits, without attempting to say anything of the characteristics of the larger divisions into which these classes may be arranged. That is a point to which I shall return on a future occasion.

But with those animals which are called "vertebrated," such a course as this would involve a great and unprofitable expenditure of time and much repetition; because the five groups of animals which pass under this name—the classes *Pisces*, *Amphibia*, *Reptilia*, *Aves*, and *Mammalia*—are obviously united and bound together by many common characteristics, and are well known to be so connected. I shall commence the present lecture, therefore, by enumerating the most important of those structural peculiarities which these five great divisions exhibit in common.

In the animals to which our attention has hitherto been confined, the external, or integumentary and parietal, portion of the blastoderm never becomes developed into more than a single saccular, or tubular, investment, which incloses all the viscera. So that if we make a transverse section of any one of these animals endowed with a sufficiently high organization to possess a nervous system and a heart, that section may be represented diagrammatically as in Fig. 30 (I.), where P represents

Fig. 30.

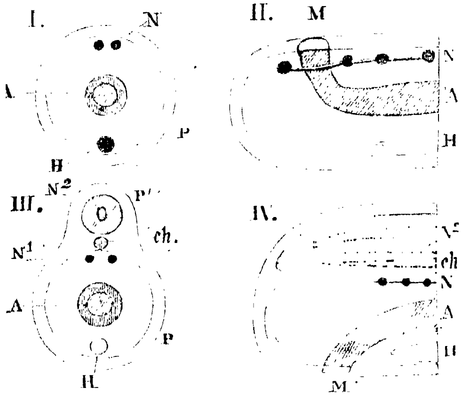


Fig. 30.—Diagrams representing generalised sections of one of the higher Invertebrates (I. II.), and of a Vertebrate (III. IV.); I. III. transverse, II. IV. longitudinal section. A, alimentary canal; H, heart; P, parietes of the body; P′, parietes of the neural canal; N, nervous centres of Invertebrate; N^1, sympathetic, and N^2, cerebro-spinal centres of Vertebrate; *ch*, notochord; M, mouth.

sents the parietes or wall of the body, A the alimentary canal, H the heart, and N the nervous centres. It will be observed that the alimentary canal is in the middle, the principal centres of the nervous system upon one side of it, and the heart upon the other. In none of these animals, again, would you discover, in the embryonic state, any partition, formed by the original external parietes of the body, between the nervous centres and the alimentary canal.

But, in the five vertebrate classes, the parietal portion of the blastoderm of the embryo always becomes raised up, upon each side of the middle line, into a ridge, so that a long groove is formed between the parallel ridges thus developed; and the margins of these, eventually uniting with one another, constitute a second tube parallel with the first, by a modification of the inner walls of which the vertebrate cerebro-spinal nervous centres are developed. Hence it follows that, after any vertebrated animal has passed through the very earliest stages of its development, it is not a single, but a double tube, and the two tubes are separated by a partition which was, primitively, a part of the external parietes of the body, but which now lies, in a central position, between the cerebro-spinal nervous centres and the alimentary canal. Hence, a transverse section of any vertebrated animal may be represented diagrammatically by Fig. 30 (III.), where, for the most part, the letters have the same signification as in the foregoing case, but where P' denotes the second, or *cerebro-spinal*, tube. The visceral tube (P) contains, as in the case of the invertebrate animal, the alimentary canal, the heart, and certain nervous centres, belonging to the so-called sympathetic system. This nervous system and the heart are situated upon opposite sides of the alimentary canal, the sympathetic corresponding in position, and in forming a double chain of ganglia, with the chief nervous centres of the invertebrate; so that the cerebro-spinal tube appears to be a super-addition,—a something not represented in the invertebrate series. The formation of the cerebro-spinal tube of vertebrates, in the manner which I have described to you, is a well-established fact; nor do I entertain any doubt that the cerebro-spinal centres, viz., the brain and the spinal cord of vertebrates, are the result of a modification of that serous layer of the germ which is continuous elsewhere with the epidermis. Two years ago, I took some pains to verify the remarkable discoveries of Remak in relation to this point, and, so far as the chick is concerned, his statements appeared to me to be fully borne out. But, as Von Baer long ago suggested, it is a necessary result of these facts that there can be no comparison between the cerebro-spinal nervous centres of the *Vertebrata* and the ganglionated nervous centres of the *Invertebrata*, and the homologues of the latter must probably be sought in the sympathetic.

Doubtless in close connection with this profound difference between the chief nervous centres of the vertebrate and the invertebrate is another remarkable structural contrast. In all the higher invertebrates, with a well-developed nervous system, the latter is perforated by the gullet, so that the mouth is situated upon the same side of the body as the principal masses of the nervous system, and some of the ganglia of the latter lie in front of, and others behind, the œsophagus. A longitudinal vertical section of such an animal, therefore, may be represented by Fig. 30 (II.).

A similar section of a vertebrated animal shows, on the contrary, the chief centre of the nervous system not to be perforated by the œsophagus; the latter turning away from it and opening upon the opposite side of the body (Fig. 30, IV.).

Another structure sharply distinctive of the vertebrate classes is the "chorda dorsalis" or "notochord," an organ of which no trace has yet been discovered in any of the invertebrates, though it invariably exists, in early embryonic life at least, in every vertebrate. Before the cerebro-spinal canal is complete, in fact, the substance of the centre of its floor, beneath the primitive median line of the embryo, becomes differentiated into a rod-like cellular structure, which tapers to both its extremities; and, in a histological sense, remains comparatively stationary, while the adjacent embryonic tissues are undergoing the most rapid and varied metamorphoses.

To these great differences between vertebrates and invertebrates, in their early condition, many others might be added. In all *Vertebrata* that part of the wall of the body which lies at the sides of, and immediately behind the mouth, exhibits a series of thickenings parallel with one another and transverse to the axis of the body, which may be five, or more, in number, and are termed the "visceral arches." The interspaces between these arches becoming thinner and thinner, are at length perforated by corresponding clefts, which place the cavity of the pharynx in free communication with the exterior. Nothing corresponding with these arches and clefts is known in the *Invertebrata*.

A vertebrated animal may be devoid of articulated limbs, and it never possesses more than two pair. These limbs always have an internal skeleton, to which the muscles moving the limbs are attached. Whenever an invertebrated animal possesses articulated limbs, the skeleton to which the muscles are attached is external, or is connected with an external body skeleton.

When an invertebrated animal possesses organs of mastication, these are either hard productions of the alimentary mucous membrane, or are modified limbs. In the latter case there may be many pairs of them—numerous *Crustacea*, for example, have eight pairs of limbs devoted to this function. In no vertebrated animal, on the other hand, are limbs so modified and functionally applied, the jaws being always parts of the cephalic parietes specially metamorphosed, and totally distinct in their nature from the limbs. All vertebrated animals, finally, possess a distinct vascular system, containing blood with suspended corpuscles of one kind, or of two, or even three, distinct kinds. In all, save one, there is a single valvular heart—the vessels of the exception, *Amphioxus*, possessing numerous contractile dilatations. All vertebrates possess a "hepatic portal system," the blood of the alimentary canal never being wholly returned directly to the heart by the ordinary veins, but being more or less largely collected into a trunk, the "portal vein," which ramifies through and supplies the liver.

These are the most important characters by which the vertebrate classes are distinguished, as a whole, from the other classes of the animal kingdom; and their number and importance go a long way to justify the step taken by Lamarck when he divided the animal kingdom into the two primary subdivisions of *Vertebrata* and *Invertebrata*.

If we seek now to construct definitions of the first two classes of the *Vertebrata*, PISCES and AMPHIBIA, we shall meet with some difficulties, arising partly from the wide variations observable in the structure of fishes, and partly from the close affinity which exists between them and the *Amphibia*.

No fish exhibits any trace of that temporary appendage of the embryo of the higher vertebrates which is termed an amnion, nor can any fish be said to possess an allantois, though the urinary bladder of fishes may possibly be a rudiment of that structure. The posterior visceral clefts and arches * of fishes persist throughout life, and are usually more numerous than in other vertebrates; while upon, or in connexion with, them are

* The relation of the perforated pharynx of *Amphioxus* to the visceral arches and clefts is not known.

developed villi, or lamellæ, which subserve the respiratory function.

Median fins, formed by prolongations of the integument, supported by one or other kind of skeleton, are very characteristic of fishes, and it is questionable if any fish exists altogether devoid of the system of median fin-rays and their supports, which have been termed inter-spinous bones and cartilages. On the other hand, no vertebrate animal, other than a fish, is known to possess them.

When the limbs, or pectoral and ventral fins, of fishes are developed, they always exhibit a more or less complete fringe of fin-rays. No amphibian is known to possess such rays in its lateral appendages, but there is some reason to believe that the extinct *Ichthyosauria* may have been provided with them.

In most fishes, the nasal sacs do not communicate directly with the cavity of the mouth, but the *Myxinoids* and *Lepidosiren* are exceptions to this rule.

The blood-corpuscles of fishes are always nucleated, and are commonly red, but by a singular exception those of *Amphioxus* (the Lancelet, which is an exception to most rules of piscine organization) are colourless.

Almost all fishes have the heart divided into two auricles and one ventricle; but *Amphioxus,* as I have previously stated, is devoid of any special heart, being provided instead with a number of contractile, vascular dilatations; while *Lepidosiren* possesses two auricles, and, at the same time, is provided with true lungs.

It is useless therefore to appeal to the olfactory organ, the blood, the heart, or the respiratory organs, for characters at once universally applicable to, and diagnostic of, fishes.

The Amphibia (or Batrachians, Salamandroids, *Cœciliæ*, and Labyrinthodonts) resemble fishes, and differ from all other vertebrates in the entire absence of an amnion, and in having only the urinary bladder to represent the allantois. They have red nucleated blood-corpuscles. Yet again they resemble fishes, and differ from all other vertebrates in the fact that filaments exercising a respiratory function, or branchiæ, are developed from their visceral arches during a longer or shorter period.

None are known to be provided with median fins supported by fin-rays, and their limbs are never fringed with fin-rays.

Furthermore, in all *Amphibia* which possess limbs, the skeleton of these limbs is divisible into parts which obviously correspond with those found in the higher vertebrates. That is to say, in the fore limbs there are cartilages, or bones, answering in their essential characters and arrangement to the humerus, radius and ulna, carpus, metacarpus, and phalanges; and, in the hind limb, to the femur, tibia and fibula, tarsus, metatarsus, and phalanges of the higher vertebrates. This is the case in no fish; for, whether fishes possess parts corresponding with the humerus, radius and ulna, &c., or not, certain it is that the elements of their limb skeletons are very differently disposed from the arrangement which obtains in *Amphibia* and in higher vertebrates.

In all *Amphibia* the skull articulates with the spinal column by two condyles, and the basi-occipital remains unossified. Furthermore, the cranial peduncle, or suspensorium, to which the lower jaw is articulated, gives attachment to the hyoidean apparatus.

These last are characters by which the *Amphibia* are sharply distinguished from the higher vertebrates.

There is a striking contrast between the close affinity of the fish and the amphibian and the wide separation of the *Amphibia* from the succeeding classes, all of which possess, in the embryonic state, a well-developed amnion and allantois, the latter almost always taking on, directly or indirectly, a respiratory function.

The amnion is a sac filled with fluid which envelopes and shelters the embryo, during its slow assumption of the condition in which it is competent to breathe and receive food from without. The mode of its formation is shown in the accompanying figures of the early stages of development of the common fowl. Fig. 31, A, represents the first step in the differentiation of the embryo from the central portion of the blastoderm—that thin membranous cellular expansion which lies on the surface of the yelk where we see the cicatricula, or "tread." A well-defined, though shallow, straight groove, the "primitive groove," bounded at the sides by a slight elevation of the blastoderm, indicating the position of the future longitudinal axis of the body of the chick. Soon, the lateral boundaries of this groove, in what will become

Fig. 31.

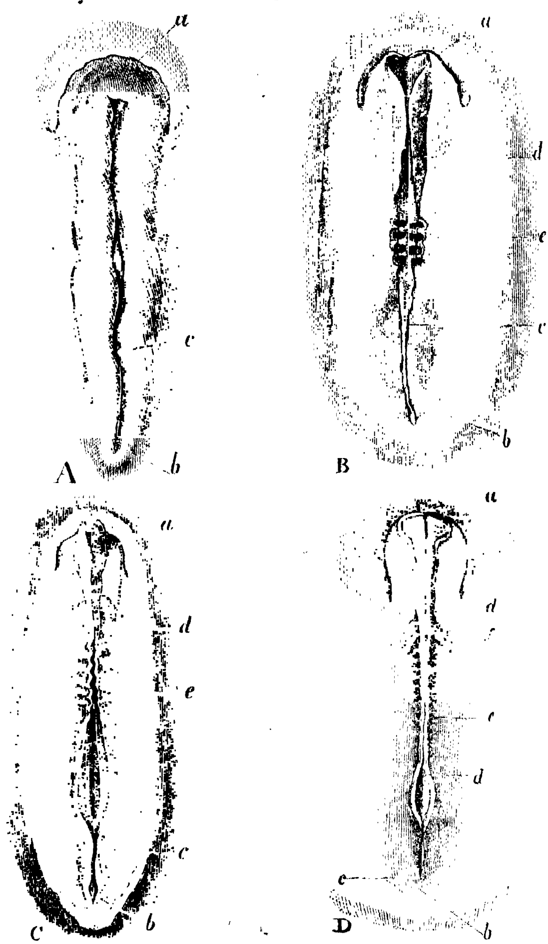


Fig. 31.—Development of the Chick.

A. First rudiment of the embryo; *a*, its cephalic; *b*, its caudal end; *c*, primitive groove.
B. The embryo further advanced; *a*, *b*, *c*, as before; *d*, the dorsal laminæ developed in the cephalic region only, and nearly uniting in the middle line; *e*, the proto-vertebræ.
C. Letters as before. The dorsal laminæ have united throughout the greater part of the cephalic region, and are beginning to unite in the anterior spinal region.
D. Embryo further advanced (second day), the dorsal laminæ having united throughout nearly their whole length. The proto-vertebræ have increased in number, and the omphalo-meseraic veins, *f*, are visible.

The embryos are drawn of the same absolute length, but it will be understood that the older embryos are, in nature, longer than the younger.

the anterior region of the body, grow up into plates—the dorsal laminæ (Fig. 31, B); and these dorsal laminæ, at length uniting, inclose the future cerebro-spinal cavity (Fig. 31, C, D). The blastoderm, beyond the region at which the dorsal laminæ are developed, grows downwards to form the ventral laminæ, and where the margins of these pass into the general blastoderm, the outer serous, or epidermic, layer rises up into a fold, which encircles the whole embryo; and the anterior and posterior parts of this fold growing more rapidly than the lateral portions, form a kind of hood for the cephalic and caudal ends of the body respectively (Fig. 32, E). The margins of the hoods and of

Fig. 32.

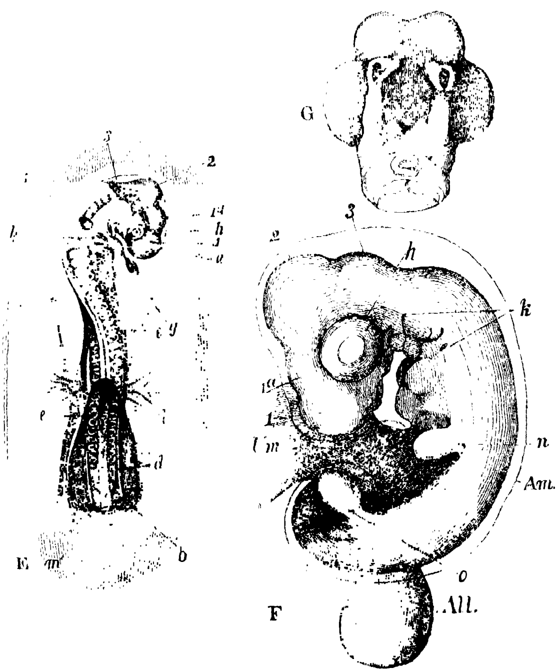


Fig. 32.—Development of the Chick.

E. Embryo at the third day; *g*, heart; *h*, eye; *i*, ear; *k*, visceral arches and clefts; *l*, *m*, anterior and posterior folds of the amnion, which have not yet united over the body; 1, 2, 3, first, second, and third cerebral vesicles; 1*a*, vesicle of the third ventricle.

F. Chick at the fifth day; *n*, *o*, rudiments of the anterior and posterior extremities; *Am*, amnion; *All*, allantois; *Um*, umbilical vesicle.

G. Under view of the head of the embryo F, the first visceral arch being cut away.

their lateral continuations at length meet over the middle line of the body, and there coalesce: so that the body is covered for a while by a double sac, the inner layer of which is formed by that wall of the fold of the serous layer which is inferior, or nearest to the body of the embryo; while the outer layer is formed by that wall which is superior, or furthest from the body of the embryo. The outer layer eventually disappears as a distinct structure, while the inner remains as the amnion. From the mode of formation which has been described, it results that the amnion is a shut sac, enveloping the body of the embryo; and is continuous, on the ventral side of the body, with the integument of a region which eventually becomes the umbilicus (Fig. 32, F).

The allantois is developed much later than the amnion, neither from the serous nor from the mucous (or epidermic and epithelial) layers of the germ, but from that intermediate stratum whence the bones, muscles, and vessels are evolved. It arises, as a solid mass, from the under part of the body of the embryo, behind the primitive intestinal cavity; and, enlarging, becomes a vesicle, which rapidly increases in size, envelopes the whole embryo, and, being abundantly supplied with arterial vessels from the aorta, serves as the great instrument of respiration during fœtal life; the porosity of the egg-shell allowing the allantoic blood to exchange its excess of carbonic acid for oxygen by osmosis.

The amnion and the external part of the allantois are thrown off at birth.

That which has just been stated respecting the development and characters of the amnion and allantois of the chick is true not only of all Birds, but of all *Reptilia*.

All embryonic REPTILIA are provided with an amnion and an allantois, like those just described in the fœtal fowl. In the embryonic state, also, they possess visceral arches and clefts, but no respiratory tufts are ever developed in the arches, nor are reptiles endowed with an apparatus for breathing the air dissolved in water at any period of their existence. The skull of all *Reptilia* is articulated with the vertebral column by a single condyle, into which the ossified basi-occipital enters largely

(Fig. 33). Each ramus of the lower jaw is composed of a number of pieces, and articulates with the skull, not directly, but by the

Fig. 33.

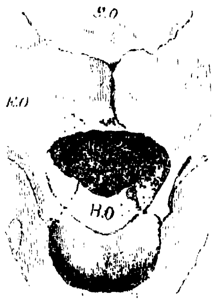


Fig. 33.—The occipital condyle of a Crocodile's skull viewed from behind.—*B.O*, Basi-occipital; *E.O*, Ex-occipital; *S.O*, Supra-occipital.

intervention of a bone—the os quadratum—with which the hyoidean apparatus is not immediately connected (Fig. 34).

Fig. 34.

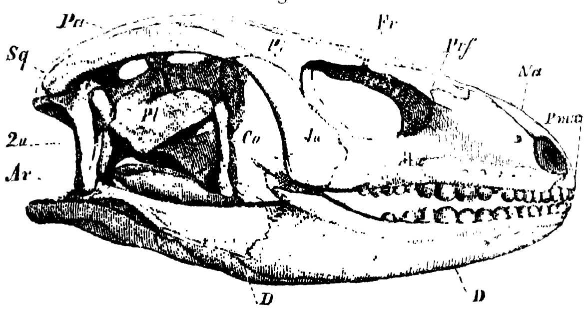


Fig. 34.—The skull of a Lizard (*Cyclodus*).—*D D*, Dentary piece of the lower jaw; *Qu*, Os quadratum; *Sq*, Squamosal.

The fore-limb of Reptiles never takes the form of a wing, such as is seen in Birds; the "wing" of the remarkable extinct flying reptiles, the *Pterodactyles*, being constructed on a totally different principle from that of a bird. In no known reptile, again, are the metatarsal and tarsal bones anchylosed into one bone.

In all *Reptilia* the greater and lesser circulations are directly connected together, within, or in the immediate neighbourhood of, the heart; so that the aorta, which is formed by the union of two arches, contains a mixture of venous and arterial blood.

The blood is cold, and the majority of the blood-corpuscles are red, oval, and nucleated. The bronchial tubes are not connected at the surface of the lungs with terminal saccular dilatations, or air-vesicles. When, as is ordinarily the case, the superficial layers of the epidermis of Reptiles are converted into horn, the corneous matter takes the form of broad plates, or of overlapping scales, neither plates nor scales being developed within pouches of the integument.

The class of AVES consists of animals so essentially similar to Reptiles in all the most essential features of their organization, that Birds may be said to be merely an extremely modified and aberrant Reptilian type.

As I have already stated, they possess an amnion and a respiratory allantois, and the visceral arches never develop branchial appendages. The skull is articulated with the vertebral column by a single condyle, into which the ossified basi-occipital enters largely. Each ramus of the lower jaw, composed, as in Reptiles, of a number of pieces, is connected with the skull by an os quadratum, to which the hyoidean apparatus is not suspended.

In no existing bird does the terminal division of the fore-limb possess more than two digits terminated by claws, and the metacarpal bones are commonly anchylosed together, so that the "manus" is of little use, save as a support for feathers.

In the hind limb of all birds the tarsal and metatarsal bones become more or less completely fixed, and the latter, anchylosed together, so as to form a single osseous mass, the "tarso-metatarsus."

The greater and lesser circulations of birds are completely separate, and there is only one aortic arch, the right. The right ventricle has a muscular valve. The blood is hot, hotter on the average than that of any other vertebrates, and the majority of the blood-corpuscles are oval, red, and nucleated. The bronchial tubes open upon the surface of the lungs into air-sacs, which differ in number and in development in different birds. Lastly, the integument of birds is always provided with horny appendages, which result from the conversion into horn of the cells of the outer layer of the epidermis. But the majority of these appendages, which are termed "feathers," do not take the form of mere plates developed upon the surface of the skin, but are evolved within sacs from the surfaces of conical papillæ of the dermis. The external surface of the dermal papilla, whence a feather is to be developed, is provided upon its dorsal surface with a median groove, which becomes shallower towards the apex of the papilla. From this median groove lateral furrows proceed at an open angle, and passing round upon the under surface of the papilla, become shallower, until, in the middle line, opposite the dorsal median groove, they become obsolete. Minor grooves run at right angles to the lateral furrows. Hence the surface of the papilla has the character of a kind of mould, and if it were repeatedly dipped in such a substance as a solution of gelatine, and withdrawn to cool until its whole surface was covered with an even coat of that substance, it is clear that the gelatinous coat would be thickest at the basal or anterior end of the median groove, at the median ends of the lateral furrows, and at those ends of the minor grooves which open into them; while it would be very thin at the apices of the median and lateral grooves, and between the ends of the minor grooves. If, therefore, the hollow cone of gelatine, removed from its mould, were stretched from within; or if its thinnest parts became weak by drying; it would tend to give way, along the inferior median line, opposite the rod-like cast of the median groove and between the ends of the casts of the lateral furrows, as well as between each of the minor grooves, and the hollow cone would expand into a flat feather-like structure with a median shaft, as a "vane" formed of "barbs" and "barbules." In point of fact, in the development of a feather such a cast of the dermal papilla is formed, though not in gelatine, but in the horny epidermic layer developed upon the mould, and, as this is thrust outwards, it opens out in the manner just described. After a certain period of growth the papilla of the feather ceases to be grooved, and a continuous horny cylinder is formed, which constitutes the "quill."

Between *Aves* and MAMMALIA there is a hiatus, not perhaps, in some respects, quite so wide as that between *Amphibia* and *Reptilia*, but still very considerable.

All Mammals possess an amnion of an essentially similar character to that of Birds and Reptiles, and all have an allantois. But the latter either ceases to exist after a very early period of fœtal life, or else it is "placentiferous," and serves as the means of intercommunication between the parent and the offspring. Of the nature and characters of the "placenta" developed in the majority of the *Mammalia* I shall speak more particularly by and by. For the present, I pass it over as a structure not universally characteristic of the class.

The visceral arches are, throughout life, as completely devoid of branchial appendages in Mammals, as in Birds and Reptiles. In the skull, the basi-occipital is well ossified, and, with the ex-occipitals, enters into the formation of the cranio-spinal articulation; the occipital condyle thus formed, however, is not single, as in Reptiles and Birds, but double, and the atlas has corresponding articular facets.

Fig. 35.

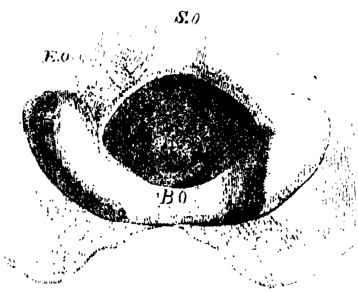


Fig. 35.—The occipital condyles of a Dog's skull viewed from behind.—Signification of the letters as in Fig. 33.

Each ramus of the lower jaw is composed of only a single piece, and this articulates directly with the squamosal bone of the skull, and not with the representative of the quadrate bone.

The greater and lesser circulations of Mammals are as completely distinct as in Birds, and there is but a single aortic arch, the left. The majority of the blood-corpuscles are red, free nuclei, and these are always discoidal, and usually circular in form. The blood is hot. There is a complete diaphragm, and none of the bronchi end in air-sacs.

Some part or other of the integument of all Mammals exhibits "hairs"—horny modifications of the epidermis—which so far resemble feathers, that they are developed upon papillæ inclosed within sacs; but, on the other hand, differ from the horny appendages of birds, in not splitting up as they are protruded, in the fashion so characteristic of feathers.

Fig. 36.

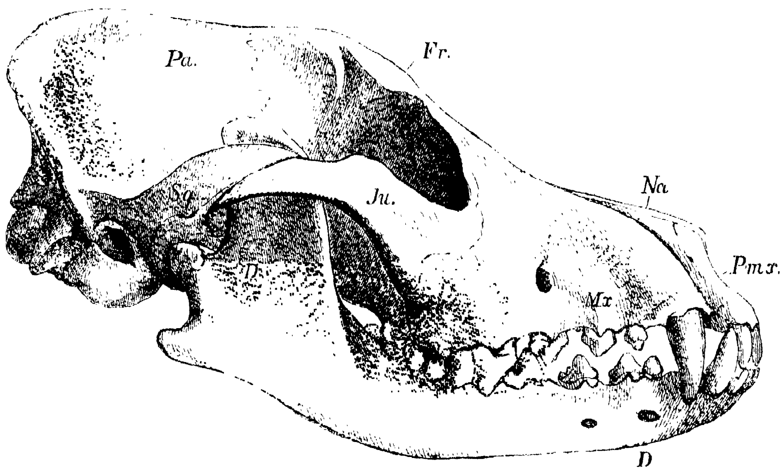


Fig. 36.—The skull of a Dog.—*D*. Ramus of the lower jaw; *Sq*. Squamosal.

Finally, all Mammals are provided with organs for the secretion of a fluid which subserves the nourishment of the young after birth. The fluid is milk; the organs are the so-called "mammary" glands, and may probably be regarded as an extreme modification of the cutaneous sebaceous glands. These glands are aggregated into two or more masses, disposed upon each side of the median line of the ventral surface of the body; and, in almost all Mammals, the aggregated ducts of each mass open upon an elevation of the skin common to all—the nipple or teat. To this the mouth of the newly-born Mammal is applied, and from it, either by suction on the part of the young, or by the compressive action of a special muscle on the part of the parent, the nutritive fluid makes its way into the stomach of the former.

LECTURE V.

ON THE CLASSIFICATION OF ANIMALS.

ON THE ARRANGEMENT OF THE CLASSES INTO LARGER GROUPS.

HAVING now arrived at the end of the list of classes, and having endeavoured to furnish you with a statement of the structural features common to, and characteristic of, each class, it will be my next object to discuss the relations of these classes one to another, and to inquire how far they present such common characters as will enable us to group them into larger divisions.

And, to commence with the highest classes, it is clear that the *Mammalia*, *Aves*, and *Reptilia* are united together by certain very striking features of their development. All possess an amnion and an allantois, and are devoid, throughout life, of any apparatus for breathing the air which is dissolved in water. In other words, they constitute what has been termed the "province" of ABRANCHIATE VERTEBRATA, in contradistinction to *Pisces* and *Amphibia*, which possess no amnion, nor allantois (or at most a rudimentary one), and, being always provided at a certain period, if not throughout life, with branchiæ, have been called BRANCHIATE VERTEBRATA.

The abranchiate, however, form a far less homogeneous assemblage than the branchiate *Vertebrata*—Mammals being so strongly separated from Reptiles and Birds that I am disposed to regard them as constituting one of three primary divisions, or provinces, of the *Vertebrata*. The structure of the occipital condyles, the structure and mode of articulation of the mandibular rami, the presence of mammary glands, and the non-nucleated red blood-corpuscles appear to separate Mammals as widely from Birds and Reptiles as the latter are separated from *Amphibia* and Fishes.

Thus the classes of the *Vertebrata* are capable of being grouped into three provinces: (I.) the Ichthyoids (comprising Fishes and *Amphibia*), defined by the presence of branchiæ at some period of existence, the absence of an amnion, the absence, or rudimentary development, of the allantois, nucleated blood-corpuscles, and, as will be seen by and by, a parasphenoid in the skull; (II.) the Sauroids, defined by the absence of branchiæ at all periods of existence, the presence of a well-developed amnion and allantois, a single occipital condyle, a complex mandibular ramus articulated to the skull by a quadrate bone, nucleated blood-corpuscles and no parasphenoid, comprising Reptiles and Birds; and (III.) the Mammals, devoid of branchiæ and with an amnion and an allantois, but with two occipital condyles and a well-developed basi-occipital and no parasphenoid; a simple mandibular ramus articulated with the squamosal and not with the quadratum, with mammary glands and with red non-nucleated blood-corpuscles.*

These five classes, whether divided into two or three provinces, again, present so many characters, already enumerated, by which they resemble one another, and differ from all other animals, that, by universal consent, they are admitted to form the group of VERTEBRATA, which takes its place as one of the primary divisions or "sub-kingdoms" of the Animal Kingdom.

The next four classes—*Insecta, Myriapoda, Arachnida, Crustacea*—without doubt also present so many characters in common as to form a very natural assemblage. All are provided with articulated limbs attached to a segmented body-skeleton—the latter, like the skeleton of the limbs, being an "exoskeleton," or a hardening of that layer which corresponds with the outer part of the epidermis of Vertebrates. In all, at any rate in the embryonic condition, the nervous system is composed of a double

* To these may be added the absence of the *corpus callosum* in the brain of Sauroids and its presence in Mammals. See note p. 89.

chain of ganglia, united by longitudinal commissures, and the gullet passes between two of these commissures. No one of the members of these four classes is known to possess vibratile cilia. The great majority of these animals have a distinct heart, provided with valvular apertures, which are in communication with a perivisceral cavity containing corpusculated blood. But the *Cirripedia* and the *Ostracoda* among Crustaceans, and many of the Mites among *Arachnida*, have as yet yielded no trace of distinct circulatory organs, so that the nature of these organs cannot be taken as a universal character of the larger group we are seeking; still less can such a character be found in the respiratory organs, which vary widely in character, and are often totally absent as distinct structures. Some years ago I endeavoured to show* that a striking uniformity of composition is to be found in the heads of, at any rate, the more highly organized members of these four classes, and that, typically, the head of a Crustacean, an Arachnid, a Myriapod, or an Insect is composed of six somites (or segments corresponding with those of the body) and their appendages, the latter being modified so as to serve the purpose of sensory and manducatory organs. I believe this doctrine to be substantially correct; and that, leaving all hypothetical suppositions aside, the head of any animal belonging to these classes may be demonstrated to contain never fewer than four, and never more than six somites with their appendages; but, until this view has received confirmation from other workers, I shall not venture to put forward any statement based upon it as part of the definition of the large group or "province" containing the four classes above mentioned, which has received from some naturalists the name of ARTICULATA, from others that of ARTHROPODA, the latter being perhaps the more distinctive and better appellation.

The members of the class *Annelida* present marked differences from all the *Arthropoda*, but resemble them in at least one important particular; and that is, the arrangement of the nervous system, which constitutes a ganglionated double chain, traversed at one point by the œsophagus. In almost all other

* "On the Agamic Reproduction and Morphology of *Aphis*," *Transactions of the Linnæan Society*, vol. xxii.

respects, Annelids differ widely from Arthropods. It may be doubted whether any Annelid is devoid of cilia in some part or other of its organization, and cilia constitute the most important organs of locomotion in the embryos of many. No Annelid possesses a heart communicating by valvular apertures with the perivisceral cavity, none have articulated limbs, and none possess a head composed of even four modified somites.

Most Annelids are provided with that peculiar system of vessels termed "pseudo-hæmal;" but, in some, that system has not yet been discovered.

In endeavouring to separate from among invertebrated animals a first large group, comparable to the *Vertebrata*, it appears to me that the resemblances between the *Annelida* and the *Arthropoda* outweigh the differences; and that the characters of the nervous system and the frequently segmented body, with imperfect lateral appendages, of the former, necessitate their assemblage with the *Arthropoda* into one great division, or "sub-kingdom," of ANNULOSA.

But what of the *Echinodermata* and the *Scolecida?* Should both these great classes be also ranged under the *Annulosa;* or do they belong to different sub-kingdoms; or, if they belong to the same, should they constitute a sub-kingdom of their own?

I will endeavour to reply to these questions in succession. Whether these two groups belong to the *Annulosa* or not, must depend upon whether they possess any characters in common with the *Arthropoda* and *Annelida* other than those which they have in common with all animals. I can find none of any great moment. No Echinoderm, or Scolecid, has a definitely segmented body or bilaterally disposed successive pairs of appendages. None of these animals has a longitudinal chain of ganglia.

On the other hand, there is much resemblance between the ciliated larvæ of some Scolecids and Echinoderms, and those of Annelids; and the form of the body of many Scolecids is so similar to that of one of the most familiar of Annelids, as to have earned for both them and the Annelids the common title of "worms." Nor must it be forgotten that, in the Annelids, there seem to be representatives of that singular system of vessels which attains so large a development as the "water-vascular" apparatus in many Scolecids.

Whatever value may be attached to these resemblances, it must, I think, be admitted that, in the present state of our knowledge, it is impossible to affirm anything absolutely common to, and yet diagnostic of, all *Annulosa* and all Echinoderms and Scolecids. On the other hand, there can be no doubt as to the many and singular resemblances which unite the Scolecids and the Echinoderms together. The nervous system of the Echinoderm may present considerable differences from that of a Trematode or Rotifer, but it must be recollected that the comparison is not a fair one, seeing that the mouth and gullet of an Echinoderm, round which its nervous ganglia are arranged, are not, strictly speaking, the same as the parts so named in a Rotifer, but are new developments.

And it is exactly in that anomalous method of development of the Echinoderm within its larva, which is so characteristic of the whole group of *Echinodermata,* that this class exhibits its strong alliance with the *Scolecida;* the *Turbellaria* and *Tæniada* exhibiting the only approach to the method of Echinoderm development known in the Animal Kingdom.

A singular larva studied by Johannes Müller, in one of his many fruitful visits to the seashore, and termed by him *Pilidium,* has furnished, in the hands of subsequent observers (more especially Krohn, Leuckart, and Pagenstecher), ample proof that a *Nemertes* (a genus of *Turbellaria*) may be developed in a manner altogether similar to that in which an Echinoderm takes its origin.

The *Pilidium* (Fig. 37) is a small, helmet-shaped larva, with a long flagellum attached like a plume to the summit of the helmet, the edges and side lobes of which are richly ciliated. A simple alimentary sac opens upon the under surface of the body between the lobes (Fig. 37, A).

In this condition, the larva swims about freely; but, after a while, a mass of formative matter appears upon one side of the alimentary canal, and, elongating gradually, takes on a worm-like figure. Eventually it grows round the alimentary canal, and, appropriating it, detaches itself from the *Pilidium* as a Nemertid—provided with the characteristic proboscis, and the other organs of that group of *Turbellaria.*

Fig. 37.

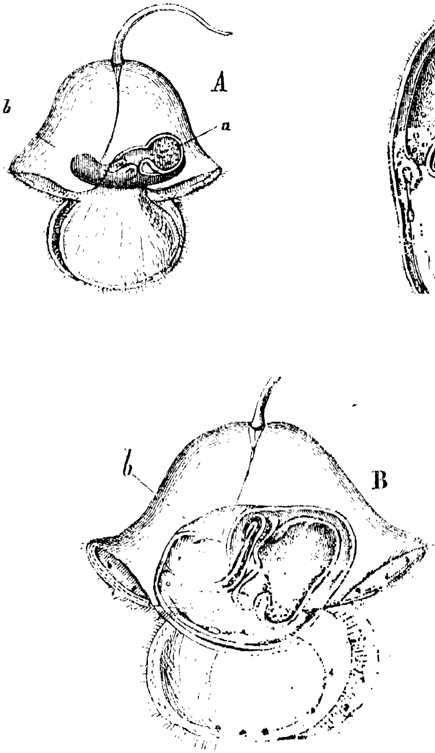


Fig. 37.—*Pilidium gyrans* (after Leuckart and Pagenstecher).
A. Young *Pilidium ; a*, alimentary canal ; *b*, rudiment of the Nemertid.
B. *Pilidium* with a more advanced Nemertid.
C. Newly-freed Nemertid.

Many *Trematoda*, and all Tænioid *Scolecida*, again, present an essentially similar process of internal gemmation, in virtue of which either a separate offspring arises, or an adult is developed within an embryonic form; but in these cases the appropriation of the intestine of the primary by that of the secondary form, which renders the ordinary development of the Echinoderm so striking, does not occur.

In discussing the characters of the *Echinodermata,* I have described at length the ambulacral system; and, in speaking of the *Scolecida*, I have no less insisted upon the peculiarities of the "water-vascular system." But it is impossible to compare these two systems of vessels without being struck by their similarity. Each is a system of canals, opening externally, and ciliated within; and the circumstance that the two apparatuses are turned to different purposes in two distinct groups of the animal kingdom, seems to me no more to militate against their homology, than the respiratory function of the limbs of Phyllopod *Crustacea* militates against the homology of these limbs with the purely locomotive appendages of other Crustaceans.

Thus it appears that the *Echinodermata* and the *Scolecida* are so closely connected that they can by no means be placed in separate sub-kingdoms; and in the course of studying the other sub-kingdoms it will be quite obvious that, unless they are to occupy an independent position, there is no place for them anywhere, save among the *Annulosa*. I have hitherto been accustomed to consider them, under the name of the ANNULOIDA, as a division of this sub-kingdom; but until some structural character can be discovered by which all the *Annuloida* agree with the *Annulosa*, and differ from other animals, I am much inclined to think it would conduce to the formation of clear conceptions in zoology if the *Annuloida* were regarded as a distinct primary division of the Animal Kingdom.

If we now turn to the other column of classes of invertebrate animals (*supra*, p. 6), the four last on the list, viz., *Cephalopoda*, *Pteropoda*, *Pulmogasteropoda*, and *Branchiogasteropoda*, have a number of well-marked characters in common. In all, the nervous system is composed of three principal pairs of ganglia—cerebral, pedal, and parieto-splanchnic—united by commissures. All possess that remarkable buccal apparatus, the odontophore,—whence I have ventured to propose the name of ODONTOPHORA for the group. The circulatory and respiratory organs vary a good deal, but none are provided with double lamellar gills upon each side of the body.

The *Lamellibranchiata* stand in somewhat the same relation to the *Odontophora* as the *Annelida* to the *Arthropoda*. The

Lamellibranchs have the three fundamental pairs of ganglia of the *Odontophora*, but they possess no trace of the odontophore. Furthermore, they are all provided with bivalve external pallial shells, the valves being right and left in relation to the body. No shell of this kind is found in any of the *Odontophora*. Almost all Lamellibranchs, lastly, have a pair of lamellar gills on each side of the body, and all are provided with auriculate hearts. No doubt the *Odontophora* and the *Lamellibranchiata* properly form parts of one and the same sub-kingdom, MOLLUSCA, and the three classes which follow, viz., the *Ascidioida*, *Brachiopoda*, and *Polyzoa*, are usually included in the same sub-kingdom.

But the difficulty of framing a definition which shall include the last-named classes with the *Lamellibranchiata* and *Odontophora* is almost as great as in the parallel case of the *Annuloida* and *Annulosa*; while, on the other hand, the Ascidians, Brachiopods, and *Polyzoa* exhibit many features in common. Thus the nervous system is greatly simplified in all three classes, consisting, in the *Ascidioida* and *Polyzoa*, of a single ganglion, sending perhaps a commissural cord round the gullet. In the *Brachiopoda* the chief ganglia, which appear to be the homologues of the pedal ganglia of the higher mollusks, and are connected by a circum-œsophageal cord, are combined with accessory ganglia, but these do not seem to be identifiable with the pedal or the parieto-splanchnic ganglia.

Again, the fact that the heart, when present, is of a simple tubular, or saccular, character, and is devoid of any separation into auricle and ventricle, constitutes a wide difference between these three classes and the higher Mollusks. On the other hand, these classes, which may be conveniently denominated MOLLUSCOIDA, resemble one another in the fact (so far as I am aware there is only one exception, *Appendicularia*) that the mouth is provided with ciliated tentacula, disposed in a circle, or in a horse-shoe shape, or fringing long arms; that it leads into a large, and sometimes an exceedingly large, pharynx; and that in two of the three, at least, that system of cavities communicating with the exterior, which has been called the "atrial system," is greatly developed.

I cannot doubt, then, that the *Molluscoida* form a natural assemblage; but, until the precise characters, if any exist, which unite them with the *Mollusca* proper can be clearly defined, I am inclined to think it might be better, as in the case of the *Annuloida*, to recognise them as a separate division of the Animal Kingdom.

The next two classes—the *Actinozoa* and the *Hydrozoa*—constitute one of the most natural divisions of the Animal Kingdom—the CŒLENTERATA of Frey and Leuckart. In all these animals, the substance of the body is differentiated into those histological elements which have been termed cells, and the latter are primarily disposed in two layers, an external and an internal, constituting the "ectoderm" and "endoderm."

Among animals which possess this histological structure, the *Cœlenterata* stand alone, in having an alimentary canal, which is open at its inner end and communicates freely, by means of this aperture, with the general cavity of the body. In a large proportion of these animals the prehensile organs are hollow tentacles, disposed in a circle around the mouth, and all (unless the *Ctenophora* should prove to be a partial exception to the rule) are provided with very remarkable organs of offence and defence, termed "thread cells" or "nematocysts." These, when well exhibited, as, for example, by the common freshwater polype (*Hydra*), are oval, elastic sacs, containing a long coiled filament, barbed at its base, and serrated along the edges. When fully developed, the sacs are tensely filled with fluid, and the slightest touch is sufficient to cause the retroversion of the filament, which then projects beyond the sac for a distance, which is not uncommonly equal to many times the length of the latter. These fine filaments readily penetrate any delicate animal tissue with which they are brought into contact, and cause great irritation in the human skin when they are of large size. Nor can it be doubted that they exert a similarly noxious influence upon the aquatic animals which are seized by, and serve as prey to, the *Actinozoa* and *Hydrozoa*. Characteristic as these organs are of the Cœlenterates, however, it must not be imagined that they are absolutely peculiar to the sub-kingdom; for some nudibranchiate *Mollusca*, such as *Eolis*, are armed with similar weapons, and the integument of certain *Turbellaria*, and even of some *Infusoria*, is provided with bodies which seem to be of a not altogether dissimilar character.

No Cœlenterate possesses any circulatory organs, unless the cilia which line the general cavity of the body can be regarded as such; and a nervous system has, at present, been clearly made out only in the *Ctenophora*. Here its central mass occupies a position which is very unlike that in which the principal masses of the central nervous system are found in other invertebrate animals, being situated upon that side of the body which is diametrically opposed to the mouth.

Whatever extension our knowledge of the nervous apparatus of the Cœlenterates may, and not improbably will, receive from future investigators, the positive characters afforded by the histological features of their substance, and the free opening of their alimentary canal into the general cavity of the body, are such as to separate them, as a sub-kingdom, as sharply defined and devoid of transitional forms as that of the *Vertebrata*, from the rest of the Animal Kingdom.

Great difficulties stand in the way of any satisfactory grouping of the remaining classes, if we are determined to remain true to the principle that the definition of a group shall hold good of all members of that group, and not of any others,—a principle which lies at the foundation of all sound classification.

In possessing cilia, as locomotive and ingestive organs; in being provided with a contractile water receptacle with canals proceeding from it (in some cases at any rate) into the substance of the body; in their tendency to become encysted and assume a resting condition, the INFUSORIA undoubtedly exhibit analogies with the lower *Annuloida*, such as the *Turbellaria*, *Rotifera*, and *Trematoda*.

But the entire absence, so far as our present knowledge goes, of a nervous system, the abrupt termination of the gullet in a central semi-fluid sarcodic mass, and the very peculiar characters of the reproductive organs, of the *Infusoria*, separate them widely from the *Annuloida*, though it seems to me not improbable that the gap may hereafter be considerably diminished by observation of the lower forms of *Turbellaria*.

At present the *Infusoria* are usually regarded as forming part of the same sub-kingdom as the *Spongida*, *Rhizopoda*, and *Gregarinida*, and as closely allied to them. But, so far as I am aware, no definition can be framed which will yield characters at once common to, and distinctive of, all these four groups; while recent discoveries tend to widen so greatly the hiatus between the *Infusoria* and the other three classes, that I greatly doubt if the sub-kingdom PROTOZOA can be retained in its old sense.

But if the *Infusoria* be excluded from it, the remaining groups, notwithstanding the imperfection of our knowledge regarding some of them, exhibit a considerable community of partly negative and partly positive characters.

The *Spongida*, *Rhizopoda*, and *Gregarinida*, in fact, are all devoid of any definite oral aperture; a considerable extent, and sometimes the whole, of the outer surface of the body acting as an ingestive apparatus. Furthermore, the bodies of these animals, or the constituent particles of the compound aggregations, such as the Sponges, exhibit incessant changes of form—the body wall being pushed out at one point and drawn in at another—to such an extent, in some cases, as to give rise to long lobate, or filamentous, processes, which are termed "pseudopodia."

Finally, all these classes agree in the absence of any well-defined organs of reproduction, innervation, or blood circulation.

In my first lecture upon Classification, I passed very briefly over the class *Rhizopoda*, intending to return to the discussion of its limits, and of the value of its subdivisions, when discussing the subdivisions of classes generally. But as time will not permit me to enter at any length upon the greater part of this branch of my subject, I will content myself with briefly stating the conclusions at which I have arrived from a careful study of the extant literature of the subject, combined with some old investigations of my own.

It appears that three, or perhaps four, types of structure obtain among the *Rhizopoda*—

1st. That of the *Amœbæ*—Rhizopods with usually short pseudopodia, a nucleus, and a contractile vesicle.

2nd. That of the *Foraminifera*—Rhizopods devoid of nuclei and of contractile vesicles, and, for the most part, with long pseudopodia, which commonly run into one another and become reticulated.

3rd. That of the *Thalassicollæ*, provided with structureless cysts containing cellular elements and sarcode, and surrounded by a layer of sarcode, giving off pseudopodia, which commonly stand out like rays, but may and do run into one another, and so form networks.

Fig. 38.

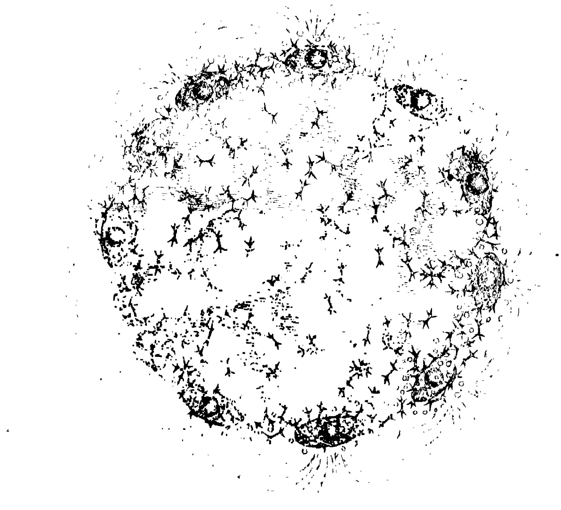


Fig. 38.—*Sphærozoum ovodimare* (after Haeckel), one of the *Thalassicollæ*.

While a fourth type of structure is probably furnished by those anomalous creatures, the *Acinetæ*, the radiating processes of which serve as suctorial tubes down which the juices of their prey are conveyed.

That the *Rhizopoda* are divisible into at least three groups, corresponding to the three first-mentioned types of organization, seems to me unquestionable; but it is another matter, and one on which I offer no opinion, what should be the exact limits of these groups, and what denominations we ought to employ for them. And it must be recollected that, so long as naturalists are unacquainted with the sexual method of reproduction of these animals, they are, to a certain extent, working in the dark.

In conclusion, I may sum up the results of this lecture by stating that, in the present state of our knowledge, the whole Animal Kingdom is divisible into eight primary categories or groups, no two of which are susceptible, in the present state of knowledge, of being defined by characters which shall be at once common and diagnostic.

These groups are the—

VERTEBRATA.

MOLLUSCA.	ANNULOSA.
MOLLUSCOIDA.	ANNULOIDA.
CŒLENTERATA.	INFUSORIA.

PROTOZOA.

I leave aside altogether the question of the equivalency of these groups; and, as I have already stated, I entertain some doubts regarding the permanency of one—the *Infusoria*—as a distinct primary division. Nor, in view of the many analogies between the *Mollusca* and the *Molluscoida*, the *Annulosa* and the *Annuloida*, do I think it very improbable that, hereafter, some common and distinctive characters may possibly be discovered which shall unite these pairs respectively. But the discoveries which shall effect this simplification have not yet been made, and our classification should express not anticipations, but facts.

I have not thought it necessary or expedient, thus far, to enter into any criticism of the views of other naturalists, or to point out in what respect I have departed from my own earlier opinions. But Cuvier's system of classification has taken such deep root, and is so widely used, that I feel bound, in conclusion, to point out how far the present attempt to express in a condensed form the general results of comparative anatomy departs from that embodied in the opening pages of the "Régne Animal."

The departure is very nearly in the ratio of the progress of knowledge since Cuvier's time. The limits of the highest group, and of the more highly organized classes of the lower divisions, with which he was so well acquainted, remain as he left them; while the lower groups, of which he knew least, and which he threw into one great heterogenous assemblage,—the *Radiata*,—have been altogether remodelled and rearranged. Milne-Edwards demonstrated the necessity of removing the *Polyzoa* from the radiate mob, and associating them with the lower Mollusks. Frey and Leuckart demonstrated the sub-regnal distinctness of the *Cœlenterata*. Von Siebold and his school separated the *Protozoa*, and others have completed the work of disintegration by erecting the *Scolecida* into a primary division, of *Vermes*, and making the *Echinodermata* into another. Whatever form the classification of the Animal Kingdom may eventually take, the Cuvierian *Radiata* is, in my judgment, effectually abolished: but the term is still so frequently used, that I have marked out those classes of which it consisted in the diagram of the Animal Kingdom (p. 6), so that you may not be at a loss to understand the sense in which it is employed.

LECTURE VI.

ON THE CLASSIFICATION OF ANIMALS.

THE SUBDIVISIONS OF THE MAMMALIA LARGER THAN ORDERS.

In my last lecture I endeavoured to point out the grounds upon which naturalists have arrived at the conclusion that the classes of the Animal Kingdom may be arranged together in larger groups or divisions, such as have been termed "provinces" and "sub-kingdoms." If the time at my disposal for the consideration of Classification permitted me to do so, I should now, in the logical order of my discourse, take the opposite course; and turning again to the list of classes, I should endeavour to indicate in what manner they must be subdivided into sub-classes, orders, and lesser divisions. But it is needless to say that such a task as this would require many lectures, while I have only one to dispose of; and I propose to devote that one to a consideration of the classification of that class, which is in many respects the most interesting and the most important of any in the Animal Kingdom,—the class Mammalia.

A great many systems of classification of the *Mammalia* have been proposed, but, as any one may imagine from the nature of the case, only those which have been published within the last forty or fifty years, or since our knowledge of the anatomy of these animals has approached completeness, have now any scientific standing-ground. I do not propose to go into the history of those older systems, which laboured more or less under the disqualification of being based upon imperfect knowledge, but I shall direct your attention at once to that important step towards dividing the *Mammalia* into large groups, which was taken by the eminent French anatomist, M. de Blainville, so far back as the year 1816. M. de Blainville pointed out that the *Mammalia* might be divided into three primary groups, according to the character of their reproductive organs, especially the reproductive organs of the female. He divided them into "Ornithodelphes," "Didelphes," "Monodelphes;" or, as we might term them, ORNITHODELPHIA, DIDELPHIA, MONODELPHIA. Now, I do not mean to assert that M. de Blainville defined these different groups in a manner altogether satisfactory, or strictly in accordance with all the subsequently discovered facts of science, but his great knowledge and acute intuition led him to perceive that the groups thus named were truly natural divisions of the *Mammalia.* And the enlargement of our knowledge by subsequent investigation seems to me, in the main, only to have confirmed De Blainville's views.

The division of the ORNITHODELPHIA comprises those two remarkable genera of Mammals, as isolated in geographical distribution as in structure,—*Ornithorhynchus* and *Echidna*,—which constitute the order *Monotremata.*

In these animals the angle of the lower jaw is not inflected, and the jaws are devoid of true teeth, one of the two genera only (*Ornithorhynchus*) possessing horny plates in the place of teeth. The coracoid bone extends from the scapula to the sternum, with which it is articulated, as in birds and most reptiles, and, as in many of the latter, there is an episternal bone. There is no marsupial pouch, though bones wrongly termed "marsupial" are connected with the pelvis. But it is to the structure of the female reproductive organs that the *Ornithodelphia* owe their name. The oviducts, enlarged below into uterine pouches, but opening separately from one another, as in oviparous vertebrates, debouch, not into a distinct vagina, but into a cloacal chamber, common to the urinary and genital products and to the fæces. The testes of the male are abdominal in position throughout life, and the vasa deferentia open into the cloaca, and not into a distinct urethral passage. The penis is indeed traversed by an urethral canal, but it is open and interrupted at the root of that organ. In both sexes, the ureters pour the renal secretion, not into the bladder, which is connected with the upper extremity of the cloaca, but into the latter cavity itself.

In the brain, the *corpus callosum* is inconspicuous, though the question how far it can properly be said to be absent requires much more thorough investigation than it has yet received.* We are but very imperfectly acquainted with the reproductive processes of these animals, but it is asserted that the young are devoid of a placenta. The mammary gland has no nipple.

Like the *Ornithodelphia*, the division DIDELPHIA contains but a single order, the *Marsupialia*, the great majority of which, like the *Ornithodelphia*, inhabit Australia. They almost all have the angle of the lower jaw inflected, and all possess true teeth. The coracoid is, as in the higher Mammals, anchylosed with the scapula, and is not articulated with the sternum. All have the so-called "marsupial" bones or cartilages—ossifications, or chondrifications, of the internal tendon of the external oblique muscle of the abdomen—and the females of almost all possess a fold of the skin of the abdomen above the pubis, constituting a "*marsupium*," or pouch, within which the young are nourished and protected in their early, helpless condition.

The oviducts open into vaginæ, which are more or less completely divided into two separate passages. The testes of the

* For a number of years I have entertained the gravest doubts respecting the accuracy of the doctrine put forth now nearly thirty years ago by Professor Owen, and almost universally received, that the *corpus callosum* is absent in Monotremes and Marsupials, and at one time I began to collect materials for the thorough investigation of the question; but other occupations intervened, and the plan was never carried out. Nevertheless, I have always expressed myself cautiously on this subject, and, as the text shows, I was particularly guarded when delivering the present lecture. At that time, in fact, I was well aware that my friend Mr. Flower had commenced a series of inquiries into the question, and such results as he had then obtained tended greatly to the increase of my scepticism. Mr. Flower has since been good enough to go carefully with me over the large series of drawings and preparations which he has made; and I am prepared to express my entire concurrence in his conclusion that the *corpus callosum* exists, distinctly developed, though not so well as in monodelphous, or placental, Mammals, in both the *Didelphia* and the *Ornithodelphia*.

males are lodged in a scrotum, which is suspended in front of the penis; and the vasa deferentia open into a complete and continuous urethra, which is also the passage by which the urine escapes from the bladder, and is perfectly distinct from the passage for the fæces, though the anus and the termination of the urethro-sexual canal are embraced by the same sphincter.

The corpus callosum is comparatively small, as in the *Ornithodelphia.*

It is stated that the allantois of the embryo is arrested in its development, and gives rise to no placenta. The umbilical sac is said to acquire a large proportional size; but whether it plays the part of a placenta for the short period of intra-uterine life, or not, is unknown.

The young are born of very small size, and in a singularly imperfect condition; but being transferred to the marsupium, and becoming attached to a long nipple, they are supplied with milk until they are able to provide for themselves—the milk being, at first, forced into their mouths by the action of a muscle spread over the mammary gland.

In the MONODELPHIA, the angle of the lower jaw is not inflected, and they may or may not be provided with teeth. They never possess "marsupial" bones. The uterine dilatation of the oviducts is always considerable, and whether they have common or distinct apertures, the vagina is a single tube, though it may be partially divided by a septum. The testes may vary much in position; but, if they are lodged in a scrotal pouch, it is never pendulous by a narrow neck in front of the penis, as in the *Didelphia.*

The urinary bladder opens into a distinct urethra, which, directly or indirectly, receives the vasa deferentia in the male.

The corpus callosum is very variable in its development, commonly attaining a much larger size than in the preceding groups; the optic lobes are divided into four portions.

The young are nourished within the uterus until such time as they are competent to suck milk from the teats of the parent, to which end the chorion always develops processes or villi, which are well supplied with vessels brought to them by the allantois. These processes becoming interlaced more or less closely with corresponding vascular developments of the wall of the uterus (and so forming a "placenta"), an interchange of constituents takes place between the fœtal and the maternal blood, through the separating walls of the fœtal and maternal vessels. In this manner, throughout its prolonged intra-uterine life, the Monodelphian fœtus is supplied with nourishment and gets rid of its effete products.

As the three groups instituted by De Blainville are capable of being thus clearly differentiated one from the other, the distinctions between them having been only more and more clearly brought out by the subsequent progress of knowledge, I can see no ground for refusing to adopt his classification, or for denying him that credit to which he is fairly entitled for apprehending these distinctions. Certainly, the later proposition, to divide Mammals into two great groups only, *Placentalia* and *Implacentalia*, cannot be regarded as any improvement upon De Blainville's system, as it ignores the important fact that the

Fig. 39.

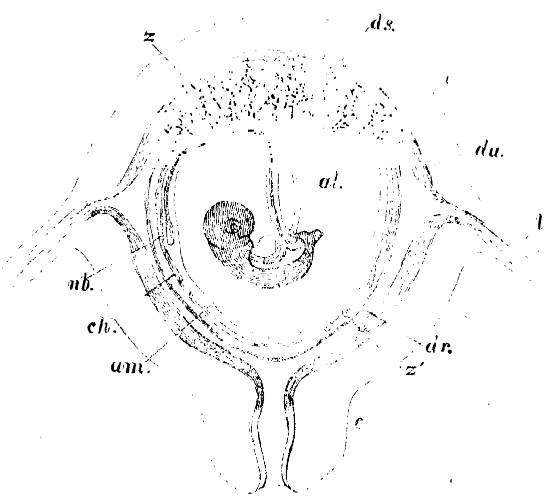


Fig. 39.—Diagrammatic section of a human pregnant uterus, with the contained ovum (Longet). *u*, uterus; *l*, oviduct; *c*, cervix uteri; *du*, decidua uteri; *dr*, decidua reflexa; *ds*, decidua serotina; *ch*, chorion; *am*, amnion; *al*, allantois; *nb*, umbilical vesicle; *z*, villi which form the fœtal part of the placenta; *z'*, villi over the rest of the chorion, which take no part in the placental function in man.

two divisions of the *Implacentalia* are separated by characters of fully as great importance as those which distinguish the *Placentalia* and *Implacentalia*.

But whether the *Ornithodelphia* and the *Didelphia* are regarded (as I believe they ought to be) as two of the three primary separate "sub-classes" of the class *Mammalia*, or whether they are looked upon only as subdivisions of the *Implacentalia*, there is no doubt that they are, and will remain, distinct natural assemblages, the subdivisions of which present no very great difficulties.

It is otherwise with the sub-class *Monodelphia*—which contains at least a dozen orders, the arrangement of which into groups, not only in detail, but in principle, is, and long has been, a subject of much difficulty, and consequently of controversy.

Sir Everard Home* is commonly quoted as the originator of one of the two systems of classification in vogue at the present day; but his vague statements and confused notions respecting the varying characters of the placenta of the *Monodelphia* hardly entitle him to that honour, which, in my opinion, belongs rather to that eminent man, Karl Ernst von Baer, of whom it can be truly said that he has touched no subject without throwing a flood of light upon it. Towards the end of his famous essay, "Untersuchungen über die Gefäsverbindung zwischen Mutter und Frucht," published in 1828, the following passage occurs:—

"In the first place, I have taken pains to show that the ova of mammals are only variations of a single type; and if we except the ova of the Marsupials, concerning which I can form no judgment, all consist of the same parts; all have a placenta; and, in all, some portion of the chorion is smooth. The fœtal placenta consists everywhere of the same elements, but offers the most remarkable differences in its external disposition. It is either—

1. Merely applied to the maternal placenta, and
   (*a*) continuous and zone-like. *First form.*
   (*b*) divided into many parts. *Second form.*

* "Comparative Anatomy," vol. iii.

Or 2. It and the maternal placenta grow together, and they lie,

(*a*) in a zone round the egg. *Third form.*
(*b*) at one end of it. *Fourth form.*

These differences, however, are developed gradually, and, at first, are less marked."

The *first form*, described in the text of the work, is that met with in the pig. It is what is now commonly termed a *diffused placenta;* but Von Baer, more accurate than most of his successors, indicates the confinement of the placental villi to the middle of the chorion—its prolonged poles remaining bare—by the term "gürtelförmig," zone-like. The *second form* is that exemplified by the cow and sheep, the *cotyledonary placenta.* The third is the carnivorous placenta, termed *zonular.* The fourth is the placenta of man, called now-a-days *discoidal.*

The most important circumstance pointed out by Von Baer, however, is one which has been greatly overlooked, if not wholly ignored, in subsequent discussions—the fact that the differences in the *form* of mammalian placentæ are subsidiary if compared with their differences in *structure*, more particularly in regard to the extent to which a maternal element enters into their composition.

Eschricht, in the admirable memoir, "De Organis quæ Respirationi et Nutritioni Fœtus Mammalium inserviunt," which he published in 1837, repeats the ideas of Von Baer, apparently without being aware of the fact, and enlarges upon them as follows (p. 30):—

"Restat, ut succinctam expositionem Mammalium afferamus secundum varias quæ in iis observantur, placentæ formas.

"A ceteris omnibus mammalibus Marsupialia et Monotremata separanda sunt, quibus nulla est placenta. Cætera omnia in duas familias dividenda, quarum alteri placenta uterina caduca, alteri non caduca est. Huic Mammalia primata et ungulata omnia adnumeranda sunt, inter quæ Ruminantia ob singularem cotyledorum formam cæteris opponi possunt.

"In mammalibus placentam uterinam caducam habentibus tres mihi occurrere videntur placentæ typi, quorum primus gliribus, secundus feris, tertius simiis et homini proprius est."

In this passage Mammals are clearly divided, in the first place, into placental and implacental; and the former are then subdivided into those which have a non-caducous and those which have a caducous uterine placenta. The *Cetacea* and Ungulate Mammals constitute the former group; the Rodents, Carnivores, Apes, and Men the latter.

In 1843, an accomplished English zoologist, Mr. Waterhouse, published a highly instructive paper on the "Classification of the Mammalia,"* in which the following passage occurs:—

"Taking the general form of the Brain into consideration, the placental Mammalia would appear divisible into two sections: first, those in which the cerebrum is generally of a rounded form, obtuse in front and provided with distinct convolutions; and secondly, those in which the cerebrum is destitute of convolutions, or nearly so, and usually contracted in front. The first division would contain the *Quadrumana*, *Carnivora*, *Cetacea*, *Pachydermata*, and *Ruminantia*, and the second would contain the *Cheiroptera*, *Insectivora*, *Edentata*, and *Rodentia*."

But although Mr. Waterhouse puts forward thus clearly the facts upon which a cerebral classification of the *Mammalia* might be based, he immediately afterwards, with his customary judgment, expresses great doubt as to the value of any such classification.

"But are we in a condition to take for a basis of classification of the *Mammalia* the structure of the brain? I think not, though, in the case of the *Marsupialia*, it has afforded characters serving to separate that from other sections, and to indicate its proper position in the system. I am not prepared to follow those naturalists who would, in the present state of information, take this organ as one of primary importance in the distribution of the orders of the placental series of Mammals. I cannot adopt the two great sections of this series as apparently

* "Annals and Magazine of Natural History," 1843, vol. xii. p. 399.

indicated by the smooth and anteriorly contracted cerebrum on the one hand, and the convoluted cerebrum, with its rounded anterior portion, on the other. Were I to do so, I should find it necessary to remove some of the Lemurs from their group in the highest order of the first section, and to place them in the second section."

In the succeeding year, 1841, M. Milne-Edwards, one of the most distinguished physiologists and zoologists of modern France, proposed, in a highly philosophical paper upon zoological classification in general,* a method of subdividing the *Mammalia*, essentially similar to that put forward incidentally by Von Baer and Eschricht, but lacking, as I conceive, what is the great merit of the latter writers, namely, the clear perception of the classificatory value of the intimate structure of the placenta and the entrance, or not, of a decidual uterine element into its composition. M. Milne-Edwards dwells with great force (as Mr. Waterhouse had previously done) upon the closeness of the general structural affinities which unite the *Rodentia*, *Insectivora*, *Cheiroptera*, *Quadrumana*, and *Bimana* of Cuvier together, and shows that these affinities are denoted by the discoid placenta which they possess in common.

The diffused placenta (under which head the cotyledonary placenta is included) is stated to be the characteristic of the *Ruminantia*, *Pachydermata*, *Edentata*, and *Cetacea;* while, lastly, the "*Carnivora* and seals (*Amphibies*) are distinguished from all the rest by their zonular placenta."

The singular genus *Hyrax*, which Cuvier endeavoured to prove to be a true Pachyderm, is considered by M. Milne-Edwards to form one of the series of Mammals with a zonular placenta; and to represent, in that series, the Pachyderms in the series with diffuse placentation, and the Rodents, in the series with discoidal placentation.

M. Gervais, in France, and M. Vogt, in Germany, have adopted the placental classification of Milne-Edwards; while, in 1857, Mr. Waterhouse's proposed, but immediately rejected, cerebral classification was substantially revived by Professor

* "Annales des Sciences naturelles." Série 3. Tome 1. "Considérations sur quelques Principes relatifs à la Classification naturelle des Animaux."

Owen, in his paper "On the Characters, Principles of Division, and Primary Groups of the class Mammalia," published in the Journal of the Linnæan Society; though it should be added that Professor Owen made certain additions to the nucleus furnished by Mr. Waterhouse, which are unquestionably original.

Thus the "*Lissencephala*" of Professor Owen is simply a new name for the group of Mammals ("in which the cerebrum is destitute of convolutions, or nearly so") indicated by Mr. Waterhouse; and "*Gyrencephala*" is a like verbal equivalent for Mr. Waterhouse's group of Mammals characterised by having the brain provided with distinct convolutions. But Mr. Waterhouse does not mention Man at all, while Professor Owen creates a new sub-class, *Archencephala*, for the genus *Homo*, and substitutes the name "*Lyencephala*" for *Implacentalia*, formerly applied to the *Ornithodelphia* and *Didelphia*.

In attempting to decide between the various classifications thus presented to us, the canons by which our judgment must be guided are simple enough. It is obvious, in the first place, that the definition of a group, whether that definition be based on cerebral or on placental characters, must be true, as a matter of fact, if any value is to be attached to the classification of which that definition forms a part.

And, in the second place, it is clear that the definition of each group must be distinctive, that is to say, it must not include the members of other groups.

Applying the second canon to the classification last mentioned, it appears to me to collapse at once.

The sub-class *Lissencephala*, for example, is thus defined:—

"The corpus callosum is present, but connects cerebral hemispheres as little advanced in bulk or outward character as in the preceding sub-class; the cerebrum leaving both the olfactory lobes and cerebellum exposed, and being commonly smooth, or with few and simple convolutions in a very small proportion, composed of the largest members of the group. The Mammals so characterised constitute the sub-class *Lissencephala*."—*L. c.*, p. 14.

On the other hand, the sub-class *Gyrencephala* receives the following definition:—

"The third leading modification of the Mammalian cerebrum is such an increase in its relative size, that it extends over more or less of the cerebellum, and generally more or less over the olfactory lobes. Save in very few exceptional cases of the smaller and inferior forms of the *Quadrumana*, the superficies are folded into more or less numerous gyri, or convolutions, whence the name *Gyrencephala*, which I propose for the third sub-class of *Mammalia*."—*L. c.*, p. 18.

I am quite unable to see what these so-called definitions define. If, for example, we place the brains of an Ant-eater, or of a Capybara, side by side with that of a Genett—the two former being *Lissencephala*, the latter one of the *Gyrencephala*—either "definition" will apply equally well to either of the three brains. All three have slightly convoluted brains; in all three the olfactory lobes and cerebellum are more or less uncovered; and nothing in the definitions of the sub-classes of this "cerebral classification" would enable an anatomist to say that any one of these three brains belonged to one sub-class rather than another.

Since Mr. Waterhouse pointed out the fact, no one has doubted that, as a general rule, the brains of the so-called "*Gyrencephala*" are more convoluted, size for size, than those of the "*Lissencephala*;" and the relations of the size and the zoological position of an animal to the characters of its cerebral surface have long since been well discussed by Gratiolet, Dareste, and others. But it is exactly because the rule is only a general one, and has many exceptions, that the degree of cerebral convolution must be rejected as the basis of the definition of any large group of Mammals.

Thus far, we meet, in Professor Owen's definitions, with a certain foundation in fact, though it may not be such as is fitted to afford ground for classification: but the group "*Archencephala*" is in a more unfortunate position. Our first canon comes into operation, and we must reject it, because the statements respecting matters of fact in its definition are untrue. The words stand thus:—

"In man the brain presents an ascensive step in development, higher and more strongly marked than that by which the preceding sub-class was distinguished from the one below it. Not only do the cerebral hemispheres overlap the olfactory lobes and cerebellum, but they extend in advance of the one and further back than the other. Their posterior development is so marked, that anatomists have assigned to that part the character of a third lobe; it is peculiar to the genus *Homo,* and equally peculiar is the 'posterior horn of the lateral ventricle,' and the 'hippocampus minor,' which characterises the hind lobe of each hemisphere."—*L. c.*, pp. 19, 20.

These are the assertions which have been repeated over and over again during the last few years; but, thanks to the exertions of the able Conservator of your Museum, it is in my power to lay before you visible and tangible facts, which prove these assertions to be wholly devoid of foundation.

The third lobe, characterised by extending further back than the cerebellum, is said to be "*peculiar to the genus Homo.*"

I place before you casts of the cranial cavity, accurately representing the relative positions of the parts of the brain of a Gorilla, of a Chimpanzee, of an Orang, of a *Cynocephalus;* and you observe that the posterior, or third lobe, of each projects further back than the cerebellum, in just the same sense as a man's can be said to do so; and in some cases, as in the baboon, to a much greater extent.

The assertion that the third lobe, as defined by Professor Owen, is "peculiar to man," is therefore demonstrably contrary to fact.

"*Equally peculiar is the posterior horn of the lateral ventricle.*"

Side by side upon the table are two dissections, made in the same way, the one of the brain of an Orang-utan, the other that of a man, taken at hazard by Mr. Flower, who has been good enough to dissect both (Fig. 40).

Every one in this theatre, I imagine, can see perfectly well that the Orang has a posterior cornu, which, in proportion to the size of its brain, is just as long and nearly as much incurved as that of the man, while it is a good deal wider at its commencement.

Fig. 40.

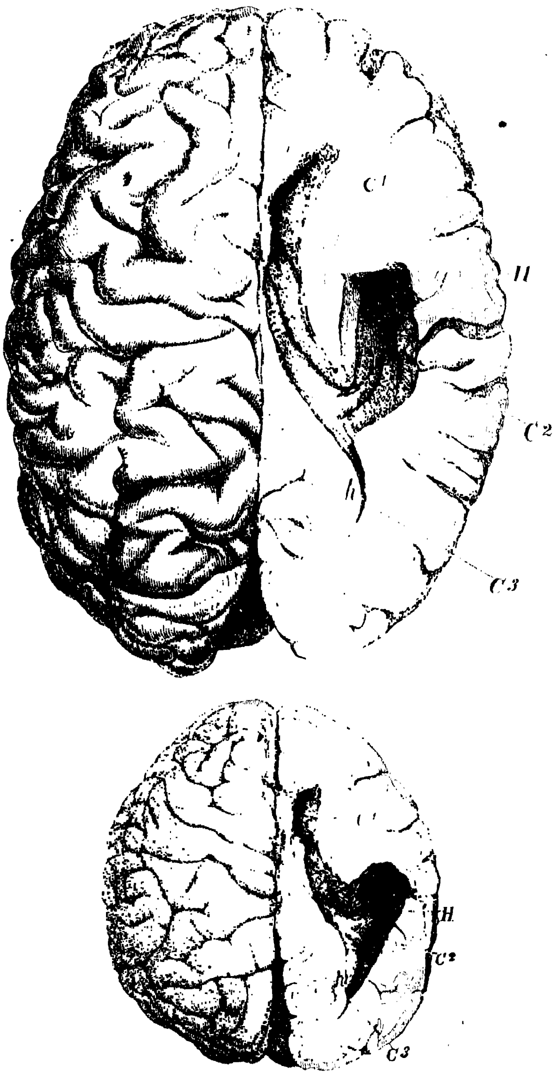


Fig. 40.—Figures [reduced to the same scale] of the dissected brains of a Man and of an Orang which were exhibited in the theatre of the Royal College of Surgeons.—C^1, anterior cornu; C^2, descending cornu; C^3, posterior cornu; *H*, hippocampus major; *h*, hippocampus minor.

In fact, even if the posterior cornu had not been demonstrated (as it has now been) in the brain of numerous genera of Apes, this one example would sufficiently demonstrate the assertion, that the posterior cornu is "peculiar to the genus *Homo*," to be simply untrue.

Lastly, as regards the hippocampus minor—which is also said to be "peculiar to man"—that structure is, as you perceive, as distinct in the Orang's as in the man's brain, so that the third term of the definition of the "*Archencephala*" is as contradictory to plain fact as the other two (Fig. 40).

Even were the posterior lobe, the posterior cornu, and the hippocampus minor peculiar to man, as supposed by the definer of the sub-class "*Archencephala*," instead of being, as they really are, structures far better developed in some of the lower apes than in him, their classificatory value would be extremely doubtful, seeing that they are among the most variable of structures in the human brain. The casts upon the table of a Tartar's and of an Australian brain-case will demonstrate to you how insignificant may be the projection of the posterior lobe in one man and how great it may be in another. While the practical anatomists and demonstrators whom I address will be familiar with the singular variability of the posterior cornu and the hippocampus minor—structures which, without any assignable cause, or noticeable modification of the structure, or of the functions, of the brain, may present every degree of development, from absence to great size.

So little, indeed, is any zoological value to be attached to such a character as the degree of projection of the posterior lobe, that closely allied apes present us with most singular differences in this respect. Thus the group of South American monkeys which comprises the Squirrel monkey (*Chrysothrix*), the posterior lobes of whose brain project beyond the cerebellum far more than they do in man, contains also the Howling monkey (Mycetes), in which the posterior lobes cannot be said to project at all. And within the last two days, Mr. Flower has discovered (and the cast upon the table enables me to demonstrate the fact to you) that in, at any rate, one species of Gibbon, the Siamang (*Hylobates Syndactylus*) the cerebellum projects behind the posterior lobes, while, in the three other genera of anthropoid apes, the posterior lobes of the cerebrum project behind the cerebellum.*

The latest form of the "cerebral" classification of the *Mammalia* having thus been shown to be devoid of any sound foundation, I proceed to inquire whether the "placental" classification does, or does not, stand upon a more secure basis, if we take, not merely, with Milne-Edwards, the form of the placenta, but with Von Baer and Eschricht, its structure, into account. It is a well-established fact that two very distinct types of placenta are to be met with in the *Monodelphia*, and that, at the present moment, we have no knowledge of any transitional forms between these two types. The first of these types is that exhibited by the human placenta, the second by that of the pig or horse.

From the commencement of gestation, the superficial substance of the mucous membrane of the human uterus undergoes a rapid growth and textural modification, becoming converted into the so-called "*decidua*." While the ovum is yet small, this *decidua* is separable into three portions,—the *decidua vera*, which lines the general cavity of the uterus; the *decidua reflexa*, which immediately invests the ovum; and the *decidua serotina*, a layer of especial thickness, developed in contiguity with those chorionic villi which persist and become converted into the fœtal placenta. The *decidua reflexa* may be regarded as an outgrowth of the *decidua vera*; the *decidua serotina* as a special development of a part of the *decidua vera*. At first, the villi of the chorion are loosely implanted into corresponding depressions of the *decidua*; but, eventually, the chorionic part of the placenta becomes closely united with, and bound to, the uterine decidua, so that the fœtal and maternal structures form one inseparable mass.

In the meanwhile, the deeper substance of the uterine

* See Mr. Flower's paper "On the Brain of the Siamang," *Natural History Review*, April, 1863. "This peculiarity of the Siamang's brain is due to two causes—firstly, the large development of the cerebellum; secondly, and I shall afterwards show, mainly, to the actual shortness of the posterior or occipital lobe of the cerebrum."—*L. c.*, p. 282.

mucous membrane, in the region of the placenta, is traversed by numerous arterial and venous trunks, which carry the blood to and from the placenta; and the layer of decidua into which the chorionic villi do not penetrate acquires a cavernous, or cellular, structure from becoming burrowed, as it were, by the innumerable sinuses into which these arterial and venous trunks

Fig. 41.

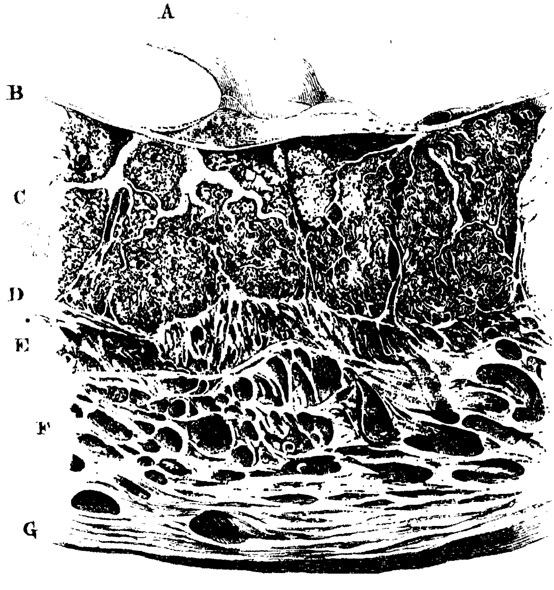


Fig. 41.—Section of the Human Uterus and Placenta at the thirtieth week of pregnancy. (After Ecker.)—A, umbilical cord; B, chorion; C, the fœtal villi separated by processes of; D, cavernous *decidua*; E, F, G, wall of the uterus.

open. In the process of parturition, the *decidua serotina* splits through this cellular layer, and the superficial part of it comes away with the umbilical cord, together with the fœtal membranes and the rest of the *decidua;* while the deeper layer, undergoing fatty degeneration and resolution, is more or less completely brought away with the *lochia*, and gives place to a new mucous membrane, which is developed throughout the rest of the uterus, during pregnancy; but, possibly, arises only after delivery over the placental area.

In the Pig the placenta is an infinitely simpler structure.

No "*decidua*" is developed; the elevations and depressions of the unimpregnated uterus simply acquire a greater size and vascularity during pregnancy, and cohere closely with the chorionic villi, which do not become restricted to one spot, but are developed from all parts of the chorion, except its poles, and remain persistent in the broad zone thus formed throughout fœtal life. The cohesion of the fœtal and maternal placentæ, however, is overcome by slight maceration or post-mortem change; and, at parturition, the fœtal villi are simply drawn out, like fingers from a glove, no vascular substance of the mother being thrown off.

The process by which the mucous membrane of the uterus returns to its unimpregnated condition after parturition in the pig has not been traced.

The extreme cases of placentation exhibited by man and by the Pig may be termed, with Von Baer and Eschricht, from the character of the maternal placenta, "caducous" and "non-caducous," or, from the degree of cohesion of the two placentæ in parturition, "coherent" and "incoherent;" or, what perhaps would be better still, the two Mammals may be spoken of as "deciduate" and "non-deciduate."* But, whatever terms be employed, the question for the classifier is to inquire what mammals correspond with Man and what with the Pig, and whether the groups of deciduate and non-deciduate *Monodelphia* thus formed, are natural groups, or, in other words, contain such orders as can be shown, on other grounds, to be affined.

With respect to the deciduate *Monodelphia*, it is certain that the apes agree, in the main, with man in placental, as in other important characters; and, so far as has hitherto been observed (though our knowledge of the placentation of the Lemurs is very defective), their placentæ differ from those of Man only in presenting a more marked lobation—a character which occurs as a variety in Man.

* It is, of course, by no means intended to suggest by these terms, that the homologue of the *decidua* does not exist in the "non-deciduate" Mammals. The mucous membrane of the uterus becomes hypertrophied during pregnancy in both the deciduate and the non-deciduate Mammals; but it is thrown off, and so gives rise to a "*decidua*" only in the one of these two groups.

The *Cheiroptera*, *Insectivora*, and *Rodentia* agree with Man in possessing a placenta which is not only as much "discoidal," allowance being made for the shorter curve of the uterine walls, as his, but also entirely resembles his in being developed in conjunction with a decidua. This *decidua* always corresponds to at least the *decidua serotina* of Man; frequently there is a well-developed *decidua reflexa*.* How far a *decidua vera* can be said to be developed is doubtful.

I am well aware that these statements are in direct opposition to some that have been very confidently put forward. Thus, Professor Owen, in arguing against the views entertained by Milne-Edwards and Gervais, makes the following assertions:—

"The degree of resemblance in outward form between the placenta of the Rat or Hare, on the one hand, and the *Mycetes* and *Macacus* on the other, seems to me to be more than counterbalanced by the difference of structure. *The pedunculate and cotyloid placenta of the Rat consists of fœtal parts exclu-*

Fig. 42.

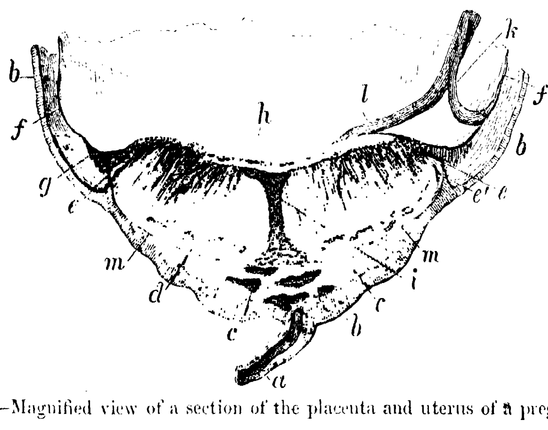


Fig. 42.—Magnified view of a section of the placenta and uterus of a pregnant Rat.

sively; the maternal areolar portion is as distinct from it as it is in the cotyledon of the Ruminant, and is a persistent structure of

* See upon this subject the recently-published valuable essay of Reichert: "Beiträge zur Entwickelungs-geschichte des Meerschweinchens." Reichert finds a complete, or almost complete, *decidua reflexa* in Rats, Mice, Guinea-pigs, and Bats; while in Rabbits, Hares, and *Carnivora*, the *decidua reflexa* only partially surrounds the ovum.

the uterus. The discoid placenta of the monkey includes a large proportion of maternal cellular structure, which comes away with the fœtal portion. The difference in the organic interblending of the circulatory organs of mother and offspring, between the *Rodentia* and *Quadrumana*, is of much more real importance than the degree of superficial similarity."—*L. c.*, p. 16, note.

Led by the extraordinary contradictions of some of the best-known facts of embryology* contained in the passage

* Eschricht described the placenta of the Rat with great precision, as the following extract will show, six-and-twenty years ago. Is it possible that a hasty perusal of a passage which I have put into italics below should have misled any of his successors into supposing that Rodents have persistent cotyledons like those of Ruminants?—"Placenta fere circularis erat; diametrus longior sex lineas cum dimidia explebat, brevior sex lineas. Superficies ovo obversa nonnihil concava erat, externa autem sat convexa, ita ut a margine ad centrum sensim in tumulum surgeret et crassitudinem placentæ ad duas lineas augeret. In superficie ejus concava, ovo obversa, tres distingui potuerunt regiones; circum centrum, a vasis umbilicalibus perforatum, laminulâ illâ pertenui obtecta erat, quam vasa umbilicalia hic circumdare jam observatum est. Circa peripheriam scabrosa apparuit, quasi fila seu vasa abrupta fuissent, in media regione autem inter periphericam et centralem lævis erat tunicâ sat distinctâ vestita. Superficies placentæ externa convexa duas regiones obtulit. Peripheriæ propior inæqualis ad axem longitudinalem ovi latior erat, unam et quartam lineæ partem explens; ad latera angustior quartam modo lineæ partem explens. Sic media et lævis hujus superficiei regio ovoidea quidem erat ut tota placenta, sed cum axe majore transverse ei insidens. In cumulo hujus superficiei permagnum vas ab utero centrum placentæ perforavit. Haud procul a centro quinque vasa minora intervallis sat æqualibus uterum cum placenta jungebant. Superficiei uterinæ proxima placentæ pars in lamellas facile dividebatur, profundior autem pars eundem illum laminarum innumerabilium contextum exhibuit quem in placenta felina fusius supra descripsi. Laminulas a centro ad peripheriam sat regulariter ordinatas esse observare mihi visus sum. Inter laminulas illas eandem esse alternationem laminularum fœtalium et uterinarum vix dubitare potui, præsertim quum non modo vasa umbilicalia sed ab altera parte sex vasa majora ab utero placentam ingredi vidissem. At uterum examinans nova orta est dubitatio. Uteri cornua antequam ova excisa fuissent, moniliformia apparuerunt, et inter singula ova fortiter constricta. Ita non modo numerus sed etiam forma ovorum extus apparuit quid quod etiam placentæ facillime observari videbantur. Intumescentiæ, ova includentes, ipsæ quidem oviformes erant, sed ad marginem superiorem ad insertionem ligamentorum latorum et ante eadem singulæ tumuli speciem præbebant, placentam aperte indicantis. Itaque placentæ in utero muris ratti non modo quoad fœtum, sed etiam quoad uterum certum occupat locum, et embryones omnes in una serie in oppositis uteri cornibus symmetrice collocati sunt, utrum autem capitibus præviis abdominibusque abdomen matris respicientibus, an clunibus præviis dorsisque abdomini matris obversis inquirere neglexi. Verum tumuli placentas indicantes non ipsæ fuerunt placentæ. Ovis excisis iidem tumuli in utero remanebant ut tubercula fusca tres lineas crassa, diametrum quinque linearum exhibentia. Quod quum

I have italicised to look into the matter afresh, I have found that the assertions made therein respecting the placenta of the Rat are as completely contrary to fact as are those respecting the brain of the apes which I have already cited from the same author.

Figure 42 represents a section of the uterus, chorion, and partially-injected placenta of a fœtal Rat, one inch and a quarter long, taken in a direction perpendicular to the long axis of the uterine cornu. *a* is the mesometrium traversed by a large uterine vein; *b* is the wall of the uterus becoming looser in texture and traversed by large venous channels in its inner substance, *c*; *d* is a decidual layer of the uterus of a cavernous structure, whence vascular processes are continued towards the chorionic surface of the placenta. A large vein (*i*) passes directly from the decidual layer (*d*), and the uterine sinuses beneath it, to near the chorionic surface of the placenta, beneath which it branches out horizontally. The chorion (*f*), rendered vascular over its non-placental part by the omphalomeseraic vessels (*k*), only begins to exhibit villous processes and folds at the point (*g*). These outermost villi appear to me to be free; but, more internally, they become closely connected with the upper surface of the placenta; and over the central third of the fœtal face of the placenta, the umbilical vessels (*l*) ramify in a radiating fashion, and send prolongations

observassem, initio tota mea de structura placentæ mammalium unguiculatorum sententia labefacta est. *Gliribus si ut ruminantibus pars uterina placentæ in partu non abstruderetur, mirum sane fuisset,* etsi theoria de placentæ structura in universum eo nihil caperet detrimenti. Quum vero superficiem uterinam placentæ lævem observassem, et idem de superficie ipsius uteri ei obversa nunc observarem, tota theoria pæne refelli mihi videbatur, secundum quam alternatio quædam utriusque systematis adsit necesse est. Attamen mox intellexi corpus illud uterinum non ipsam partem uterinam placentæ esse. Supra jam de vase majore centrali et quinque minoribus circumstantibus sermo erat, quæ placentæ superficiem uterinam transibant. Eadem vasa jam in ipsius uteri superficie observavam et in aperto erat ramificationem eorum in laminulis ipsius placentæ fieri. Corpus uterinum transcissum cellulas plurimas exhibuit, ni fallor, sanguinis coagulati nonnihil etiamtunc continentes. Sic constructum eidem functioni inservire mihi videtur ac similes uteri humani cellulæ vel sinus venosi; nec placentam murinam aliter a placenta felina discrepare video nisi quod vasa uterina pauciora sed sat magna partem uterinam intrant. Quibus observationibus ductus etiam GLIRIUM PLACENTAS EX PARTE FŒTALI ET UTERINA CADUCA HAC ET ILLA LAMINULIS INNUMERIS ALTERNANTIBUS COMPOSITAS ESSE putabo donec melioribus observationibus refutatus fuero."

down between the decidual lamellæ. The slightest traction exerted upon the cord causes the placenta to separate along the line *e, m, m, e*, bringing with it, of course, the cup-shaped *decidua, d.**

It is obvious, from the above description, that the "pedunculate and cotyloid" placenta of the Rat does *not* "consist of fœtal parts exclusively," but that, on the contrary, as Eschricht has so well pointed out, "the organic interblending of the circulatory organs of mother and offspring" is as complete in the Rat as in Man; and that, therefore, the concluding paragraph of the citation from Professor Owen's paper ought to be reversed.

The *Carnivora* develop a well-marked *decidua*, and their

* My friend Professor Rolleston has made the following statements in a paper which will shortly appear in the Zoological Society's *Transactions*.

1. The Rat's afterbirth consists of a saucer-shaped deciduous serotina, and a button shaped placenta proper. Afterbirths made up of these two elements may be found in the stomachs of animals of this species after parturition, as they, like many other Mammals below the *Simiadæ*, devour them. Under these circumstances, the two constituent factors of the afterbirth may either be found in their normal connection, or they may be separated one from the other.

2. The non-deciduous part of the serotina forms in the Rat, after parturition, a hernial protrusion into the mesometrium, which has been mistaken for a developing ovum (see Hunterian Catalogue, Phys. Ser. Prep. 3466); just as the homologous structures in the human subject form a hernial protrusion into the cavity of the uterus, which may persist as a more or less elevated area for several years. (Cf. Robin, Mem. Imp. Acad. Med., tom. xxv., p. 137.)

3. The homologue of the saucer-shaped deciduous serotina of the Rat is, in the human subject, the thin layer of laminated albuminous tissue, which, in a placenta expelled without suffering much violence, is seen clothing its uterine surface. It is smaller, relatively, to the other structures concerned in the nutrition of the fœtus, in the human than in any other species. It is more easily demonstrable in the Monkey (*Macacus Nemestrinus*, e. g.), as being a more coherent and stouter membrane than in Man. It is, however, here still a condensed and membranous structure, as compared with its pulpy homologues in *Carnivora*, *Insectivora*, and Rodents.

4. In early periods of utero-gestation in the common Shrew and Hedgehog, the deciduous serotina is a very much larger structure than the placenta proper, which it entirely covers, except on the fœtal aspect. But in the Tenrec, near the full time, the *decidua serotina* is of but wafer-thickness.

5. Dr. Matthews Duncan and M. Robin have shown that the muscular coat of the uterus is never left denuded after parturition in the human subject. The same remark holds good in the case of the "deciduate" *Mammalia*, in all of which a more or less modified mucous tissue, the "non-deciduous serotina," is left, after parturition, upon the utero-placental area, from which the deciduous serotina and placenta proper have been separated as "afterbirth."

placenta in all genera which have been examined (except the Polecat, according to Von Baer) has the form of a complete zone,

Fig. 43.

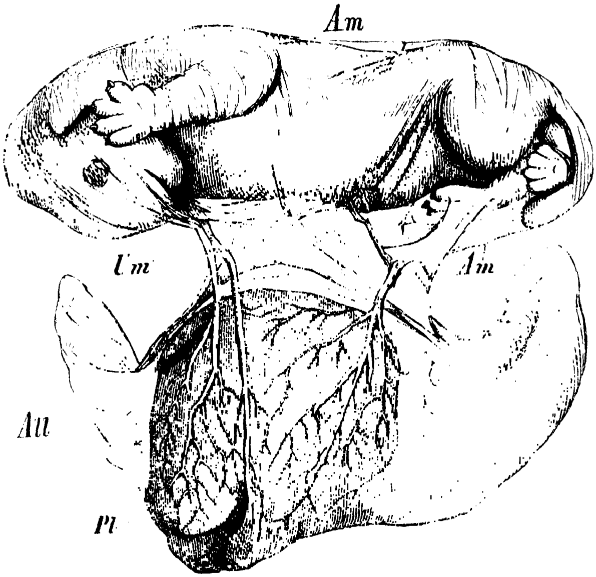


Fig. 43.—Fœtal kitten, with its membranes and placenta. The latter is seen from within, the chorion and allantois being open and everted.—*Am*, amnion; *All*, allantois; *Pl*, placenta; *Um*, umbilical vesicle.
(From a preparation in the Museum of the Royal College of Surgeons.)

or broad girdle, surrounding the middle of the chorion and leaving the poles bare (Fig. 43).

Thus Man; the Apes, or so called *Quadrumana;* the *Insectivora;* the *Cheiroptera;* the *Rodentia,* to which the lowest apes present so many remarkable approximations; and the *Carnivora* (united into one group with the *Insectivora* by Cuvier) are all as closely connected by their placental structure as they are by their general affinities.

With the Pig, on the other hand, all the *Artiodactyla,* all the *Perissodactyla* (save one, taking the group in its ordinarily received sense) and all the *Cetacea* which have been studied, agree in developing no decidua, or, in other words, in the fact that no vascular maternal parts are thrown off during parturition. But considerable differences are observed in the details of the disposition of the fœtal villi, and of the parts of the uterus which receive them. Thus, in the Horse, Camel, and *Cetacea* the villi are scattered, as in the Pig, and the placenta is said to be *diffuse;* while, in almost all true Ruminants, the fœtal

Fig. 44.

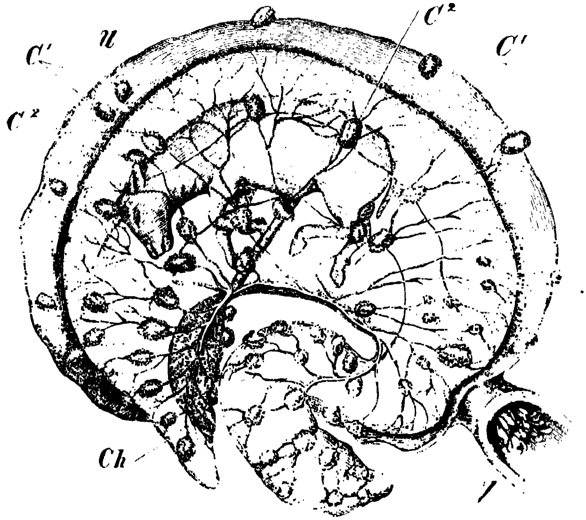


Fig. 44.—Uterus of a Cow in the middle of pregnancy laid open.—*V*, vagina; *U*, uterus; *Ch*, chorion; C^1, uterine cotyledons; C^2, fœtal cotyledons (after Colin).

Fig. 45.

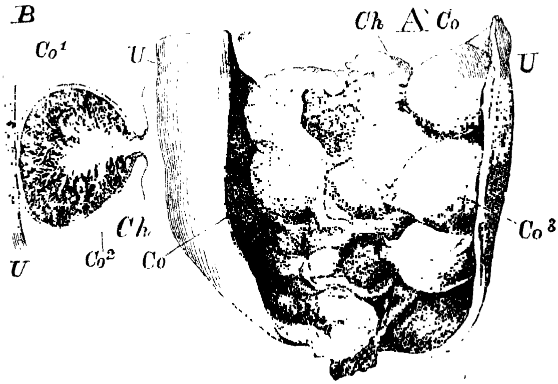


Fig. 45.—A. Horn of the Uterus of a pregnant Ewe, laid open to show, *Ch*, the chorion; with *Co*, the cotyledons.
B. Diagrammatic section of a Cotyledon.—*U*, uterine wall; Co^1, uterine cup of the cotyledon; Co^2, chorionic villous tuft of the cotyle lon.
(From a preparation in the Museum of the Royal College of Surgeons.)

villi are gathered into bunches, or cotyledons, which in the Sheep (Fig. 45) are convex, and are received into cups of the mucous membrane of the uterus; while in the Cow, on the contrary, they are concave, and fit upon corresponding convexities of the uterus (Figs. 44 and 46).

Fig. 46.

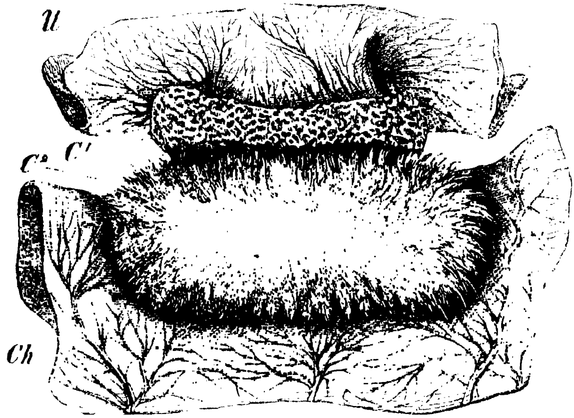


Fig. 46.—A fœtal cotyledon, C^2, half separated from the maternal cotyledon, C^1, of a Cow. *Ch*, chorion. *U*, uterus (after Colin).

No one, probably, would be inclined to object to the association of the orders just mentioned into one great division of the *Monodelphia*, characterised by its placental structure. But such grouping leaves several important points for discussion. The Elephant, as Professor Owen* has shown, has a zonary placenta, and the genus *Hyrax* has been known since the time of Home to be in like case. Hence, as the elephants are commonly supposed to be closely allied with the *Pachydermata*, which possess diffuse, non-deciduate placentæ, and as *Hyrax* is now generally, if not universally, admitted into the same order as the Horse, which has a diffuse, non-deciduate placenta, it is argued that placental characters do not indicate natural affinities. A question, indeed, arises, which has not been answered by those who have described the placentæ of *Elephas* and *Hyrax*. Is the placenta of these animals simply a zone-like arrangement of villi

* "Description of the Fœtal Membranes and Placenta of the Elephant." *Philosophical Transactions*, 1857.

or cotyledons, in connection with which no decidua is developed, or is it a true deciduate placenta, resembling that of the *Carnivora* in the essentials of its internal structure as in its external form? Recent investigation has convinced me, that, in both these animals, the placenta is as truly deciduate as that of a Rodent; so that most unquestionably, if the placental method of classification is to be adopted, both *Elephas* and *Hyrax* must go into the same primary division of the *Monodelphia* as the *Rodentia* and *Carnivora*.

But do these facts really present obstacles to the placental system of classification?

So far as the case of the Elephants is concerned, I must confess that I see no difficulty in the way of an arrangement which unites the *Proboscidea* more closely with the *Rodentia* than with the *Artiodactyla* and *Perissodactyla*, the singular ties which unite the Elephants with the Rodents having been a matter of common remark since the days of Cuvier.

In the absence of any definite knowledge of the placental structure of *Rhinoceros* and *Tapirus*,* it would, perhaps, be premature to discuss the position of *Hyrax*, as determined by its placenta; but if it should eventually appear, as is very probable, that *Rhinoceros*, like *Tapirus* and *Equus*, has a diffuse, non-deciduate placenta, I should have no hesitation in regarding *Hyrax* as the type of a distinct order of deciduate Monodelphous *Mammalia*. *Hyrax*, in fact, hangs by *Rhinoceros* mainly by the pattern of its molar teeth,—a character which affords anything but a safe guide to affinity in many cases.†

Concerning the placentation of the *Sirenia* we have no information.

Among the *Edentata*, the Sloths have presented a cotyledonary placenta, and the Armadillos have been affirmed to possess a discoidal one. I am not aware that the minute structure of the placenta has been examined in either of these groups, but I am

* Home's description of the fœtal membranes of the Tapir is very poor, but Bauer's beautiful figures show clearly that the villi are diffuse, as in the Horse.

† See, in reference to this point, the late Professor A. Wagner's excellent remarks on Cuvier's exaggeration of the Rhinocerotic affinities of *Hyrax*, in Schreber's "Säugethiere." Supp. Band, Abth. iv. p. 307.

indebted to Dr. Sharpey for valuable information respecting the placental structure of *Manis.* The surface of the chorion is covered with fine reticulating ridges, interrupted here and there by round bald spots, giving it an alveolar aspect, something like the inside of the human gall-bladder, but finer. The inner surface of the uterus exhibits fine low ridges or villi, not reticulating quite so much. The chorion presents a band, free from villi, running longitudinally along its concavity, and there is a corresponding bald space on the surface of the uterus. The ridges of the chorion start from the margins of the bald stripe, and run round the ovum. The umbilical vesicle is fusiform. This is clearly a non-deciduate placenta, and the cotyledonary form of that of the Sloth leads me to entertain little doubt that it belongs to the same category.

Admitting all these difficulties and gaps in our information, it still appears to me that the features of the placenta afford by far the best characters which have yet been proposed for classifying the Monodelphous *Mammalia*, especially if the concomitant modifications of the other fœtal appendages, such as the allantois and yelk-sac, be taken into account. And it must be recollected that any difficulties offered by the placental method attach with equal force to the systems of classification based upon cerebral characters which have hitherto been propounded. If any objections, on the ground of general affinities, are offered to the association of *Elephas*, *Hyrax*, *Felis*, and *Cercopithecus* in the same primary mammalian division of deciduate *Monodelphia*, they are not removed by constructing that primary division upon other principles, and calling it *Gyrencephala.*

LECTURE VII.

ON THE VERTEBRATE SKULL.

THE STRUCTURE OF THE HUMAN SKULL.

The human skull is by no means one of the simplest examples of a vertebrate cranium which can be studied, nor is the comprehension of its structure easy; but, as all vertebrate anatomy has started from the investigation of human organization, and the terms osteologists use are derived from those which were originally applied to definite parts of the organism of man, a careful investigation of the fundamental structure of man's skull, becomes an indispensable preliminary to the establishment of anything like a sound comparative nomenclature, or general theory, of the Vertebrate Skull.

Viewed from without (Fig. 47), the human cranium exhibits a multiplicity of bones, united together, partly by sutures, partly by anchylosis, partly by moveable joints, and partly by ligaments; and the study of the boundaries and connections of these bones, apart from any reference to the plan discoverable in the whole construction, is the subject of the topographical anatomist, to whom one constantly observed fact of structure is as valuable as another. The morphologist, on the other hand, without casting the slightest slur upon the valuable labours of the topographer, endeavours to seek out those connections and arrangements of the bony elements of the complex whole which are fundamental, and underlie all the rest; and which are to the craniologist that which physical geography is to the student of geographical science.

Perhaps no method of investigating the structure of the skull conduces so much towards the attainment of a clear understanding of this sort of architectural anatomy, as the study of sections, made along planes which have a definite relation to the principal axes of the skull.

Fig. 47.

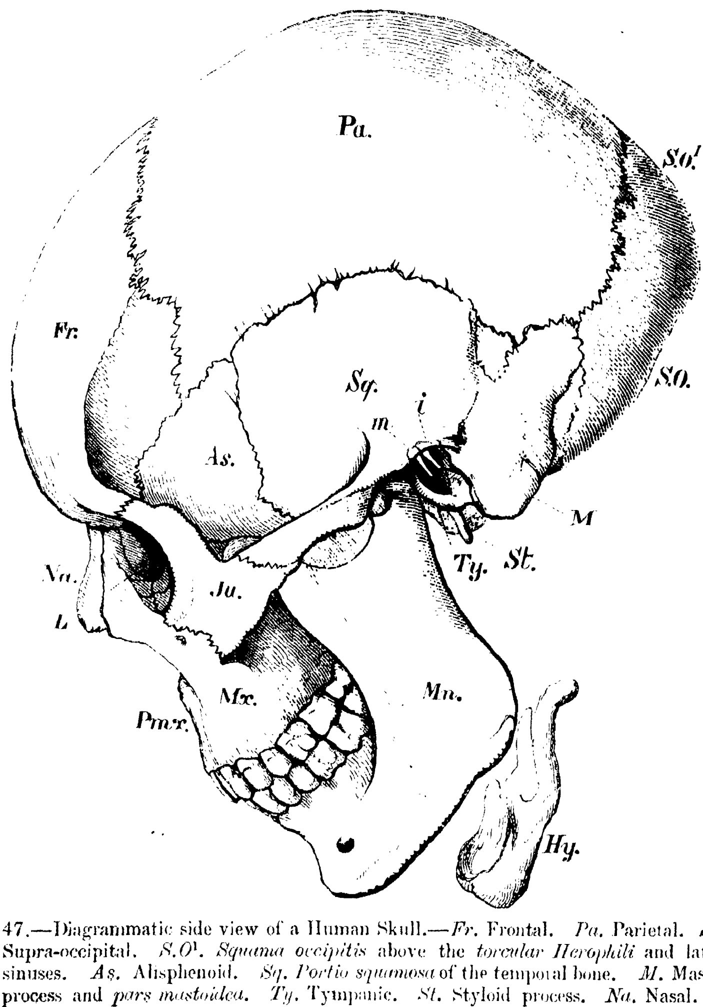


Fig. 47.—Diagrammatic side view of a Human Skull.—*Fr.* Frontal. *Pa.* Parietal. *S.O.* Supra-occipital. *S.O*[1]. *Squama occipitis* above the *torcular Herophili* and lateral sinuses. *As.* Alisphenoid. *Sq. Portio squamosa* of the temporal bone. *M.* Mastoid process and *pars mastoidea*. *Ty.* Tympanic. *St.* Styloid process. *Na.* Nasal. *L.* Lachrymal. *Ju.* Jugal, or Malar. *Pmx.* Premaxilla. *Mx.* Maxilla. *Mn.* Mandible. *Hy.* Hyoid. *m.* Malleus. *i.* incus. [These letters will bear the same signification throughout the series of figures of crania.]

If a vertical and transverse section be taken through the cranium, in such a manner that the plane of the section shall traverse both external auditory meatuses, the skull will be divided into two unequal portions—an anterior, larger, and a posterior, smaller. The former, if viewed from behind, will present the appearance represented in Fig. 48.

Fig. 48.

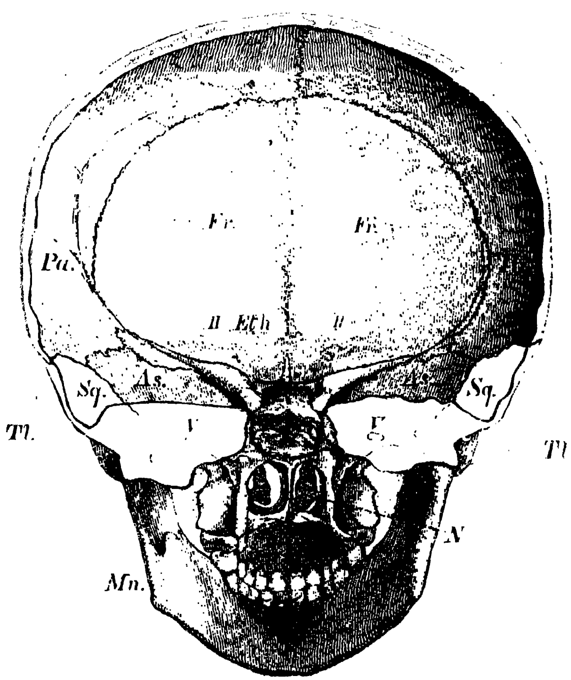


Fig. 48.—Anterior half of the skull of a young person (six or seven years of age) transversely bisected. The temporal bone (*Tl*) on each side is left in outline, and the contour of the alisphenoid is supposed to be seen through it.—*II*, optic foramina between the roots of the orbito-sphenoids; *V*, *foramen ovale* for the third division of the trigeminal; *N* indicates the nasal chamber, *Mn* is placed in the buccal chamber.

A stout median floor (*BS*) whence lateral continuations (*AS*) are prolonged to meet an arched roof (*Pa*), divides a capacious upper chamber, which, during life, lodged a part of the brain, from a lower chamber, formed by the bones of the face. This lower chamber itself is again separable into two parts,—an upper, divided into two by a median septum, the *nasal passages*: and a lower, the *oral cavity*.

The posterior portion of the bisected skull (Fig. 49) presents, in like manner, a strong floor (*BO*) and a large upper chamber for the lodgment of parts of the brain; but the lower chamber seems at first to be absent in the skeleton, being represented, in fact, only by the styloid processes (*St*), the so-called stylo-hyoid ligaments, and the hyoidean bone (*Hy*) which is suspended by these ligaments to the skull.

Fig. 49.

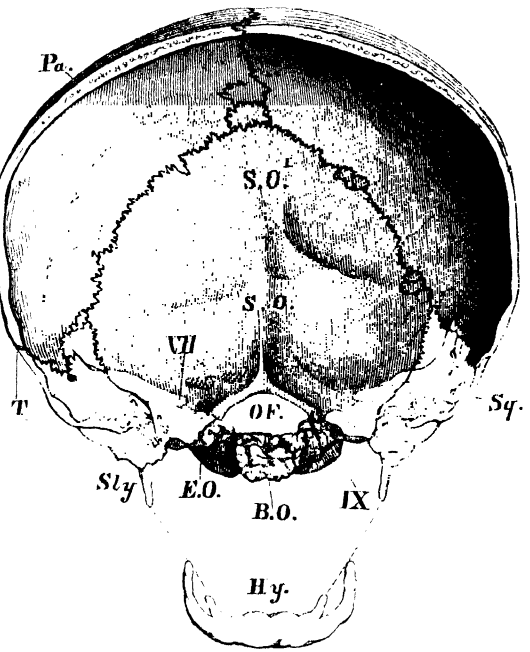


Fig. 49.—The posterior half of the transversely bisected skull, Fig. 48.—*B.O.*, the basi-occipital; *E.O.*, *E.O.*, the ex-occipitals; *T*, the temporal bone left in outline; *O.F.*, occipital foramen; *VII.*, canal for the portio dura and portio mollis; *IX.*, foramen for the ninth or hypoglossal nerve.

A longitudinal and vertical section of the skull (Fig. 50) enables us to observe the same relations of the parts from another point of view. The central bones (*BO*, *BS*, *PS*, *Eth.*, *Vo*), which lie between the arches of the brain-case above, and the arches of the face below, are, in such a section, found to constitute a continuous series, from the occipital foramen to the anterior extremity of the nasal passage, which, as it forms the common centre or axis, not only for the bones of the brain-

Fig. 50.

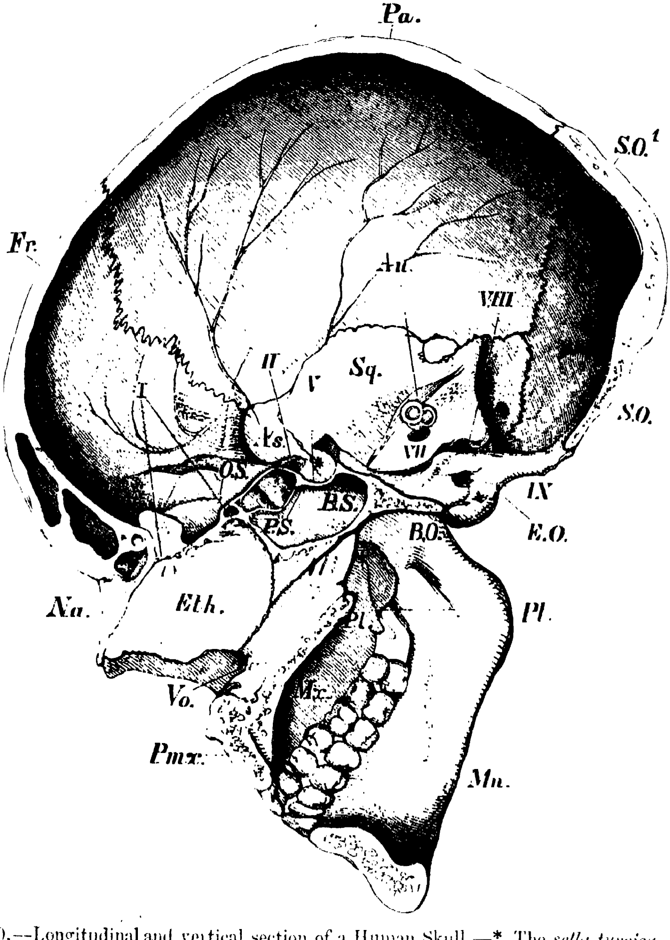


Fig. 50.—Longitudinal and vertical section of a Human Skull.—* The *sella turcica*. *Au.* The position of the superior and posterior vertical semicircular canals. *I.*, *II.*, *V.*, *VIII.*, *IX.* The exit of the olfactory, optic, third division of the fifth, eighth, and ninth nerves. *Vo.*, the Vomer.

case or cranium proper, but also for those of the face, may be termed the *Cranio-facial axis.*

It will be useful to divide this axis into two portions,—a posterior *basi-cranial* (*BO, BS, PS*), which forms the centre of the floor of the proper cranial cavity; and an anterior, *basi-facial* (*Eth., Vo.*), which constitutes the axis of the front part of the face.

Fig. 51.

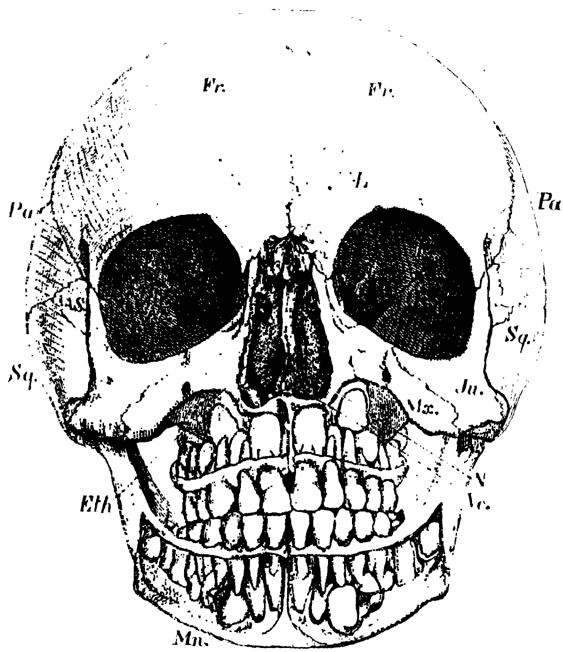


Fig. 51.—Front view of the skull, the halves of which are shown in Figs. 48 and 49.—N, nasal chamber; *Or*, orbit. The nasal bones are removed, and so much of the upper and lower jaws as is necessary to show the permanent teeth.

Three pairs of chambers, destined for the lodgment of the organs of the higher senses, are placed symmetrically upon each side of the double bony box thus described. Of these, two pair are best seen in a front view of the skull (Fig. 51), the inner pair being the *olfactory*, or *nasal chambers* (N), the outer pair, the *orbits* (*Or*). The other pair are better displayed in the transverse sections, Fig. 48 and Fig. 49, and are formed by the temporal bones of anatomists (*T, Tl*), and especially by the petrous and mastoid portions of those bones.

There is an obvious difference between the relations of these sensory chambers to the contained sensory organ, in two of these chambers as compared with the third. The sensory apparatuses of the nose and of the ear are firmly fixed to, or within, the bony chambers in which they are lodged. That of the eye, on the other hand, is freely moveable within the orbit.

An axis, upper and lower arches, chambers for the sensory organs,—such are, speaking generally, the components of the skull. The special study of these components may be best commenced from the cranio-facial axis. Viewed either from above (Fig. 52) or from below (Fig. 53), the cranio-facial axis is seen to be depressed, or flattened from above downwards, behind, and thick and nearly quadrate in the middle; while, in front, it is so much compressed, or flattened from side to side, that it takes the shape of a thin vertical plate. In such a young skull as that from which the Figures 52 and 53 are taken, the depressed hindermost division of the axis is united with the rest, and with the bones *EO, EO,* only by synchondroses; and is readily separable, in the dry skull, as a distinct bone, which is termed the *Basi-occipital* (*BO*). This basi-occipital furnishes the front boundary of the occipital foramen; and its postero-lateral parts, where they abut against the bones *EO*, contribute,

Fig. 52.

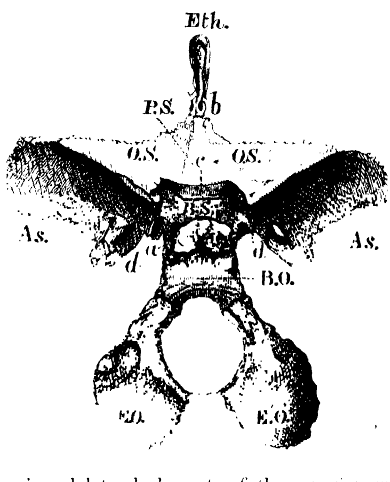


Fig. 52.—Cranio-facial axis and lateral elements of the superior arches of a human skull viewed from above.—*a*, the spheno-occipital synchondrosis; *b*, the ethmo-sphenoid synchondrosis; *c*, the *tuberculum sellæ*, indicating the line of demarcation between the basi-sphenoid and the presphenoid; *d*, the *lingulæ sphenoidales*.

to a small extent, to the formation of the two occipital condyles. In the adult skull the basi-occipital anchyloses completely with the ex-occipital, on the one hand, and with the next bone of the basi-cranial axis on the other, so that the saw must be called to our aid in order to demonstrate the bone.

Fig. 53

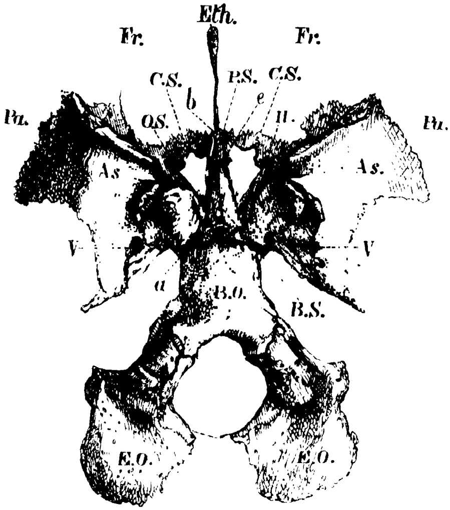


Fig. 53.—Cranio-facial axis and lateral elements of the superior arches (as in Fig. 52), with the pterygoid bones, and without the vomer, viewed from below.—*e*, junction of the basi-sphenoid and presphenoid with the internasal cartilage; *C.S.*, *cornua sphenoidalia*, or bones of Bertin.

From the synchondrosis *a* to the point *b*, in even so young a skull as that here represented, the basi-cranial axis is formed by one continuous ossification, the *Basi-sphenoid* bone, excavated superiorly (Figs. 50 and 52) by a saddle-shaped cavity, the *sella turcica*, which lodges the pituitary body,—an organ of no great physiological moment, so far as we know, but of first-rate morphological significance.

On each side of the hinder part of the *sella turcica*, the basi-sphenoid presents a groove for the internal carotid artery, and this groove is completed in front and externally, by an osseous mass, tapering from behind forwards, the *lingula sphenoidalis*, which lies between the basi-sphenoid and ali-sphenoid. At the front part of the *sella*, separating it from the depression for the optic commissure, there is a transverse ridge, the *tuberculum sellæ*.* The region between the synchondrosis and the tuberculum is the upper surface of the *basi-sphenoid*. Its under-surface (Fig. 53) exhibits a median, wedge-shaped portion, terminating abruptly at the point *e*, on each side of which are stuck on, as it were, two delicate bones, shaped somewhat like sugar-bags, with their wide and open ends directed forwards and their apices backwards. These are the bones of *Bertin*, or *cornua sphenoidalia*, which do not properly belong to the basi-sphenoid, but coalesce with it in the course of growth.

From the *tuberculum sellæ* (*c*) to the point (*b*) in the upper view (Fig. 52), and from the point *e*, to *b* of the lower view (Fig. 53), the middle region of the cranio-facial axis belongs to a third bone, the *presphenoid* (*PS*) which terminates the basi-cranial axis.

I say *terminates* the basi-cranial axis, because the appearance of a continuation forwards of that axis by the *crista galli*, or upper margin of the *lamina perpendicularis* of the ethmoid (see Fig. 50), is altogether fallacious, depending, as it does, upon a special peculiarity of the highest Mammalian skulls, which arises from the vast development of the cerebral hemispheres. In the great majority of *Mammalia* below the Apes, in fact, the free edge of the *lamina perpendicularis* is not horizontal, but greatly inclined, or even vertical; and in these cases the whole *lamina* plainly appears to be, what it really always is, beyond, or anterior to, the floor of the brain-case; while the true basi-cranial bones are parts of the floor of the brain-case.

During fœtal life, the basi-sphenoid and presphenoid are united only by synchondrosis, traces of which may even be discovered (as Virchow has shown) as late as the thirteenth year, or later. Even before birth the two bones become anchylosed superiorly, their junction being marked by the *tuberculum sellæ*; and the remains of the synchondrosis extend

* Where the terms employed in our ordinary handbooks of Human Anatomy do not suffice for my purpose, I adopt those used by Henle in his classical "Handbuch der Systematischen Anatomie des Menschen," a work of great accuracy and comprehensiveness, now in course of publication.

obliquely from this spot, downwards and forwards, to the point *e* (Fig. 53) on the under-surface of the axis, where its cartilage becomes continuous with the osseo-cartilaginous internasal septum.

It is this osseo-cartilaginous septum between the two nasal cavities, the upper free edge of which constitutes the *crista galli*, while the lower free edge supports the *septum narium*, which terminates the *basi-facial axis*.

All the upper and middle part of this septum is formed by a thin osseous plate, the *lamina perpendicularis* of human anatomy, or true *Ethmoid* (*Eth.*), which abuts, in front, upon the frontal and nasal bones; behind, upon the presphenoid; and below, upon a rod-like mass of cartilage, which becomes connected with the *septum narium* and the premaxillary bones anteriorly and inferiorly, and is obliterated with age.

The inferior and posterior part of the septum is constituted by a bone with a gutter-like upper and anterior boundary, which embraces the whole rounded inferior and posterior edge of the cartilage in question, and thus extends from the under-surface of the basi-sphenoid, posteriorly and superiorly, to the middle of the roof of the bony palate, anteriorly and inferiorly. This bone is the *Vomer* (*Vo.*, Fig. 50).

Thus there are three bones in the *basi-cranial axis*,—the basi-occipital, basi-sphenoid, and presphenoid; and there are two bones in the *basi-facial* axis,—the ethmoid and the vomer; the essential difference between these two sets of bones being that the former constitute the middle part of the floor of the brain-case, while the latter are altogether excluded therefrom.

We may now turn to the upper arches of the skull, or those bones which form the walls and roof of the brain-case. In the young skull from which the Figures 52 and 53 are taken, the postero-lateral margins of the basi-occipital are united with the rest of the occipital bone, only by synchondrosis. The parts of the latter which are thus united with the basi-occipital, and which limit the sides of the great occipital foramen, are primitively distinct bones,—the *Ex-occipitals* (*Eo.*); while the squamous part, which bounds the posterior segment of the foramen, is known as the *Supra-occipital* (*So*, *So'*). All these bones, eventually becoming anchylosed together, form the occipital bone of the human anatomist; or what we may term the first, posterior, or *Occipital segment* of the skull.

From the sides of the basi-sphenoid, external to the *lingulæ*, two wide processes, well-known as the "greater wings of the sphenoid" or *Alisphenoids* (*AS*) spring, and unite suturally with the expanded *Parietal* bones (*Pa*), which form the dome-like crown of the skull, and unite in the middle line in the sagittal suture. In this way a second, middle, or *Parietal segment* of the skull is distinguishable.

In like manner, the presphenoid passes, on each side, into the smaller processes, the "lesser wings of the sphenoid," *alæ minores*, or wings of Ingrassias; which, on account of their relations to the orbits, have been well named the *Orbito-sphenoids* (*OS*). And these, externally and anteriorly, unite by suture with the arched and expanded *Frontal* bones (*Fr*), originally double, and separated by a median frontal suture, which ordinarily early disappears. These bones not only meet in front, but send in processes which roof over the orbits and unite with the free anterior edges of the orbito-sphenoids, thus leaving only a long and narrow vacuity, on each side of the *crista galli*, and in front of the presphenoid.

The presphenoid, the orbito-sphenoid, and the frontals are the constituents of the third, anterior, or *Frontal segment* of the skull.

It will be observed, however, that this enumeration of the bones of the three great segments of the skull does not account for all the distinct osseous elements, which enter, directly and indirectly, into its boundaries. If all the bones mentioned are put together, there still remain four considerable vacuities; two small, already mentioned, in the proper front wall of the skull, on each side of the *crista galli*; and one on each side, posteriorly, between the occipital and parietal segments, of very much larger size, and extremely irregular form. The anterior vacuities are filled up by those spongy osseous masses, united with the *lamina perpendicularis* in the adult skull, which are called "lateral masses of the Ethmoid," or "superior and middle spongy bones," and more immediately by the perforated cribriform plate, which allows of the passage of the filaments of the olfactory nerve, and connects these lateral masses with the *lamina perpendicularis*, or proper ethmoid. Looking at the bones which form the immediate walls of the upper and middle part of the nasal chambers, with reference only to the olfactory organs, we might say, in fact, that the anterior vacuity of the cranium proper is stopped by the ossified walls of the olfactory sacs, consisting of the ethmoid and vomer in the middle line, of the superior and middle spongy bones (or so-called lateral masses of the ethmoid) supero-laterally, of the inferior turbinal bones infero-laterally. And to these ossifications must be added, as members of the olfactory group, the bones of Bertin, posteriorly and superiorly, and the nasal bones, anteriorly and superiorly.

The great posterior vacuity on each side is filled up by the *Temporal bone*, which consists of a very considerable number of distinct elements, only distinguishable by dissection and by the study of development in Man, but which remain permanently distinct, and undergo very strange metamorphoses in many of the lower Vertebrates. Some of these constituents of the temporal bone, such as the squamous portion or *Squamosal* (*Sq.*), and the *Malleus*, *Incus*, and *Stapes*, are discriminated by the student of ordinary human anatomy; but there are many others which he is not in the habit of regarding as distinct osseous elements. Thus the bony "external auditory meatus" is primitively a distinct bone, termed *Tympanic* (*Ty.*) on account of its affording the frame in which almost the whole of the tympanic membrane is set. The *Styloid* process (*St.*) is originally a distinct bone. And, lastly, the *pars petrosa* and *pars mastoidea* of human anatomy are, in reality, made up of three distinct ossifications, of which I shall have to say more presently, but which I shall speak of for the present under the collective name of the *Periotic* bones, because they immediately surround the organ of hearing.

Not merely the periotic, but also the squamosal and tympanic bones are so closely related to the auditory organ, that the postero-lateral apertures of the cranium may be said to be stopped by the osseous chambers of the auditory organ, in the same way as the anterior apertures are closed by the osseous chambers of the olfactory organs. As the eye is contained only in a mobile fibrous capsule, the sclerotic, the apertures which lead to the orbit—the spheno-orbital fissures and the optic foramina—are not closed by any special bones pertaining to the sensory organ lodged therein.

Thus the brain-case may be said to be composed of three superior arches connected respectively with the three divisions of the basi-cranial axis, and of two pair—an anterior and a posterior—of bony sense capsules interposed between these arches. A middle, third pair of sense capsules is not represented by bone in the cranial walls.

In like manner, the face may be resolved into a series of bones, occurring in pairs from before backwards, and forming more or less well-defined lower arches, some of which embrace the nasal cavity, being placed in front of, or above, the oral aperture, while others enclose the buccal chamber, and are situated behind and below the oral aperture. Of the former, *pre-oral* bones, there are four pairs—the *Premaxillæ* (*Pmx.*), the *Maxillæ* (*Mx.*), the *Palatines* (*Pl.*), and the *Pterygoids* (*Pt.*).

The *Premaxillæ*, which lodge the upper incisor teeth, so early lose their distinctness in man, by becoming anchylosed with the maxillary bones (at any rate externally and anteriorly) that they are rarely recognised as separate bones. Nevertheless, a suture extending upon the bony palate from the posterior margin of the alveolus of the outer incisors to the incisive foramen, very commonly persists, as an indication of the primitive separation of these bones. The most important character of the premaxillæ, regarded morphologically, is, that they are connected, superiorily, with the anterior termination of the cranio-facial axis, and that this connection is a primary one. Each premaxilla passes from its inner end, which is united with the axis, outwards and backwards, and two of the other three pair of pre-oral bones have similar relations to the cranio-facial axis. The anterior of these are the *Palatine* bones; the inner, or sphenoidal, processes of which are connected with the basi-sphenoid and with the vomer; while the outer, or orbital, processes articulate with the so-called lateral masses of the ethmoid and with the maxilla; so that the upper part of each palatine bone is directed, from the cranio-facial axis, with which its inner end is connected, outwards and forwards (Fig. 54). The third pair of bones, the *Pterygoids*, are the internal pterygoid processes,—bones which are originally quite distinct from the sphenoid, while the external pterygoid processes are of a very different character, being mere outgrowths of the alisphenoids. These are connected with the basi-sphenoid (or rather with the *lingulæ sphenoidales*), above, and, in front, with the palatines, while their planes are directed backwards and somewhat outwards. The fourth pair of pre-oral bones—the *Maxillæ*—are connected in front and internally with the premaxillæ, and behind and internally with the palatines, but they nowhere come into direct contact with the cranio-facial axis, at least primarily.

I make the latter qualification because the vomer articulates with the superior surface of the palatine plates of the maxillæ, and it may be said that, in this way, the maxillæ do unite with the cranio-facial axis. This articulation, however, has nothing to do with the primitive connections of the bones, but depends upon a modification of the maxillæ peculiar to the higher vertebrata. The bony apertures—called "posterior nares"—in Man, for example, are structures of a totally different character from, and superadded to, what are called the posterior nares in a frog, or ordinary lizard, or bird. In these lower Vertebrates, the posterior nares are apertures, bounded on the inner side, by the vomer; on the outer side and behind, by the palatine bones; in front, by the premaxillæ and maxillæ. In Man, on the other hand, the apertures so called are limited, it is true, on the inner side by the vomer, and on the outer side by the palatine bones; but they are also bounded below and in front by the palatine bones, and the premaxillæ and maxillæ have nothing to do with them. On looking closely into the matter, however, it will be found that that region of the palatine which forms the outer and inferior boundary of the posterior nares of Man is a something which has no representative in the lower Vertebrate.

But if, with a fine saw, the greater part of the perpendicular plate of the palatines, and the corresponding part of the maxillaries, and, with these, their palatine plates, be cut away, leaving only the premaxillæ, vomer, and upper parts of the maxillary and palatine bones; it will be found that hinder nares are left, which entirely correspond with the "posterior nares" of a bird or of an amphibian; that is to say, they are passages between the vomer in the middle line, the premaxillæ and maxillæ in front and externally, and the palatines externally and behind.

Fig. 54.

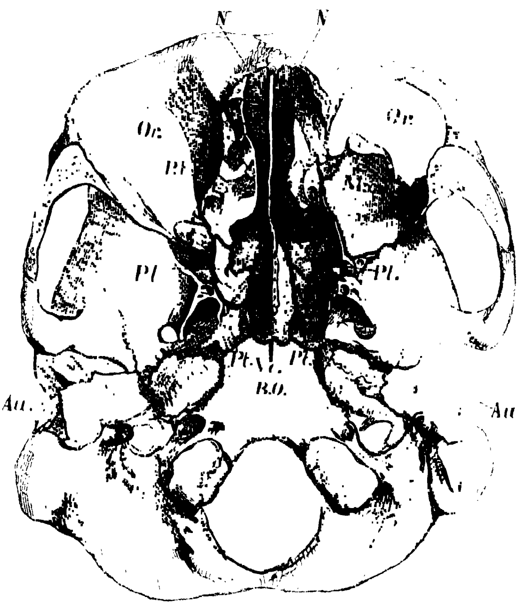


Fig. 54.—The base of a human skull—the nasal, ethmoid, vomerine, maxillary, palatine, and pterygoid bones being cut through horizontally, and their lower portions removed. The entire right maxilla is taken away. The posterior pair of letters, *NN*, are situated in the median nares, which are incomplete, in front, in consequence of the removal of the premaxillæ.

In fact, the apertures of the nasal chamber into the mouth, thus artificially exposed, are those which originally exist in Man and the higher *Vertebrata;* but the downward growth of the maxilla into its alveolar process, and of the palatine bone into its perpendicular plate, together with the production inwards of the palatine plates of these bones, which eventually unite with the vomer, give rise to the apertures, which are ordinarily called posterior nares. So that in Man, for example, there are three pairs of "nares:"—the *external*, situated between the anterior end of the internasal septum, the nasal bones, and the premaxillæ, as in the lower Vertebrates; the *median*, between the vomer, the palatines, and the premaxillæ, which correspond with the posterior nares of the lower Vertebrates; and the *posterior*, between the vomer, internally, and the palatines above, at the sides, and below, which are peculiar to the higher Vertebrates.

And, to return to the maxilla, we find that it really differs altogether from the other pre-oral bones, and is, as it were, fastened on to the outer sides of the premaxillary and palatine bones, without having any primary direct connection with the cranio-facial axis.

The *post-oral* bones surround the buccal cavity, and form two distinct arches—the *mandibular* and the *hyoidean*. Neither of these arches is directly connected with the cranio-facial axis, nor with the segments of the brain-case, but both are suspended to different parts of the temporal bone, which is so singularly intercalated between the middle and posterior of those segments.

The lower jaw or *Mandible* (*Mn*) consists of two rami, anchylosed at the symphysis, and each consisting of a single piece, the condyle of which articulates with the squamosal.

The *Hyoid* bone (*Hy*), composed of its body and two pairs of cornua, does not articulate directly with the temporal bone, but ligaments connect it with the styloid processes, and these last bones unite with the posterior part of the periotic capsules.

Thus, the natural connections of the bones by no means allow of the separation of the walls of the lower chambers of the human skull into a series of arches springing from, and corresponding with, the axial parts, as we found to be the case with the walls of the upper chambers.

If the temporal bone be detached, the hyoidean and mandibular arches come with it, and exhibit no connection with the occipital or the parietal segments. Indeed, the latter is preoccupied by the pterygoid and the palatine, both of which are connected with the basi-sphenoid (at least with the *lingulæ*), while the anterior part of the palatine is also connected, in the adult state, with the presphenoid, by the intermediation of the *cornua sphenoidalia.*

Two bones yet remain to be mentioned which come neither into the category of axial bones, nor of superior or inferior arch bones, nor, strictly speaking, of sense-capsule bones. These are the *Lachrymal* (*L*), intercalated between the nasal, maxillary, and lateral mass of the ethmoid, and serving to lodge the conduit which places the orbit and the nasal cavity in communication; and the *Jugal* or *Malar* (*Ju*), which connects the bones of the orbital chamber with the squamosal element of the temporal bone.

The skull, thus composed, serves as a protection to the organs which are lodged within it, and which are of as great importance in their morphological, as in their physiological, aspect.

The cerebral hemispheres and cerebellum, with their dependent parts, fill the cranial cavity, the lower lateral margin of the posterior cerebral lobes corresponding with the *torcular Herophili* and the lateral sinuses, on the inner surface of the occipital bone; or, in other words, with the line of attachment of the tentorium. Certain axial parts of the brain have definite relations to the axial parts of the cranium. Thus, the medulla oblongata lies upon the basi-occipital. The pituitary body rests upon the upper surface of the basi-sphenoid, this bone constituting the chief part of the front as well as of the hinder wall of the *sella turcica.* The *chiasma* of the optic nerves rests upon the hinder portion of the upper face of the presphenoid, and the peduncles of the olfactory nerves upon the front portion of that face. The termination of the axial parts of the brain in the *lamina terminalis* of the third ventricle corresponds pretty nearly with the termination of the basi-cranial axis in the anterior extremity of the presphenoid.

Not less important are the relations of many of the cerebral nerves to the lateral elements of the arches of the brain-case.

The filaments of the olfactory nerves pass out through the cribriform plates, leaving the ethmoid proper, or *lamina perpendicularis*, upon their inner side, and the lateral masses of the ethmoid, or superior and middle spongy bones, upon their outer sides.

The optic nerves pass out through the optic foramina, situated between the roots of the orbito-sphenoids, from the *chiasma*, which rests, as has just been stated, upon the posterior and upper part of the presphenoid. Hence it follows, that the presphenoid lies in front of, and between, the optic nerves, which embrace it, as in a fork, from behind.

The third and fourth pairs are not of so much morphological importance that I need dwell upon them, but the trigeminal affords first-rate cranial landmarks by its nasal branch and its whole third division. The nasal nerve enters the orbit by the *foramen lacerum anterius*, passes to the inner side of the eye, and then, traversing the anterior of the two ethmoidal foramina, perforates the "lateral mass of the ethmoid," and entering the cavity of the bony cranium, though it always lies beneath the dura mater, skirts the olfactory aperture, and passes out into the nasal cavity, by an aperture in the front part of the cribriform plate. We shall find this irregular perforation of the "lateral mass of the ethmoid," by the nasal division of the fifth nerve, to be an excellent guide to the determination of the homologue of the bone in the lower *Vertebrata*.

The third division of the trigeminal traverses the *foramen ovale* in the posterior part of the alisphenoid, so that it makes its exit behind the greater part of that bone, and altogether in front of the periotic bone.

The *portio dura* enters the internal auditory foramen in the periotic mass, runs along its canal, situated above the *fenestra ovalis*, and eventually passes out by the stylo-mastoid foramen. It therefore perforates the fore part of the periotic, passing in front of the membranous labyrinth. The *portio mollis* also enters the periotic bone by the internal auditory foramen, and it terminates in the membranous labyrinth.

The eighth pair passes out through the *foramen lacerum posterius* completely behind the periotic (which thus lies between the exits of the fifth and of the eighth pairs), and in front of the ex-occipitals.

The ninth pair perforates the ex-occipitals in front of the condyles.

With regard to the relations of the nerves to the inferior arches of the skull, only one circumstance calls for particular notice,—the distribution of the terminal divisions of the *portio dura*. This nerve divides, as it is about to leave the temporal bone, into two portions, the larger of which passes out by the stylo-mastoid foramen, and, besides giving off many other branches, supplies certain muscles of the hyoidean apparatus.

The smaller division of the nerve, of comparatively insignificant size—the *chorda tympani*—returns to the tympanic cavity, crosses it, and leaving it by an aperture internal to, and above the tympanic element, runs down upon the inner side of the lower jaw. In Man, the great development of the facial muscles gives a predominance to the branches of the *portio dura* which supply them; but, in the lower Vertebrates, the nerve becomes more and more completely represented by simple mandibular and hyoidean divisions, corresponding respectively with the *chorda tympani* and the branches distributed to the stylo-hyoid and digastric.

In the preceding description of the architecture of the human skull, I have, as far as possible, avoided complicating the general view of its structure which I have desired to give, by enter-

Fig. 55.

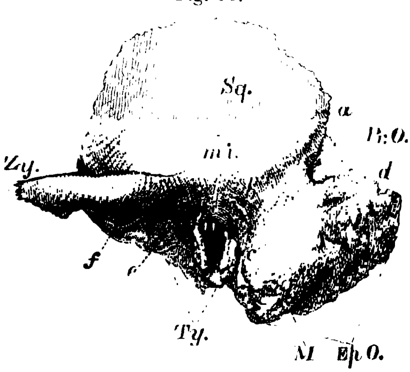


Fig. 55.—Human left temporal bone, half the natural size.—*a b*, posterior root of the zygomatic process; *e*, middle root; *f*, anterior root; *b*, post-auditory fossa; *m i*, long processes of the malleus and of the incus.

ing into any details which were not strictly necessary; but there remains one part of the cranium—the temporal bone—the structure of which must be carefully and thoroughly investigated, if we desire to understand the modifications undergone by the bones which correspond with its constituent elements in other *Vertebrata.*

Viewed from without, the temporal bone presents the well-known *pars squamosa (Sq.)* and *pars mastoidea (M)*, in the re-entering angle between which, the tympanic element (*Ty.*) is fixed (Fig. 55).

No suture separates the *pars squamosa* from the *pars mastoidea*, but the posterior limits of the former are indicated, in the first place, by the curved ascending portion of the posterior root of the zygoma (*a b*), which bounds the attachment of the temporal muscle; and secondly, by a curved ridge, convex backwards and differently defined in different subjects—the *margo tympanicus* of Henle—which passes downwards, behind the auditory meatus, until it cuts the contour of the tympanic bone. Near the upper end of this ridge, or "post-auditory process," is an elongated "post-auditory fossa" (*b*), more marked in old than in young subjects.

The portion of the squamosal element, the free edge of which terminates in this ridge, forms an arch, of which the posterior pillar constitutes the posterior and upper wall of the auditory meatus, while the anterior pillar forms the front boundary of the glenoid cavity. The centre of the arch is interrupted by the middle root of the zygoma (*e*), or "the post-glenoidal process" of the squamosal, which runs, as a wedge-shaped ridge, transversely to the span of the arch.

The upper edge of the anterior wall of the gutter-shaped tympanic bone (which forms the hinder boundary of the glenoid cavity), unites with this ridge, crossing its direction obliquely inwards and forwards. Beyond the ridge it is no longer united with the squamosal, but, keeping its oblique direction, crosses rather to the inner side of the lower edge of that bone, and leaves the Glaserian fissure between the squamosal and itself.

A section taken through both the external and the internal auditory meatuses (Fig. 56) shows that this arched plate of the squamosal is interposed between the upper half of the tympanic and the upper parts of the *pars petrosa* and *pars mastoidea*, the depth of the interposed squamosal being greatest posteriorly, while it diminishes to nothing anteriorly.

The upper region of the *pars petrosa*, however, does not directly abut, by its thick mass, against the squamosal, but by a thin horizontal plate, which roofs over the tympanum, the

Fig. 56.

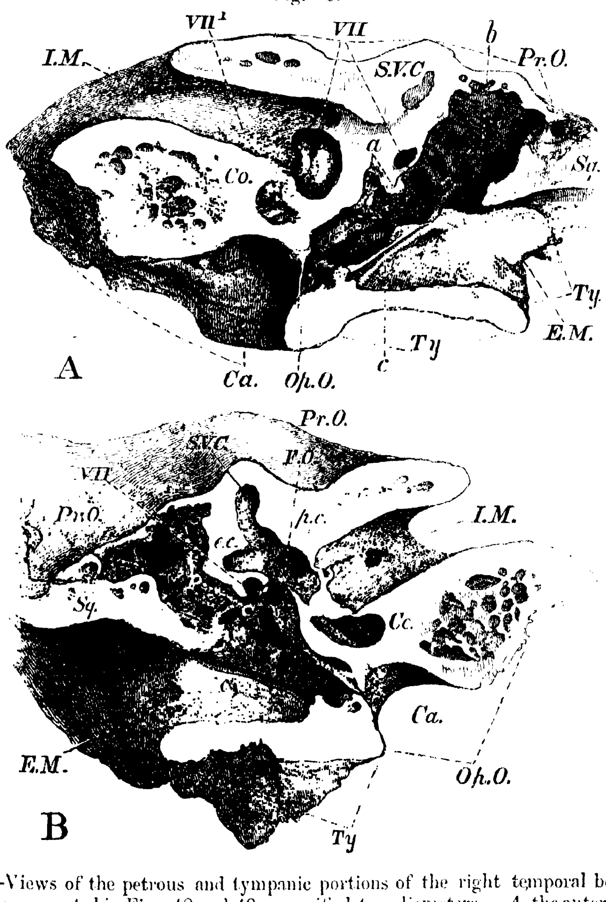


Fig. 56.—Views of the petrous and tympanic portions of the right temporal bone of the skull represented in Figs. 48 and 49, magnified two diameters.—*A*, the anterior half of the bone; *B*, its posterior half; *I.M.*, internal meatus; *E.M*, external meatus; *a*, processus cochleariformis; *b*, chamber in which the heads of the malleus and incus lie; *c*, groove for the tympanic membrane; *S.V.C.*, superior vertical semicircular canal; *e.c.*, external semicircular canal; *p.c.*, posterior vertical semicircular canal; *Co*, cochlea; *P*, Pyramid; *F.O.*, fenestra ovalis; *VII*, canal for portia dura; *VII*[1], for portio mollis.

Eustachian tube, and the *antrum mastoideum,* and is the *tegmen tympani.**

The lower region of the *pars petrosa* in like manner gives off a thicker and shorter plate, which forms the floor of the Eustachian tube and the outer or inferior boundary of the carotid canal, in front; the floor of the tympanum, in the middle; and then, becoming gradually thicker, constitutes the lower boundary of the *antrum mastoideum.* It is with the outer edge of this inferior, or floor-plate, of the tympanum that the lower portion of tympanic bone becomes anchylosed. The inner wall is of course constituted by the outer surface of the more massive part of the *pars petrosa.* Thus, the roof and part of the floor of the tympanum are formed by the superior and inferior prolongations of the *pars petrosa,* while the outer wall of the tympanum is constituted above by the squamosal, and below by the tympanic. A section taken vertically and transversely to the axis of the skull through the middle of the *fenestra ovalis,* in the way described above, shows that the squamosal limits, externally, an upper chamber of the tympanum (*b*, Fig. 56), which is nearly as deep as, and is wider than, the lower division, bounded externally by the tympanic membrane and tympanic bone (Fig. 56). It is in this upper chamber that the heads of the malleus and incus are lodged, the handle of the one and the long process of the other, only, depending into the proper tympanic cavity. Hence, in looking into the tympanum from without (Fig. 55) when the ear-bones are *in situ,* only these processes are seen, the heads of both malleus and incus being hidden by the arched plate of the squamosal.

Thus, the tympanum is formed by a very complicated adjustment of bony elements, and we shall by and by see reason to believe that it is even more complex than it now appears to be, inasmuch as the so-called *pars petrosa* will prove to be composed of two distinct elements; an inferior, *opisthotic,* bone, containing the lower part of the cochlea, and a superior, *pro-otic,* sheltering the greater part of the vestibule, the upper part of the cochlea, the anterior vertical semicircular canal, part of the posterior vertical canal, and the external semicircular canal.

* It lies immediately beneath the letters *Pr.O.*, Fig. 56, A.

Behind the posterior boundary of the squamosal, constituted by the two diverging lines above described (Fig. 55), lies all that portion of the temporal bone which is known as the *pars mastoidea.* But, as I shall have occasion to demonstrate, when explaining the mode of development of the temporal bone, this *pars mastoidea* is, in reality, made up of extensions of two of the primitive constituents of the *pars petrosa,* and of a third element, the *epiotic.* The posterior margin of the squamosal, as above described, may be said roughly to form two sides of a parallelogram. The third side is the thick part of the upper edge of the *pars mastoidea,* corresponding with the termination of the upper and anterior surface of the *pars petrosa* on the inner side of the bone. If a fourth side is made by an imaginary line connecting the ends of the others, the bony surface which lies above and in front of the line will, as nearly as possible, belong to the *pro-otic* element, while that which lies below and behind it, including the mastoid process, appertains to the *epiotic.* On the other hand, a certain amount of the *pars mastoidea* internal to the digastric groove belongs to the *opisthotic.*

LECTURE VIII.

ON THE STRUCTURE OF THE SKULL.

THE DEVELOPMENT OF THE HUMAN SKULL.

As might be expected from the nature of the case, it has not yet been possible to obtain a series of human embryos, in every stage of development, sufficiently large to enable embryologists to work out all the details of the formation of the human skull. But all higher vertebrate embryos so nearly follow one and the same type of early developmental modification, that we may reason, with perfect confidence, from the analogy of the lower Vertebrates to man, and fill up the blanks of our observations of human embryos by investigations of the chick, the dog, the rabbit, or the pig.

In the chick,* the first indication of the body of the embryo is an elongated, elevated area of the blastoderm, the axis of which is traversed by a linear groove. The one end of the elongated area is wider and more distinctly raised up from the rest of the blastoderm, than the other: it is the cephalic end (Fig. 31, A, *a*), and the linear groove stops short of the rounded extremity of this part of the elevated area. A peculiar cellular cylinder, tapering off at each end, the notochord, is soon discerned occupying the bottom of this groove, beneath the outer, serous, or neuro-epidermic layer of the germ.

A laminar outgrowth of the convex summits of the ridges which bound the primitive groove now takes place, in that part of the embryo, which will eventually become the middle region

* See Lecture IV., pp. 64—66.

of the head; and the *dorsal laminæ*, thus produced, extending forwards and backwards, like parapets, upon each side of the primitive groove, lay the foundations of the lateral walls, not only of the skull, but of the spinal column.

Very early, however, the boundary line between skull and spinal column is laid down, by the appearance in the substance of the bases of the dorsal laminæ and the adjacent middle layer of the blastoderm, of the first pair of those quadrate masses of condensed tissue, the *proto-vertebræ* ("Urwirbel" of the German writers), which are the foundations, not only of the bodies of the vertebræ, but of the spinal muscles and ganglia. The proto-vertebræ increase in number from before backwards; and, at length, extend through the whole range of the spinal column, while none ever make their appearance in the region which will be converted into the skull.

The edges of the dorsal laminæ now unite, the coalescence taking place first in the middle cephalic region, and extending thence backwards and forwards; at the same time, the cephalic canal becomes separated into three distinct dilatations, or cerebral vesicles, of which the anterior is by far the most marked (Fig. 57, A, *I*, *II*, *III*).

The rudimentary cranial cavity next becomes bent upon itself in such a manner, that the longitudinal axis of the first cerebral vesicle takes a direction at right angles to the axis of the third, and of the spinal canal generally. In consequence of this change, the middle cerebral vesicle occupies the summit of the angulation, and becomes the most anterior point of the whole body (Fig. 57, C, D).

The bend thus produced is the *cranial flexure*. It results in the division of the floor of the cranial cavity into two parts, an anterior and a posterior, which are at right angles to one another (Fig. 57, C, D, E). Hitherto, no trace of the notochord has been observed in the anterior division, that structure ending in a point behind the flexure (Fig. 57, D, E, *h*).

As development proceeds, the anterior cerebral vesicle becomes divided into two portions,—an anterior, the vesicle of the cerebral hemispheres (I^a); and a posterior, the vesicle of the third ventricle (I^b). In the upper wall of the vesicle of the third

Fig. 57.

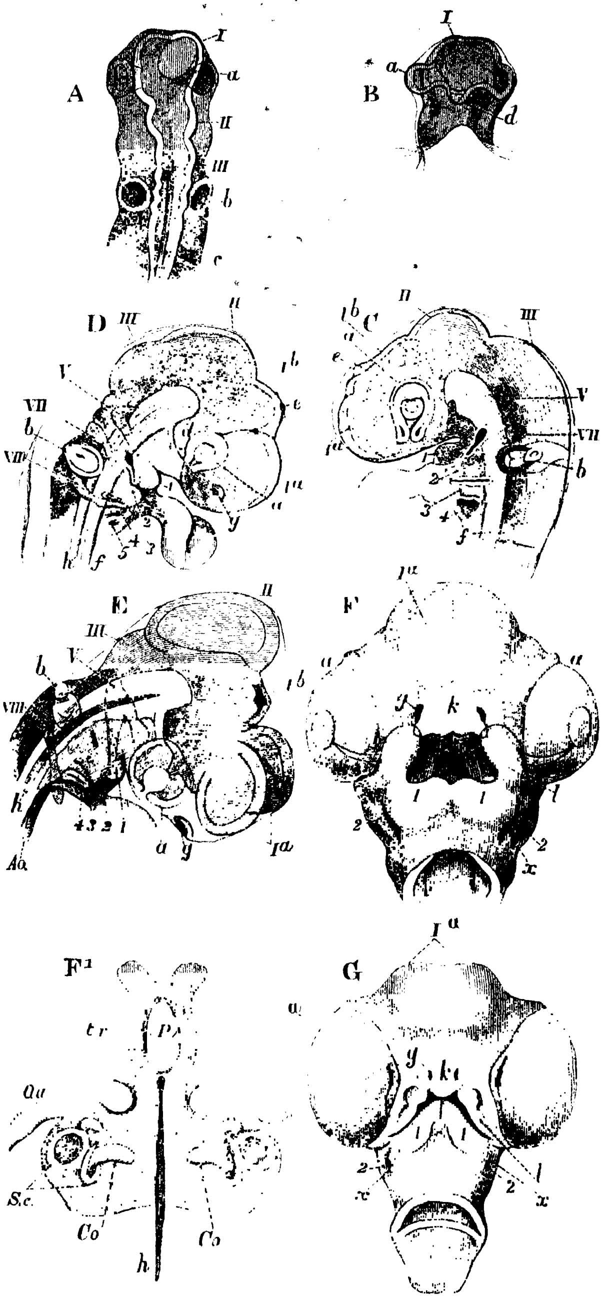


Fig. 57.—Successive stages of the development of the head of a chick.—*I*, *II*, *III*, first, second, and third cerebral vesicles; I^a, vesicle of the cerebral hemispheres; I^b,

ventricle the rudimentary pineal gland (*e*) makes its appearance in the middle line. From the middle of the lower wall grows out a process, the *infundibulum*,* terminating in a glandular appendage, the pituitary body, which last is lodged in the deep fossa situated in the floor of the anterior division of the skull, immediately in front of, and beneath, the termination of the notochord (Fig. 57, B, D, *d*).

The three pairs of sensory organs appertaining to the higher senses,—the nasal sacs, the eyes, and the ears,—arise as simple cæcal involutions of the external integument of the head of the embryo. That such is the case, so far as the olfactory sacs are concerned, is obvious; and it is not difficult to observe that the lens and the anterior chamber of the eye are produced in a perfectly similar manner. It is not so easy to see that the labyrinth of the ear arises in this way, as the sac resulting from the involution of the integument is small, and remains open but a very short time (Fig. 57, C, *b*). But I have so frequently verified Huschke's and Remak's statement that it does so arise, that I entertain no doubt whatever of the fact.* The outer ends of the olfactory sacs remain open, but those of the ocular and auditory sacs rapidly close up, and shut off their contents from all direct communication with the exterior. The olfactory nerve is developed from the anterior division of the anterior cerebral vesicle. The optic nerve is primarily developed from the posterior division of that vesicle, its connection with the middle vesicle (which eventually gives rise to the *corpora quadrigemina*)

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vesicle of the third ventricle; *a*, rudiments of the eyes and optic nerves; *b*, of the ears; *g*, of the olfactory organs; *d*, the infundibulum; *e*, the pineal gland; *c*, protovertebræ; *h*, notochord; 1, 2, 3, 4, 5, visceral arches; *V*, *VII*, *VIII*, the trigeminal, portio dura, and eighth pair of cranial nerves; *k*, the fronto-nasal process; *l*, the maxillary process; *x*, the first visceral cleft.

A, B, upper and under views of the head of a chick at the end of the second day.

C, side view at the third day.

D, side view at seventy-five hours.

E, side view of the head of a chick at the fifth day, which has been subjected to slight pressure.

F, head of a chick at the sixth day, viewed from below.

F[1], the cartilaginous cranium of the same.

P, pituitary space; *tr*, trabeculæ; *Qu*, quadrate cartilage; *Sc*, semicircular canals; *Co*, cochlea.

G, head of a chick at the seventh day, from below.

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* See also Kölliker's "Entwickelungs Geschichte," p. 300, *et seq.*

being only secondary. The auditory nerve is developed in the blastoderm adjacent to the third cerebral vesicle, so that the three pairs of sense-capsules do not correspond with the three primary cerebral vesicles.

While these changes have been going on in the proper cranial portion of the embryo, the rudiments of the face have made their appearance under a very singular guise. As the homologues of the dorsal laminæ in the head have grown upwards to inclose the cephalic cavity, so, plates, which correspond with the visceral laminæ of the trunk, have grown downwards, to constitute the posterior walls of the buccal, pharyngeal, and cervical regions. These visceral plates, however, do not remain entire and undivided, as do those of the trunk, but grooves appear in them, directed transversely to the axis of the trunk, and, the grooves deepening, eventually become converted into slits—the *visceral clefts*—which open into the pharyngeal cavity, and bound corresponding *visceral arches.* The first slit is situated immediately below and in front of the auditory sac, and separates the first and second visceral arches,—the anterior boundary of the former being determined by the edges of a depression of the integument which will eventually become the buccal cavity (Fig. 57, C). A third, fourth, and fifth visceral arch are developed in successive order behind the first and second (Fig. 57, D, and Fig. 32, F); but as they are of no great moment in reference to the human skull, our attention may be confined to the latter.

It is particularly worthy of notice that, from the moment at which it is discernible as a distinct part, the root of the first visceral arch passes into the rudimentary cranium below, and in front of, the forepart of the auditory sac, while the root of the second is attached below and behind that sac. We shall find that the parts developed within these arches retain the same position in the adult state; so that any hypothesis which involves the supposition of an extensive change of place of these parts in the course of development is, *ipso facto,* unworthy of consideration.

Both the first and second visceral arches are connected with that part of the cranium which lies behind the flexure; but the inflected portion of the cranium in front of the bend exhibits, on each side, running from the root of the first visceral arch beneath the eye to the nasal sac, a ridge or elevation, which is called the *maxillary process,* and might be regarded as a visceral arch of the anterior division of the skull, from the base of which it is developed (Fig. 32, G, and *l*, Fig. 57, F).

Lastly, the middle part of the floor of the anterior cerebral vesicle, between the nasal sacs, thickens and gives rise to a broad, flat median process, with an expanded extremity, the terminal contour of which is excavated and slightly produced at the angles—the *fronto-nasal process* (Fig. 57, F, *k*).

At first, the cranium and all its arches are membranous, or composed of mere indifferent tissue, with the exception of the axial notochord; but, very early, chondrification commences. The indifferent tissue surrounding the notochord (the "investing mass" of Rathke) (Fig. 57, C, D, *f*), is converted into cartilage, and the same histological change takes place in the walls of the auditory capsules, and around the foramen magnum; the cartilage stops in the middle line, behind the pituitary body, but sends two processes, one on each side of that body, into the floor of the anterior division of the skull (Fig. 57, F^1, *tr*). These processes, the *trabeculæ cranii*, of Rathke, unite in front, and the cartilage formed by their union ends in the fronto-nasal process. The roof of the skull, and the greater part of its side-walls, except in the region of the foramen magnum, are, at first, entirely membranous. Chondrification next takes place in the visceral arches; a rod of that substance, which coalesces with its fellow in the middle line, being formed in the axis of the several arches on each side.

Purposing to return to the visceral arches by and by, I shall now trace out the modifications which are undergone by the chondro-membranous brain-case. In the occipital region, and about the auditory capsules, which early attain a very large proportional size, the cartilage extends for some distance upon the infero-lateral parietes of the skull; on the floor of the posterior division of the skull it thickens notably, and forms a sort of model of the future basi-occipital and basi-sphenoidal regions, the interspace between the trabeculæ becoming rapidly obliterated and converted into the floor of the pituitary fossa.

In front, the coalesced trabeculæ become changed into a plate of cartilage, compressed from side to side, which occupies the middle of the gradually-narrowing fronto-nasal process, as the ethmo-vomerine, or internasal, cartilage.

From the sides of the basi-sphenoid cartilaginous plates are developed, which foreshadow the form and relations of the alisphenoids; at the sides of the presphenoidal region of the cartilage, similar plates represent the orbito-sphenoids. In front of these the upper part of the internasal, or ethmoidal, cartilage passes laterally into broad deflected cartilaginous lamellæ, which curve round the olfactory sacs, and occupy the places of the lateral masses of the ethmoid and the inferior turbinal bones.

Thus far the terms of my description are almost as applicable to the embryonic cranium of Man as to that of the chick.

The human cranium has been observed forming part of an open groove; it undergoes a flexure, and develops visceral arches altogether similar to those of the chick, nor is there any reason to doubt that the organs of sense are developed in the same manner. The very earliest condition of the cartilaginous cranium of the human embryo has not been observed; but, at the beginning of the second month, it consists wholly of cartilage and of membrane, disposed in a manner which differs only in detail from that seen in the chick. Thus the occipital foramen is surrounded by cartilage, continuous with that which extends through the basi-sphenoidal, presphenoidal, and ethmoidal regions to the anterior end of the face. The alisphenoids and orbito-sphenoids are represented by cartilage, and cartilaginous plates arch down from the summit of the internasal cartilage, on each side, to form the substratum on which, the nasal bones and, in which, the spongy bones will be developed. That part of the cranial cartilage which lodges the auditory organ is exceedingly large, and constitutes, not only an oval capsule for the membranous labyrinth, but sends back a continuation which fills the space corresponding to the *pars mastoidea*, and extends somewhat higher than it beneath the parietal region of the skull. All the upper part of the cranium is and remains simply membranous.

The relations of the regions of the chondro-cranium thus formed to the parts of the brain and to the exits of the nerves are the same as those which are observed in the bones which they prefigure.

When these bones begin to be developed, some of them make their appearance in the cartilage of the embryonic skull, some in the perichondrium, others in the membranous roof which is continuous with the perichondrium.

A single ossification appears around the notochord in the basi-occipital region, and lays the foundation for the basi-occipital bone. The ex-occipitals commence as single centres of ossification in the cartilage bounding the sides of the foramen magnum. The supra-occipital (*SO*) is developed from two ossifications in the cartilage above the foramen magnum, and

Fig. 58.

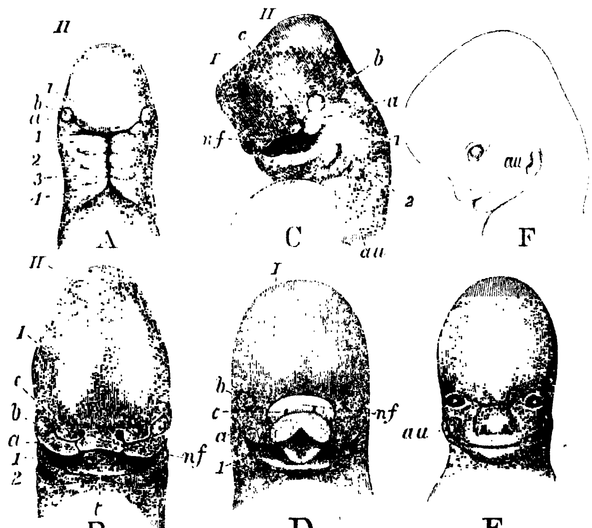

Fig. 58.—Successive embryonic conditions of the human head (after Ecker).—*I*, *II*, the first and second cerebral vesicles. 1, 2, 3, 4, the visceral arches; *a*, the maxillary process; *b*, the eye; *nf*, the middle naso-frontal process; *c*, the lateral naso-frontal process; *t*, the tongue; *au*, the outer part of the first visceral cleft, which eventually gives rise to the external auditory meatus.

A, at three weeks.
B, at five weeks.
C, at six weeks.
D, at seven weeks.
E, at eight weeks.
F, outline side view of E.

from two others which appear, not in cartilage, but in the membranous roof of the skull above the limits of the cartilage, and so give rise to that part of the squama occipitis marked *SO'*.

The basi-sphenoid is developed from two centres of ossification which appear in the floor of the *sella turcica*, but speedily coalesce into one. Two separate centres of ossification appear in the cartilage between these and the alisphenoids, and form the *lingulæ sphenoidales*. Each alisphenoid is developed from a

Fig. 59.

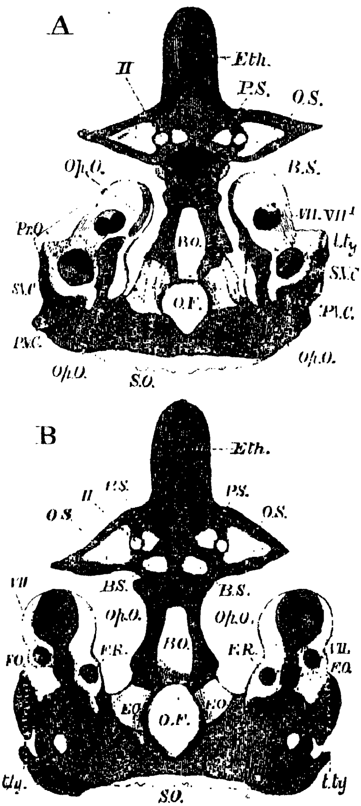

Fig. 59.—A, upper, and B, under view of the basis cranii and periotic cartilage of a human fœtus eight inches long. The alisphenoidal and immediately adjacent parts of the basi-sphenoid are omitted. The cartilage is darkly shaded, while the osseous deposits are left white, or but lightly shaded. The greater part of the supra-occipital is cut away. The clear spaces close to the dotted lines leading from *t.ty* are apertures in the cartilage. The epiotic classification has not yet appeared, and the pro-otic and opisthotic ossifications are quite distinct on the right side.

single centre in its cartilaginous predecessor, but the parietals are the result, not of the ossification of cartilage, but of that of the membrane which roofs in the skull. Each has its own centre of ossification in this membrane.

The presphenoid arises by two separate centres of ossification, one on the inner side of each optic foramen. (Fig. 59, *P.S.*) These centres coalesce with the orbito-sphenoids of their own side before they unite with one another.* The osseous orbito-

* The mode of ossification of the sphenoid bone is one of the most difficult questions in osteogenesis. Meckel has worked out the problem at great length in his "Archiv," Bd. i., and thus sums up his results in the "Handbuch der Menschlichen Anatomie," Bd. ii., pp. 102-4 :—

"In the third month, the first osseous nuclei appear in the two great wings, and soon afterwards the internal pterygoid processes begin to ossify as separate bones. Next, a third pair of ossifications appears in the external circumference of the alæ minores; and then, about the fourth month, a seventh and eighth nucleus, which lie side by side in the body of the sphenoid. In the fifth month is formed, alongside this fourth pair, a fifth, between it and the great wings. Upon this the two median nuclei of the body coalesce. Soon arises a sixth nucleus, on the inner side of the optic foramen, and then a seventh appears between this and the fourth, so that, about the beginning of the seventh month, the sphenoid consists of thirteen separate bony nuclei, since, notwithstanding seven pairs have arisen, the two primary nuclei of the body early coalesced into one.

"From this time forth the number of the nuclei diminishes still more considerably by coalescence. Those nuclei coalesce earliest which give rise to the portions of the sphenoid, which persist in a separate state longest. The fourth, fifth, and seventh pair soon unite into one piece; the first and second, coalescing on each side, constitute two other pieces; the third and sixth two others; whereby, in the eighth month, the sphenoid consists of five pieces—the two greater wings, the lesser wings, and the body. Somewhat later the two lesser wings coalesce into one, and the sphenoid now consists of four pieces; thereupon the body and the anterior pieces unite, so that in the fully-formed fœtus the sphenoid consists of three pieces, the greater wings and internal pterygoid processes being still distinct; but in the first month after birth these three pieces unite into one."

The fifth pair of ossifications here mentioned are the *lingulæ*; the sixth, those which give rise to the presphenoid. Meckel's seventh pair of ossifications, which arise between the fourth (basi-sphenoidal) and the sixth (presphenoidal), and are said, in the "Archiv," to coalesce first with one another, and then with the basi-sphenoid, appear not to have been observed by other anatomists. I have not seen them, and they are not mentioned by Virchow, the latest writer on the subject. Virchow writes ("Entwickelung des Schädel-grundes," 1857) :—"The posterior sphenoid arises (if we leave out of consideration the internal pterygoid processes which are developed as separate and independent bones), according to most authors, from three nuclei, but, according to my observations, from six. Two of these belong to the alæ magnæ (alæ temporales), or lateral arches (Bogenstücken) of the parietal vertebra. They arise in the third month, and the external pterygoids are produced by direct outgrowths from them. In the third month, I also find two other centres sphenoids arise each by one centre in the corresponding cartilages. The frontals, on the other hand, are developed, like the parietals, each from one centre in the membranous roof of the skull.

Thus we arrive at the singular result that, while all the bones of the basi-cranial axis, and all the lateral bones of the three

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of ossification which belong to the apices of the *lingulæ*, and are separated by distinct layers of cartilage from the others. The ossification of the *lingula* is almost complete in the fourth month, and its size is out of all relation to the dimensions of the other parts. It is a thick, obtusely-cylindrical process, which coalesces primarily with the body, and has nothing to do with the alæ. The *lingula* is therefore similar to an anterior or inferior transverse process (Parapophysis, Owen); and the *sulcus caroticus*, notwithstanding its position in the inner side of the *lingula*, resembles an open *foramen vertebrale*. However, Arnold's opinion that the Vidian canal answers to the canal for the vertebral artery, notwithstanding it is placed on the inner side of the lingula, deserves the careful attention of comparative anatomists. The ossification of the body begins in the third month, exactly under the pituitary fossa, which is already preformed in cartilage. Kerckring was the first to point out that here the adjacent osseous centres at first arise, and that they unite and form a biscuit-shaped mass in the fifth month. Once he saw this 'semilunula' even in the middle of the third month. Kölliker and I myself have met with it in fœtuses of three months. Other observers, as Nesbitt and Mayer, speak of a single centre in the third month, and in the fourth of two centres, which must be regarded as the result of the erroneous combination of different individual cases. I find constantly, in the beginning of the third month, two nuclei, which arise near the upper surface in the anterior wall of the pituitary fossa, and are separated by a broad layer of cartilage. Very soon, however, only a single osseous mass is present in the interior of the body, which extends through the whole thickness of the cartilage, while anteriorly and posteriorly it is still enveloped in cartilage. In a fœtus 19 centimètres [$7\frac{1}{2}$ inches] long, I saw the simple osseous nucleus in the bottom of the sella, as a transverse plate which had not yet united with the lingula."

"The anterior sphenoid is developed by the gradual coalescence of four osseous centres, of which again two belong to the body and one to each of the lesser wings. The latter are developed earlier than the former. They commence early in the third month, in the anterior clinoid processes, which are quite thick and osseous at a time when everything else in the anterior sphenoid is hyaline cartilage, and therefore are quite similar to the *lingulæ*. From this point ossification progresses rapidly, at last creeping round the circumference of the optic foramen to the body of the ala and to its anterior root. About the fifth month the lesser wing is completely solid in all parts. On the other hand, the nuclei in the body mostly appear somewhat later, usually in the fourth month, and at the inner edge of the optic foramen, so that they are at first separated by a tolerably broad median lamella of cartilage, which is continued into the ethmoid cartilage and *septum narium*. A union now very soon takes place between the centres of the body and those in the lesser wings, so that the optic foramen is surrounded by bone. . . . . Later, at times, as it appears, as early as the fifth month, the two lateral masses unite into a larger central piece, which is free superiorly, while below and anteriorly, in the middle line, it is surrounded by broad masses of cartilage."—Virchow, *loc. cit.*, pp. 15-18.

cranial arches, are primarily developed in cartilage, only one of the superior elements of these arches—the supra-occipital (*SO*) —is so; while the upper or "interparietal" portion of the *squama occipitis* (SO^1) and the two other pairs of superior elements of the arches are developed altogether from membrane.

Fig. 60.

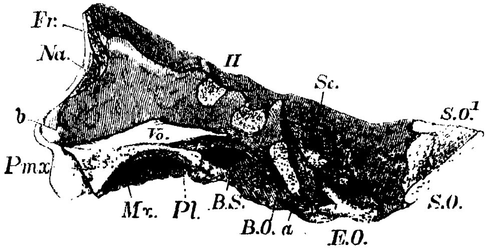


Fig. 60.—Longitudinal and vertical section of the *basis cranii* of a fœtus somewhat older than the foregoing (Fig. 59). The basi-sphenoidal and presphenoidal centres have coalesced; but they and the basi-occipital are severally separated by wide interstices of cartilage, of which the whole ethmoidal region is still constituted.

The ethmoid is developed from a single centre, arising in the internasal cartilage. Its so-called lateral masses, with the two upper spongy bones, are likewise developed each from a single centre within the superior part of the inflected lateral cartilages which wall in the olfactory sacs. The inferior turbinals are ossifications of the lower parts of these cartilages. But the nasal bones are developed within the perichondrium, which is continuous with the membrane in which the frontal bones are developed, and the vomer is produced within the perichondrium on the under-surface of the internasal septum. The bones of Bertin are also said to be developed from membrane—the perichondrium of the presphenoidal cartilage, or the walls of the olfactory sacs.

The development of the temporal bone is particularly worthy of attentive consideration. The squamosal and the tympanic elements are developed in membrane, and, at first, lie perfectly loose in this membrane, upon the outer side of the periotic cartilage. The tympanic is a delicate ring, open above; the squamosal is a mere rod, the *zygoma*, with an expanded posterior end, the *squama temporis*. The periotic mass, the styloid element, and the auditory ossicles are all preformed in cartilage.

The manner in which the cartilaginous capsule, which has the form of the subsequent periotic bones and lodges the membranous labyrinth, becomes ossified, has been much misunderstood; and as it is a point of vital importance in comparing the skull of man with that of the lower *Vertebrata*, I shall enter into some detail regarding it, as a matter of fact and as a matter of anatomical history.

Nearly two hundred years ago, Kerckringius, in his excellent "Osteogenia Fœtuum" (1670), laid the foundation for a proper understanding of this process:—

"Quarto mense mirum visu, quàm citò et quanta perfectione os squamosum magnam partem factum sit osseum. Os petrosum jam rubicundâ cartilagine signavit cavitatis suæ formam organorum auditûs capacem, nihil tamen adhuc præ se fert osseum, præterquam unam in longitudinem protensum crassiusculam et inæqualem lineam, annulo seu circulo, antea nominato, subjectam, et paulo longiùs protensam. Os itaque temporum hoc mense tribus constat ossiculis; annulo scilicet, osse squamoso, et illo jam commemorato.

"Quinto mense os squamosum ita adauctum est ut os syncipitis ferè, os autem cuneiforme omninò attigerit. Ossis petrosi pars illa quæ processum mammillarem constituit, terna de novo acquisivit ossicula: unum pyriformâ, acutiore, sui parte squamoso annectitur; alterum, scutum ovale referens, magnitudine priori vix cedens, mediâ cartilagine ab eo separatur; uti et tertium ab utroque, quamvis hoc magnitudine neutri sit æquiparandum, vix aciculæ majoris caput adæquans; sunt autem eo situ et ordine collocata, quem tabula fœtûs v. mensium, usurpata oculis facilius ad mentem quàm verba transmittet." . . . .

"Constat ergo os temporum hoc quinto mense sex distinctis ossiculis; osse videlicet squamoso, annulo, osse internam cavitatem efformante et tribus notabilibus quæ hoc mense exorta esse diximus."—*L. c.*, pp. 222, 223.

The explanation of the third figure in the thirty-fifth plate, referred to in this passage, runs thus:—"Tria in osse petroso ossicula ostendit, e, e, e. Tria petrosi ossis distincta ossicula."

"Sexto mense pyriforme et ovale scutiforme coaluerunt in unum, tertium nonnihil auctum est magnitudine."—*L. c.*, p. 224.

The third figure of the thirty-sixth plate exhibits the condition thus described, and the explanation is :—"Bina in osse petroso ossicula ostendit. *D*, ossis petrosi pars quæ jam ex duobus coaluit; *e*, tertium ossis petrosi ossiculum."

"Septimo mense jam tertium illud ossiculum duobus mense superiore inter se coalitis accessit. . . . .

"Nihil ergo de mense octavo nonoque addendum, nisi quòd ne tum quidem fœtus ullum habeat processum mamillarem, et quod adhuc insigni cartilagine distet os petrosum ab occipitis et syncipitis ossibus."—*L. c.*, p. 224.

The temporal bone of a seven months' fœtus is represented in Plate xxxvii., Fig. 2, with the explanation :—"Quæ primo tria, deinde bina, fuerunt in petroso ossicula, jam in unum coaluisse, ostendit. C, ossis petrosi substantia, ex tribus jam sæpe dictis in unum coalita."

Cassebohm ("Tractatus quatuor de Aure Humana," 1734, pp. 19 and 45; "Tractatus Quintus," 1735, p. 15) discovered that the little linear ossification mentioned in the first extract from Kerckringius is developed in the immediate vicinity of the *fenestra rotunda*, eventually surrounds it, and extends upon the base of the *pars petrosa*. But the first definite light thrown upon the signification of Kerckringius' "Tria ossa" is in the following extract from Meckel's "Handbuch der Vergleichenden Anatomie" (1820. Bd. iv., p. 49), though Meckel does not take the trouble to refer to and explain the older observer's statements :—

"4. *Bony labyrinth.*—In investigating the formation of the bony labyrinth, the origin of the bony substance of the petrous bone is very carefully to be distinguished from that of the labyrinth itself. The former begins earlier than the latter, according to the ordinary type of ossification, by the development of a loose, soft, reticulated tissue in the previously existing homogeneous cartilage, and extends from before backwards.

"The first part to ossify, about the end of the third month, is the circumference of the *fenestra rotunda*, which is remarkable by reason of the analogy of the *fenestra rotunda* to the tympanic annulus. The ossification begins above, descends posteriorly, and, after a ring has been formed in this manner, extends forwards.

"At the same time arises a proper centre of ossification, completely separated from this, at the external end of the superior vertical canal.

"After this, a third little scale is produced, opposite about the middle of the internal vertical semicircular canal.

"At the same time ossification extends swiftly backwards and downwards from the first piece, so as to give rise to the floor of the labyrinth.

"The second piece increases in size still more rapidly, so that, soon, the whole vertical semicircular canal, with the exception of its lower concave surface, is ossified. Simultaneously ossification is continued from its inner end over the inner surface of the petrous bone, surrounds the internal auditory meatus, penetrates into it, and so forms the floor of the cochlea.

"The horizontal semicircular canal begins to ossify, on its outer side, in the fifth month, by elongation of the bone forming the upper vertical semicircular canal: this is continued backwards, from without and below, round the horizontal semicircular canal. At least, I could discover no proper osseous centre for this canal, and it seems merely to become inclosed by the increase of the first and second."

All this is accurate, but, unfortunately, Meckel goes on to say, at page 51 of the work cited, that "the osseous labyrinth is at first perfectly separate from the bony mass of the petrous bone which surrounds it, is developed earlier than it, and is provided with quite a smooth surface, though the two lie close together;" and that "the bony labyrinth arises independently of the osseous substance of the petrous bone."

How Meckel arrived at this conclusion I do not know; but it is certainly erroneous, and it has been the means of creating a great deal of unsound speculation as to the ossified labyrinth being a something distinct from the proper *pars petrosa.*

It is further singular that, in this passage, Meckel not only, as I have said above, makes no reference to Kerckringius, but that he does not attempt to refer the regions of the *pars petrosa* and *mastoidea* to their separate origins. This is the more remarkable as, in his well-known paper on the "Ossification of the Vertebral and Cranial Bones" (Meckel's "Archiv," 1815), p. 636, he states expressly that the mastoid process arises from a special centre. Possibly the omission arose from Meckel's supposing that the exterior of the periotic mass is developed distinctly from the proper bony labyrinth.

Hallmann, in his well-known work, "Die Vergleichende Osteologie des Schläfenbeins" (1837), does not cite the account given by Meckel, and does not really improve upon the views of Kerckringius.

"In man, after, in the first place, the squamosal and then the *annulus tympanicus* are formed, the *os petrosum* and *mastoideum* is still a common cartilage, which fills, externally, the gap between the squamosal, the parietal, the supra-occipital and the ex-occipital. When, in the fourth month, the cochlea and a part of the semicircular canals, viz., the upper canal and the anterior crus of the external canal, already consist of porous bony substance, while the ossification of the posterior canal (and probably of the posterior crus of the external canal) has not proceeded so far; the *pars mastoidea* appears as a single or double nodule of the size of a millet-seed, which is deposited upon the arch of the posterior canal, contributes to its ossification, and now soon spreads over the whole cartilage, the four neighbouring bones growing towards it. In Nos. 2543 and 9420 of the Berlin Museum, the insertion of this nodule upon the petrous bone is quite distinct. This osseous centre appears in the dry skeleton as an oval nodule, which I could easily scratch off without injuring the canals, which proves that it arises as a separate part."

Lastly, Kölliker, in his recently published "Entwickelungs Geschichte" (1861), sums up the present state of our knowledge respecting the ossification of the periotic cartilage as follows (p. 320):—

"The ossification of the labyrinth does not appear to have been investigated since the time of Cassebohm ('Tract. de Aure Hum.,' Hal. et Magdeb., 1734 and 1735) and J. Fr. Meckel ('Handb. d'Anat.' iv. p. 42, *et seq.*), which seems to be the reason why certain incorrect statements are repeated year after year in almost all handbooks. It is not the case that the external part of the pyramid of the petrosal bone and the labyrinth ossify separately, nor is it true that ossification begins as a thin crust on the wall of the labyrinth; on the contrary, ossification commences in the whole thickness of the wall of the labyrinth; in such a manner, however, that it appears externally sooner than internally, and the whole pyramid becomes ossified from centres which make their appearance first upon the cartilaginous semicircular canals and the cochlea. The number of these is, as has been rightly stated, three—one on the first turn of the cochlea, and one on each of the upper and posterior semicircular canals, whence, by degrees, the whole *pars petrosa*, together with the cartilaginous *pars mastoidea*, which is united with it, ossifies in a manner, the details of which would not especially interest you. On the other hand, I do not agree in the statements that have been made as to the time at which this ossification arises. Neither in the third, nor in the fourth month, as is commonly stated, is there a trace of ossification; in fact, I have found the entire pyramid cartilaginous in an embryo five inches long at the eighteenth week, or, in the middle of the fifth month. Only at the end of the fifth, and especially in the sixth month, do the osseous deposits commence, but these increase very rapidly. In the sixth month, however, one meets with nothing but a beautiful reticulated cartilage ossification, and, as yet, no indication of true bone, which only arises, in the later months, from the periosteum of the labyrinth and from the external periosteum, whilst, contemporaneously, the internal cartilage ossification is reabsorbed and is replaced by a vascular true bone, which, by degrees, becomes finely spongy. The *Modiolus* and *Lamina spiralis*, in the sixth month, are still quite membranous, and only ossify at the end of fœtal life, without ever having been cartilaginous."

There is no doubt that the statement of Meckel, confirmed by Kölliker, that the periotic cartilage ossifies from three centres, is perfectly correct; there is no doubt, further, as Meckel, followed less clearly by Hallmann, has affirmed, that one of these centres gives rise to the future mastoid process;

but it is equally indubitable that Kerckringius' original statement is true, and may be readily verified in the dry skulls of fœtuses of the age he mentions. The beautiful series of human fœtuses presented by Mr. MacMurdo, in the Museum of the Royal College of Surgeons, enable one easily to reconcile the teachings of the older and the later observers, when taken in conjunction with the study of the same parts in wet preparations.

Fig. 61, A, represents the periotic capsule of a human fœtus five and a quarter inches long.

One ossification in the cartilage (*Op.O.*) is seen surrounding the *fenestra rotunda* (*F. R.*), and extending a little way upon the promontory. A second, very small, quadrate ossification (*Pr.O.*) is situated at the outer end of the superior vertical semicircular canal, and apparently extends into the cartilaginous *tegmen tympani*. There is no other ossification in the cartilage than these two. As the upper part of the periotic mass in man answers to the front part, and as the lower part corresponds to the hind part of the same mass in the majority of the *Vertebrata*, I term the ossification on the superior vertical semicircular canal the *pro-otic* bone, that on the cochlea the *opisthotic* bone.

In some dry fœtal skulls of this age the opisthotic ossification only is seen, just as it is described by Kerckringius, who seems not to have observed the pro-otic ossification at this period.

The pro-otic ossification rapidly extends, as Meckel states, over the superior vertical semicircular canal (see Fig. 59, A, p. 144), and reaching its posterior end, it includes the front and upper part of the posterior vertical canal; while, from the outer end of the anterior vertical canal, or the primitive centre, a mass of bone extends backwards in the periotic cartilage and, in the dry skull, appears conspicuously immediately behind the edge of the squamosal. (*Pr.O.*, Fig. 61, B.) This part of it is, in fact, that one of the "tria ossicula" of which Kerckringius says, "pyriformâ, acutiore sui parte, squamoso annectitur."

The opisthotic ossification likewise extends backwards and, its hinder extremity becoming apparent in the dry skull behind the tympanic, is Kerckringius' ossicle, "vix aciculæ majoris caput adæquans." (Fig. 61, B, *Op.O.*)

Fig. 61.

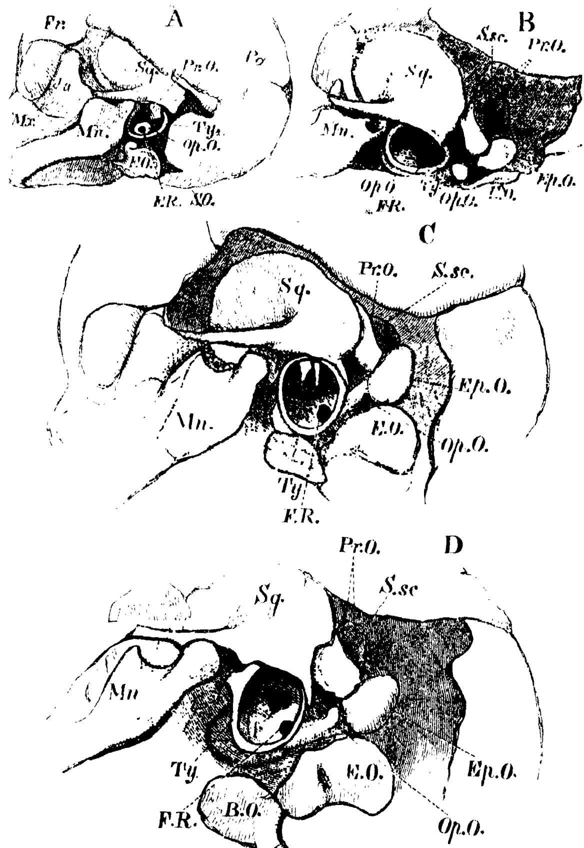


Fig. 61.—Development of the temporal bone.

A, from a fœtus $5\frac{1}{4}$ inches long, showing the commencing pro-otic and opisthotic ossification.

B, from a fœtus $8\frac{1}{2}$ inches long. The ossification in the tegmen tympani is no longer visible from without, but its continuation backwards over the superior, and part of the posterior, vertical semicircular canal is visible behind the squamosal. The epiotic ossification has made its appearance, and the hinder extremity of the opisthotic ossification appears behind the tympanic as the "third ossicle" of Kerckringius.

C, from a fœtus $10\frac{1}{4}$ inches long, the "tria ossicula" beginning to unite into the *pars mastoidea*.

D, from a fœtus $10\frac{1}{2}$ inches long, the tria ossicula anchylosed.

F.R., *foramen rotundum*.

S.sc, superior semicircular canal.

Lastly, the third ossicle, "scutum ovale referens," is that developed upon the posterior part of the posterior vertical semicircular canal, which gives rise to the mastoid process. (Fig. 61, B, *Ep.O.*)

Thus, in a fœtus between the fifth and sixth months, the "*pars mastoidea*" exhibits the appearance represented in Fig. 61, B. Its upper part is cartilaginous, but its lower part is occupied by the three "*ossicula*" of Kerckringius, which have now come into contact, and begun to unite, though their primitive contours are perfectly distinct.

The "*pars mastoidea*" of human anatomy is therefore not a single bone, but one, the "*scutum ovale*," combined with parts of two others; and as the "*scutum ovale*" is certainly the homologue of the bone I have termed *Epiotic* in the oviparous *Vertebrata*,* I propose to get rid of the confusing term "mastoid" altogether, and to call the specially "mastoid" part of the *pars mastoidea*, *Epiotic*.

Of the three periotic bones thus developed, the pro-otic gives rise to most of the *pars petrosa*, which is visible in the interior of the skull (Fig. 59, A), investing, as it does, the roof of the cochlea, the superior, and part of the posterior, vertical semicircular canals, the internal auditory meatus, and forming the *tegmen tympani*. To it, in addition, is due the upper half of the circumference of the *fenestra ovalis*, and a considerable portion of the *pars mastoidea*, as has been stated above.

The opisthotic bone constitutes all the *pars petrosa* visible on the base of the skull, furnishes the floor of the cochlea, surrounds the *fenestra rotunda*, and contributes half the contour of the *fenestra ovalis*; gives rise to the carotid canal by developing a lamella of bone, which gradually wraps itself round the carotid, and so converts the primitive groove for the vessel into a complete tube, at the same time furnishing the inner part of its floor to the tympanum.

The lower edge of the squamosal is at first nearly straight,

* Croonian Lecture. *Proceedings of the Royal Society*, 1858. In the absence of a sufficient knowledge of the development of the human temporal bone, I followed Hallmann in identifying the opisthotic of oviparous vertebrates with the mastoid of Mammals at the time this lecture was delivered.

but it soon sends a curved process downwards behind the auditory meatus and between the tympanic ring and the periotic bones. In the fœtal skull represented in Fig. 61, D, it is obvious that this process corresponds with the *Margo tympanicus* or post-auditory process of the adult temporal bone; and the manner in which the hinder end of the pro-otic ossification is fitted in between it and the representative of the ascending part of the posterior root of the zygoma is very well shown.

The tympanic bone is at first a delicate ring, interrupted above, and with tapering ends, which approach one another very closely. The anterior end is thicker than the posterior, however, exhibiting a sort of flange, or internal process, which corresponds in position with the middle root of the zygoma, and eventually unites with it. The lower arched part of the tympanic ring becomes anchylosed with the floor of the tympanum, while its posterior and upper end unites with the squamosal.

In the process of ossification thus commenced and advancing in the fœtal cranium, certain centres, at first distinct, unite, and become hard to distinguish from one another even before birth.

At this period a considerable interval of cartilage separates the basi-occipital from the basi-sphenoid; but the latter has, as at *a*, Fig. 62, A, become firmly united with the presphenoid, though traces of the original separation, and remains of the primitive cartilage, are readily discernible.

The ex-occipitals are still distinct from the supra- and basi-occipital, and the alisphenoids are only suturally united with the *lingulæ sphenoidales*, which are still large in comparison with the basi-sphenoid, though they very early unite with it. The orbito-sphenoid and the presphenoid are completely anchylosed together by the superior root of the former, but the inferior root of the orbito-sphenoid, or middle clinoid process, abuts against the basi-sphenoid. (Fig. 63.)

In the temporal bone—the pro-otic, opisthotic, and epiotic are indistinguishably united into the *pars petrosa* and *pars mastoidea*. The latter and the squamosal are firmly united, but the petro-squamosal suture between the *tegmen tympani* of the former and the squamosal bone is obvious. The tympanic bone, still little more than a mere ring, is firmly anchylosed with the squamosal and with the opisthotic portion of the *pars petrosa*, but the indication of the primitive distinctness of the two latter can be readily traced. (Fig. 62, C.)

Fig. 62.

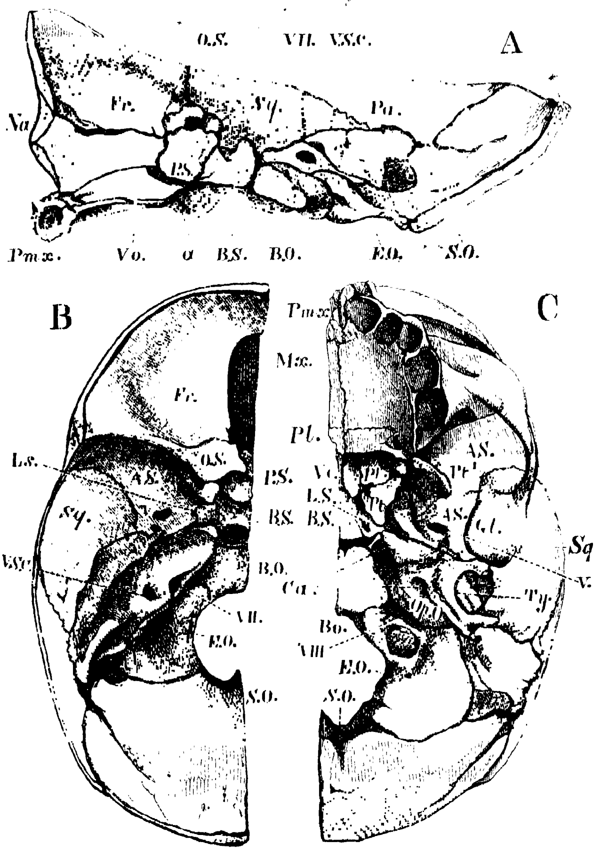


Fig. 62.—The human cranium at birth.—A, vertical and longitudinal section of the basal half of the cranium; B, upper, and C, under, view of the same preparation.

It is only after birth, and with the gradual advance towards adult years, that the spheno-occipital and the spheno-ethmoid synchondroses are obliterated, and the vomer becoming anchylosed with the ethmoid, the whole cranio-facial axis is fused into one bone, to which the ex-occipitals and supra-occipital, the alisphenoids and orbito-sphenoids, add themselves by a similar obliteration of the primitive separations. By addition of bony matter to its free margin, more especially to that of its lower part, the tympanic bone becomes converted into the gutter-like external auditory meatus. The epiotic grows out, inferiorly, into the mastoid process. The cavity beneath the bony arch in which the superior vertical semicircular canal is lodged, at first filled only by a plug of dura mater, becomes obliterated by bone.

Fig. 63.

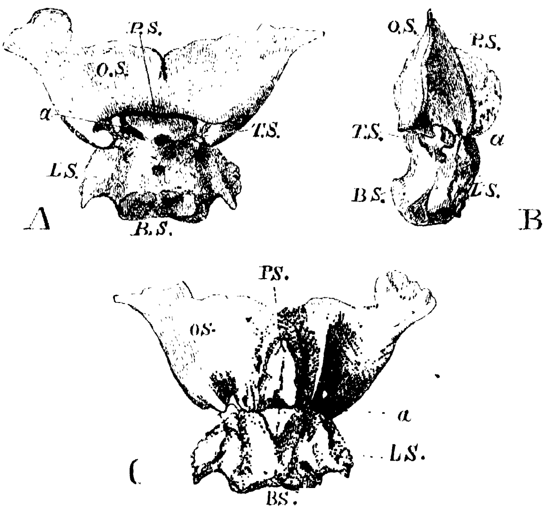


Fig. 63.—The basi-sphenoid and presphenoid, with the orbito-sphenoids of a human skull at birth.—A, viewed from above; B, from the right side; C, from below. *T.S.*, *tuberculum sellæ*: *L.S.*, *Lingula sphenoidalis*; *a*, basi-presphenoidal synchondrosis.

The basi-sphenoid acquires larger dimensions in proportion to the *lingulæ sphenoidales*, and the posterior clinoid processes, at first cartilaginous, become completely ossified. The bones of Bertin unite with the under-surface of the presphenoid, and the latter becomes almost obliterated, or converted into a mere vertical lamina of bone, by the extension of the olfactory chambers backwards to give rise to the sphenoidal sinuses.

The lateral masses of the ethmoid become anchylosed with the *lamina perpendicularis*, and form one bone—the ethmoid of human anatomy.

Of the facial bones, the premaxilla is developed within that part of the naso-frontal process which forms the anterior boundary of the mouth. The maxilla, the palatine, and pterygoid bones are produced within the maxillary process—the former from its external, the latter from its internal part. The internal pterygoid is, even before birth, united with the external pterygoid, the latter being simply an outgrowth downwards of the alisphenoid. None of these bones are at present known to be developed from cartilage, and the lachrymal and jugal are, similarly, membrane bones.

The cartilaginous rods within the first and second visceral arches undergo very remarkable changes. That of the first arch becomes modified into an upper portion, the future *incus*, and a lower portion, articulated with this, the future *malleus*, from which the rest of the cartilage is continued, as "Meckel's cartilage," along the inner side of the visceral arch (Fig. 64).

The incudal and malleal portions of the cartilage are, at first, proportionally very large, but their growth soon becomes arrested, and, a centre of ossification appearing in each, they become the *incus* and *malleus*. As the root of the first visceral arch is close to the outer and front part of the periotic capsule, so the *incus* and *malleus* have a corresponding position, and the tympanic bone, which is developed around the circumference of the modified first visceral cleft (which becomes converted into the auditory meatus, the tympanum, and the Eustachian tube), necessarily lies outside them, so that Meckel's cartilage passes between the tympanic bone and the periotic capsule, in its course from the malleus forwards and downwards. In front, the tympanic circlet marks the limit of its ossification. So far, it constitutes the *processus gracilis* (*Pg.*, Fig. 64), while, beyond this point, it eventually becomes obliterated. Very early, however, ossification takes place in the membrane of the first visceral arch, adjacent to the middle of the cartilage, and extending upwards towards the squamosal bone and, downwards and inwards, towards the symphysis, lays the foundation for each ramus of the lower jaw. The lower jaw, therefore, arises from membrane, and is not preformed in cartilage.

The axis of the second visceral arch becomes converted above into the *stapes*, below into the styloid cartilage, the stylohyoid ligament, and the lesser cornua of the hyoid bone, the body and greater cornua of which are developed from the third visceral arch. Between the styloid cartilage and

Fig. 64.

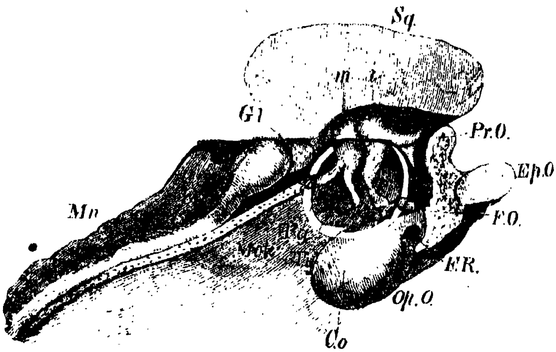


Fig. 64.—Part of the skull of a human fœtus at about the sixth month, dissected to show the auditory ossicles and Meckel's cartilage, *Mck.* *Gl*, the glenoid cavity. The *margo tympanicus* and adjacent parts of the squamosal are represented as if they were transparent, in order to show the position of the malleus (*m*) and incus (*i*). The tympanic bone (*Ty*) is merely indicated. *Co.*, the cochlea.

the *stapes* it is modified so as to form the stapedius muscle. A centre of ossification appears in the styloid cartilage, and, extending upwards and downwards, gives rise to the pyramid and the styloid process.

Some authors, however, give a somewhat different account of the metamorphoses of the cartilaginous axes of the first and second visceral arches to that which I have detailed, and which is based chiefly upon the researches of Meckel, Rathke, and Reichert. Thus Gunther,* while he agrees with Reichert that the cartilaginous axis of the first visceral arch divides into three portions, the uppermost of which (that which is primitively connected with the skull) early disappears, while the middle and lower become converted respectively into the *incus* and the *malleus* with Meckel's cartilage, differs from

* Beobachtungen über die Entwickelung des Gehörorgans bei Menschen und höheren Säugethieren. 1842.

him regarding the origin of the stapes. According to this writer :—"The middle division of the cartilaginous axis applies itself to the vesicular cartilaginous labyrinth, and when it comes into contact with the labyrinth, it sends out a small nodule, which is received by a pit, the future *fenestra ovalis.*" The nodule grows out into a process, the lower part of which becoming bent on the upper, and eventually articulated, is converted into the stapes, while from the upper part originates the long process of the incus.

The auditory ossicles are at first altogether outside the tympanic cavity; and as the latter enlarges, its mucous membrane is reflected around the ossicles. The deposit of osseous matter for each ossicle commences in the perichondrium, and the stapes has three ossific centres, independently of that for the *os orbiculare.*

It can hardly be doubted that there is much yet to be learned respecting the first steps in the development of the *ossicula auditus;* but the investigation is one fraught with difficulties.*

* See Magitot et Robin, "Cartilage de Meckel." *Ann. des Sc. Nat.* Sé. IVe. tome xviii.

LECTURE IX.

ON THE STRUCTURE OF THE SKULL.

THE SKULL OF THE PIKE COMPARED STRUCTURALLY AND DEVELOPMENTALLY WITH THAT OF MAN.

In the series of animals possessing a bony skeleton, osseous fishes and man may be regarded as the extreme terms; and I now select the skull of an osseous fish—the Pike—for comparison with that of Man. Whatever community of structure obtains between these must be expected to persist throughout the intermediate terms; while the differences between them will be more or less completely bridged over by the subsequent study of the skulls of the lower Mammals, Birds, Reptiles, and Amphibians.

At first sight, the skull of a pike (Fig. 65) presents the most

Fig. 65.

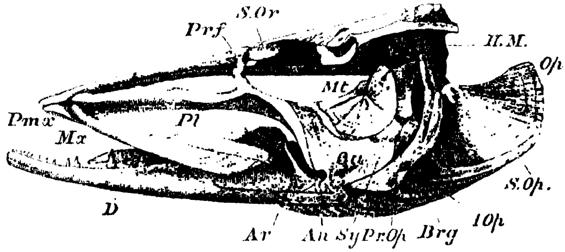


Fig. 65.—Side view of the skull of a Pike (after Agassiz).—*Prf*, prefrontal; *H.M.*, hyomandibular bone; *Op.*, operculum; *S.Op.*, sub-operculum; *I.Op*, inter-operculum; *Pr.Op*, pre-operculum; *Brg.*, branchiostegal rays; *Sy*, symplectic; *Mt*, meta-pterygoid; *Pl*, palato-pterygoid arch; *Qu.*, quadratum; *Ar*, articular; *An*, angular; *D*, dentary; *S.Or.*, supra-orbital bone.

striking dissimilarity to that of a man. The skull proper is flattened, narrow, and elongated, its vertical height and transverse diameter being insignificant when compared with its antero-posterior length, the predominance of which is due chiefly to the disproportionate enlargement of the anterior half of the cranio-facial axis, *i. e.*, the presphenoidal and ethmo-vomerine regions. The brain-case is relatively very small and much depressed, instead of presenting the capacious dome of the human skull, while, on the other hand, the facial apparatus is very large and complex, and its components are almost all moveable upon the skull. Another circumstance, which at once strikes the observer, is the fact that the lower jaw is not, as in Man, articulated directly with the skull; but is connected with the latter by the intermediation of a complex, mobile, suspensorial apparatus (Fig. 65, *H.M.* to *Qu.*), which articulates with the skull above and with the lower jaw below. A part of the same apparatus gives attachment to the hyoidean arch, and to the bones of the gill covers.

A certain fundamental resemblance may, however, be readily traced beneath these external differences. Thus, if a transverse and vertical section be taken through the pike's skull, so as to traverse the organ of hearing, and to divide the suspensorium longitudinally into two parts, the posterior and anterior moieties of the skull will present the appearances represented in Figs. 66 and 67. The posterior segment (Fig. 66) is obviously comparable with the corresponding segment of the human skull (Fig. 49), consisting, as it does, of a floor, with an upper arch, which, in the recent state, inclosed part of the brain, and with a lower arch formed by the various parts of the hyoidean apparatus.

Furthermore, certain of the bones (*Ep.O*, *Op.O*, &c.) which enter into the composition of the upper arch are especially related, as in the corresponding section of the human skull, to the organ of hearing, and it is with some of these that the inferior arch is connected.

The anterior segment (Fig. 67) presents a similar general correspondence with the corresponding segment (Fig. 48) of the Man's skull. That is to say, there is a floor with which is connected an upper arch, forming part of the brain-case, and a lower arch which enters into the composition of the face. The sides of this arch in the sectional view are partly constituted (compare Fig. 48) by bones specially connected with the auditory apparatus, and the peduncle of the lower arch is articulated with these bones. The chamber contained within the lower arch, however, differs from that seen in the section of the human skull in that it is entirely devoted to the buccal cavity, and is not subdivided by processes of the palatine and maxillary bones into an upper, nasal, and a lower, oral, passage.

Fig. 66.

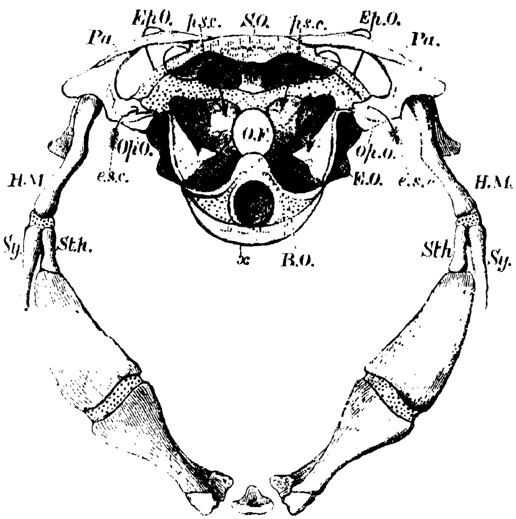


Fig. 66.—The posterior segment of the skull of a Pike which has been vertically and transversely bisected. The bones of the inferior arch are represented diagrammatically. The epiotic, opisthotic, pro-otic, and squamosal bones are left unshaded, as in the corresponding section of the human skull. *p.s.c.*, *e.s.c.*, arrows indicating the positions of the posterior and external semicircular canals; *x*, parasphenoid.

The comparison of the transverse sections of the Pike's with those of the Man's skull thus enables us to perceive certain resemblances between the two. In each there is an axis, upper and lower arches; in each the section separates the bones which lodge the auditory organs; and the most apparent difference between the two is the vastly greater proportionate size of the periotic bones in the Pike.

The comparison of the longitudinal section of the Man's skull with that of the Pike (Fig. 68) confirms the conclusions arrived at from the study of the transverse sections. A "cranio-

Fig. 67.

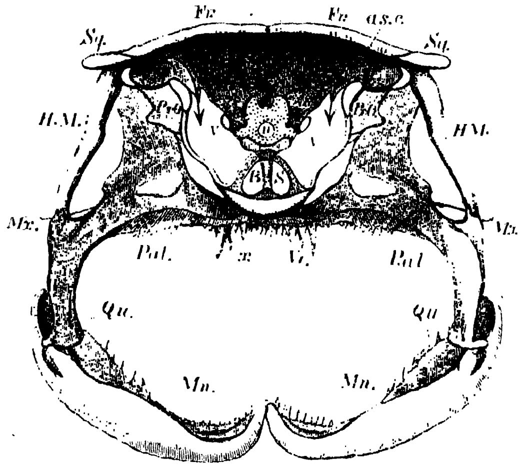


Fig. 67.—The anterior segment of the skull represented in Fig. 66.—*Mn*, mandible. *a.s.c.*, arrow indicating the position of the anterior semicircular canal. The letters *B*, *S*, one on each side of the basi-sphenoid, are seen through the canal for the orbital muscles. The pro-otic bone is left unshaded. In this, and in the preceding figure, the dotted shading indicates cartilage; but, as the drawings were made from a dry skull, it must be remembered that the whole of the cartilage entering into the cranium is not represented.

facial axis," composed partly of bone and partly of cartilage, extends from the occipital foramen to the anterior extremity of the snout of the fish. The posterior part of this constitutes the floor of the cranial cavity, and is the basi-cranial axis. The anterior part, excluded from the cranial cavity, is, as in Man, the basi-facial axis.

Again, as in Man, three pair of chambers, destined for the lodgment of the organs of the higher senses, are placed symmetrically upon the sides of the Pike's skull. The olfactory chambers are situated just in front of *Prf.*, in Fig. 65, and the orbits beneath *S.Or.*, while the auditory organs are inclosed within the posterior bony walls of the brain-case, as indicated in the transverse sections. And, as in Man, the olfactory and auditory apparatuses are fixed within their chambers, while the eye is freely moveable within the orbit.

Thus, for the Pike, I may repeat the phraseology which I employed in giving a general description of the skull of Man. It consists of an axis, of upper and lower arches, and of chambers for the sensory organs.

The next point is to ascertain how far this correspondence, thus traced generally, extends into the details of the composition of the skull; and here we may conveniently begin, as before, with the study of the cranio-facial axis.

Viewed as a whole, this axis is rounded and thick behind, compressed from side to side in the median region, and thickened and depressed in front. It is composed, as I have said, partly of bone and partly of cartilage. Behind, it consists of a single well-ossified mass (*B.O.*), which offers, posteriorly, a deeply excavated conical articular facet, quite similar to that presented by the body of the first vertebra, with which it articulates. Anteriorly, it is also excavated in the middle, its conical cavity terminating the canal for the orbital muscles behind. Its upper face forms the hinder part of the floor of the cranial cavity and the inferior boundary of the occipital foramen. Its lower face is bevelled off in front, and articulates with the hinder part of the upper face of the bone *æ*, Fig. 68.

Laterally and posteriorly, it articulates with the bones (*E.O.*), which constitute the lateral boundaries of the occipital foramen; while, laterally and anteriorly, its deeply-excavated surface is free, and forms part of the deep chamber in which the sacculus of the auditory organ is lodged. The greater part of this bone is solidly ossified throughout, but its conical anterior cavity is lined by a thin shell of bone, which is separated by a continuous layer of cartilage, thicker above than below, from the rest of the osseous mass.

In a longitudinal section (Fig. 68) of a fresh Pike's skull, the upper part of this layer of cartilage is readily seen, and can be traced without interruption, from the axis of the bone under description as far forwards as the posterior margin of the pituitary fossa, and therefore, for a long distance in front of the anterior termination of the bone *B.O.* The layer of cartilage bends down at the sides, and so enters into the lateral walls of the cavity for the orbital muscles. The cartilage, however, does not immediately constitute the floor of the skull, or the roof and side walls of the canal for the orbital muscles, seeing that it is coated over, on both its faces, by bony matter, which is continuous with that forming the inner and the outer faces of the bone *Pr.O.*

Although there can be no doubt, then, that the cartilaginous lamella in question forms part of the basi-cranial axis, it does not, strictly speaking, form part of the floor of that skull, being shut out therefrom by the extension over it of the ossifications (*Pr.O.*), towards the middle line. Leaving these ossifications out of consideration, however, it may be said that the free edge of the middle part of the cartilaginous lamella forms the posterior boundary of the fossa for the pituitary body, which dips down, surrounded by membrane, through the centre of the canal for the orbital muscles, and rests upon the concave surface of an elevation of the bone *x* at *P*, Fig. 68. Immediately in front of

Fig. 68.

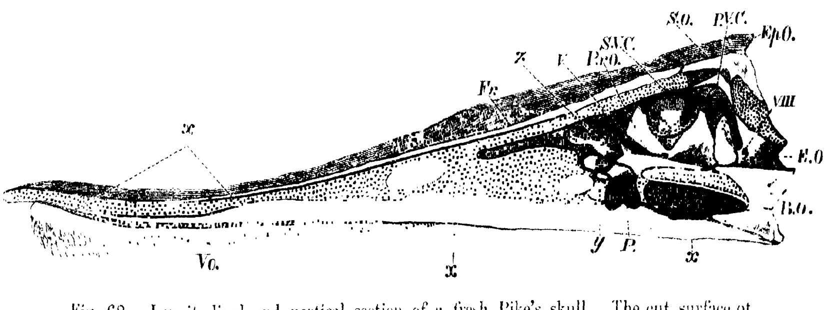


Fig. 68.—Longitudinal and vertical section of a fresh Pike's skull. The cut surface of cartilage is dotted. For *S.V.C.*, *P.V.C.*, read *a.s.c.*, *p.s.c.*, as in Figs. 66 and 67.

this elevation cartilage reappears, and extends, as an inter-orbital, ethmoidal, and internasal septum, to the end of the snout. The cranial cavity rapidly narrows above the cartilaginous inter-orbital septum, and ends where the olfactory lobes abut against the olfactory sacs. It appears to terminate much sooner, however; for the olfactory lobes, after running parallel with one another for some distance, diverge, and become separated by a plate of cartilage, which corresponds to a certain extent with the *crista galli* of the human skull.

Fig. 69.

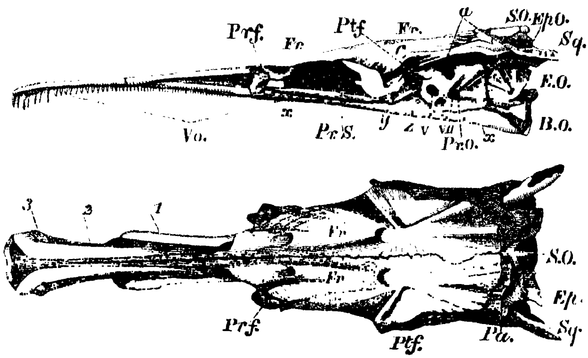


Fig. 69.—Side and upper views of a Pike's skull (after Agassiz).—*a*, the articular facet for the hyomandibular bone; *x*, the "*parasphenoid*;" *y*, the true basi-sphenoid; *z*, the alisphenoid.

Immediately in front of the pituitary fossa a thin plate-like ossification, *y*, is developed in the cartilage, and this plate sends off backwards and a little upwards, upon each side, a process which is connected posteriorly with the cranial floor. These two processes consequently lie at the sides of the pituitary fossa, and the "Y-shaped bone," as it has been well termed, thus furnishes part of the front and side walls of that fossa.

The next ossification to be noted in the cranio-facial axis of the Pike is the great bone *x* (Figs. 66 to 69), which stretches, like a splint, along the greater part of the length of the base of the skull.

The lower face of the hinder half of this bone is free, while that of its front half is covered by the bone, *Vo.* The upper face of its hinder half articulates, at first, with the lower surface of *B.O.*, but is then free for some distance, forming the floor of the canal for the orbital muscles, and articulates by expanded aliform processes of its sides with the lateral walls of that canal. At the front part of the canal it exhibits the elevation which forms the floor of the pituitary fossa, and then, depressed at the sides, but exhibiting a median superior ridge, it underlies the inter-orbital and ethmoidal cartilages.

The last ossification of the cranio-facial axis is a depressed bone *Vo*, thicker in front than behind, which fits on to the under-surface of the anterior half of the bone just described, and extends beyond it to the front end of the snout. The under-surface of this bone is free, enters into the middle of the roof of the palate, and bears teeth.

In comparing the cranio-facial axis of the Pike with that of Man, two pair of bones appear, at once, to correspond so closely that no reasonable doubt can be entertained as to their homology. These are the posterior and anterior bones of the series in each case. The former, in its relation to the spinal column, to the medulla oblongata, and to the lateral arches of the skull of the Pike, is precisely comparable with the basi-occipital of Man; while the anterior bone as exactly answers to the vomer of man; except that the fish, being devoid of any communication between the olfactory chambers and the cavity of the mouth, the vomer has a different form, and has of course no relation to nasal passages.

Again, it seems obvious that the ethmoid is represented only by cartilage, as in the fœtal state of the human skull, for there is no ossification in that portion of the cranio-facial axis which lies between the olfactory sacs.

And the like appears to be true of the presphenoid, for all that vertical plate-like portion of the cranio-facial axis which lies between the orbits, and beneath the peduncles of the olfactory lobes, and in front of the crossing of the optic nerves, is merely cartilaginous.

The Y-shaped bone forms part of the front and side walls of the pituitary fossa, and its upper prolongations are connected behind with the bones *Pr.O*, and with the floor of the cranial cavity. In this floor, the long cartilaginous plate, already mentioned, constitutes the hinder boundary of the fossa, and separates the Y-shaped bone from the basi-occipital. Now, the proper basi-sphenoid (that is to say, the central ossification taken apart from the *lingulæ*) forms the front boundary of the pituitary fossa in Man, but extends obliquely downwards in front of it as the stem of the Y-shaped bone does in the Pike.

Furthermore, in the fœtal human skull, the basi-sphenoid contributes nothing towards the posterior boundary of the pituitary fossa, which is formed by the long cartilaginous synchondrosis which connects the rudimentary basi-sphenoid with the basi-occipital. I identify the lamella of cartilage which I have described in the Pike with this synchondrosal portion of the fœtal human *basis cranii.*

But the basi-occipital, basi-sphenoid, presphenoid, ethmoid, and vomer of Man being now accounted for in the Pike's cranio-facial axis, what, it may be said, is the nature of the bone *x* to which the term "basi-sphenoid" is commonly applied?

It differs from any of the ossifications of the basi-sphenoidal cartilage in Man, not only by extending backwards beneath the basi-occipital, but by stretching forwards, beneath the pre-sphenoidal and ethmoidal cartilages, to within a short distance of the anterior extremity of the cranium; and in the still more important circumstance that it is an ossification within the perichondrium, which can be stripped off, in skulls which have been macerated, or steeped for a short time in boiling water, without injury to the cartilage upon which it is developed.

Mr. Parker has shown, in his valuable paper on *Balæniceps*,* that the so-called basi-sphenoid of birds is developed from three ossifications, a central one, the true basi-sphenoid, and two lateral and inferior centres—the "*basi-temporals*" (Parker), which appear to correspond with the *lingulæ* of Man.

The thought readily arises that the single bone *x* may correspond with these two basi-temporal ossifications. The latter, however, appear to be cartilage ossifications like the *lingulæ* themselves: and, upon the whole, I think it will be safer, at any rate for the present, to regard the bone *x* as peculiar to the branchiate *Vertebrata*, and to confer upon it the special name of "*parasphenoid.*"

Connected with the bones of the basi-cranial axis are upper arches, and, as in Man, the hindermost of these arches consists of three elements, two of which are lateral and one superior. Each lateral bone articulates below with the basi-sphenoid, and forms the lateral boundary of the occipital foramen. Above, it

* Transactions of the Zoological Society, vol. iv.

unites with its fellow for a short distance, and so constitutes the upper boundary of that foramen, shutting out the superior bone from any share in its formation. Except in this point, it will be observed that the three bones quite correspond with the ex-occipitals and supra-occipital (*S.O.*) of Man. The ex-occipital (*E.O.*), however, further differs from that of Man in that it is perforated and not merely notched, by the foramen for the eighth pair, and that it is produced in front of, and external to, this foramen, so as to enter largely into the chamber which lodges the lower and posterior part of the organ of hearing. Furthermore, there is no perforation for any hypoglossal nerve, that nerve not being represented in a distinct form in the fish.

Fig. 70.

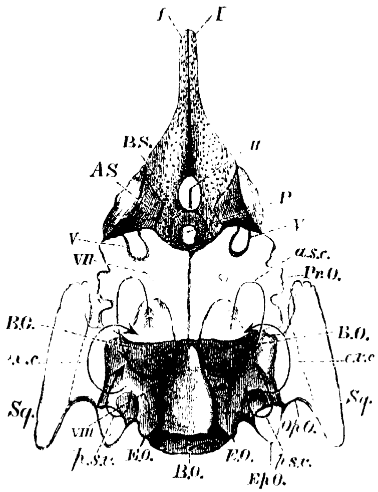


Fig. 70.—The basal and lateral bones of the skull of a Pike viewed from above. The squamosal and the three periotic bones are left unshaded. *P*, the pituitary fossa.

In the Pike, no bony wall separates the membranous labyrinth from the cavity of the skull, the periotic ossifications being all situated, as they are when they first appear in Man, upon the outer side of the capsule of the labyrinth; and this capsule is still less complete than that of the human fœtus, seeing that its inner wall is not even cartilaginous, but remains in the condition of membrane. Notwithstanding the comparatively incomplete condition of the periotic bones of the fish, however, they are as clearly and distinctly identifiable as any bones of the skull.

The large bone, *Pr.O.*, which occupies a great part of the wall of the cranial cavity, in front of the ex-occipital, has its front margin deeply notched for the exit of the third division of the trigeminal. It presents a foramen through which the *portio dura* passes; it protects the anterior part of the vestibule and the anterior vertical semicircular canal. In other words, it has exactly those relations to the auditory organ and to the cranial nerves which especially characterise the pro-otic ossification of Man—which, it will be recollected, also protects the anterior part of the organ of hearing, lies behind the exit of the third division of the trigeminal, and is perforated by the *portio dura*.

In minor respects, on the other hand, the pro-otic of the Pike differs from that of Man; as, for example, in its vast proportional size; in its remaining distinct from the other periotic bones; in the wide ossification which extends from it over the basal cartilage of the skull towards the middle line; and in coming into contact with the ex-occipital and basi-occipital behind. But none of these modifications really interfere with the homology of the bone—which we shall find to be identifiable by the same essential characters throughout the vertebrate series.

The epiotic element is not less distinctly recognisable. The upper and lower crura of the great posterior vertical semicircular canal traverse notches in the supra-occipital and ex-occipital respectively, but the summit of the arch of the canal is inclosed within a distinct conical ossification, the "external occipital" of Cuvier. This ossification is, in fact, perched upon the posterior vertical semicircular canal, just as the human epiotic ossification is perched upon the summit of the arch of the same canal when it first appears; and if the semicircular canals of man were to grow in the same proportion to the brain-case as those of the fish, the epiotic would be carried out as far, and would leave a considerable space between the pro-otic and itself, into which the adjacent supra-occipital and ex-occipital bones might intrude, as they do in the fish.

The third of the periotic ossifications—the opisthotic—seems at first not to be discoverable in the Pike. But in some specimens of this fish, and in a great many other fishes, there is a distinct bone (which is particularly large and conspicuous in the *Gadidæ*) connected below and behind with the ex-occipital, in front with the pro-otic, internally and behind with the epiotic, and externally with the squamosal. It enters especially into the outer and posterior wall of the labyrinth, and protects a great part of the external semicircular canal, sharing this function with the pro-otic.

As there is neither *fenestra ovalis* nor *rotunda* in the fish, and as it is by no means certain whether the sacculus does or does not correspond with the cochlea of the higher *Vertebrata*, some of the best marks by which the opisthotic may be identified are wanting; but the relations of this bone to the other periotic ossifications seem to me to be decisive as to its real nature.

The periotic bones being thus identified, they are all eliminated from comparison with the proper supero-lateral constituents of the cranial arches. And there remains only one bone in the lateral walls of the Pike's cranial cavity which can answer to any of these, which is that marked *z* in Figure 68, *A.S.* in the other figures.

This bone has the form of a triangle, with its apex turned downwards. The hinder side of the triangle abuts against the anterior margin of the pro-otic, and closes the trigeminal notch in that bone anteriorly. The front margin ends in the cartilaginous side walls of the skull; the apex approaches, but stops a little short of, the lateral wing of the Y-shaped bone, or basisphenoid. The relations of this bone are therefore essentially those of the alisphenoid, though I think it quite possible that the orbito-sphenoid may, to a certain extent, be represented by its anterior portion.

The bones which enter into the roof of the skull (Fig. 69) remain for consideration. Of these, the supra-occipital, which has no additional constituent comparable to *S.O′* in Man, has already been mentioned. It articulates in front with two very large and long bones (*Fr.*), separated by a median suture, which narrow in front of the orbits and end in a point beyond the nostrils, and but a short distance from the extremity of the snout. The supra-occipital lies between, and separates two other comparatively small and insignificant bones (*Pa.*), which are situated between the posterior edges of the parietals and the epiotics, and, strictly speaking, do not enter into the roof of the cranial cavity at all. Of these two pairs of bones, the anterior represent the frontals of Man, and the posterior his parietals. The position and proportions of the bones are, indeed, remarkably altered; but we shall find by and by, that these very variable cranial elements undergo almost as great changes of proportion and relation even within the limits of the Mammalian class.

The three bones which correspond with the *pars petrosa* and *pars mastoidea* have already been identified. In Man another element, the squamosal, situated above and external to the pro-otic and opisthotic enters into the composition of the temporal bone. In the Pike there is a corresponding bone, which forms the external and posterior angle of the skull, and lies above and external to the pro-otic and opisthotic, being usually anchylosed with the latter. The under and outer surface of this squamosal bone contributes towards the formation of the articular facet for the suspensory apparatus of the lower jaw. There appears to be no ossification in the ethmoidal cartilage, which answers to the *lamina perpendicularis* of the ethmoid. But, separating the orbits from the nasal chambers, there is on each side of the frontals, and partially overlapped by them, a bone which helps to bound the hinder wall of the nasal chamber, which lies external to the olfactory nerve, and which is in immediate relation with the nasal division of the trigeminal nerve. This is the bone termed "pre-frontal" by Cuvier, and it obviously corresponds with the lateral mass of the ethmoid in Man, which, in like manner, enters into the wall of the olfactory chamber, lies external to the olfactory nerves, and is traversed by the nasal division of the fifth.

Thus far the bones entering into the composition of the Pike's cranium (with the exception of the "parasphenoid") have been identified without much difficulty with those met with in Man. But there remain several others which seem to be without human homologues. These are, firstly, the bones called post-frontal, *Pt.f.*, which form the posterior, superior, and external angles of the orbits, and are wedged in between the alisphenoids and the pro-otics; secondly, the bones marked 1 and 2, developed upon the ethmoidal cartilage external to the points of the frontals. The pair 1,1, which immediately overhang the external nares, are probably to be regarded as the nasals of Man; but the nature of the second pair, 2,2, which lie internal to them, and extend to the end of the snout, is doubtful. Still less does there appear any reason to identify the bones 3,3, which are minute triangular ossifications in the substance of the cartilage between the bones 2,2 and the vomer, with any which exist in man. I consider them to be peculiar to the fish.

And now to sum up, in a few words, the structure of the brain-case of the Fish. We find, as in Man, a posterior, *occipital*, segment, consisting of basi-occipital, ex-occipital, and supra-occipital; a middle, *parietal*, segment, consisting, as in Man, of a basi-sphenoid, alisphenoids, and parietals, but in which the latter, in consequence of the disproportionate size of the frontals, are thrown far back out of connection with the alisphenoids; and, finally, an anterior, or, *frontal*, segment, of which only the frontals are separately distinguishable in the osseous state. The orbito-sphenoids and the presphenoid are alike represented only by cartilage and membrane, unless, indeed, as has been suggested, a part of the alisphenoid may take the place of the former bones.

Of the bony elements connected with the sense-capsules in Man, the pro-otic, opisthotic, and epiotic, together with the squamosal, have been clearly identified in the Pike; as have the pre-frontals and the vomer.

But certain bones present in Man have not been recognised in the Fish; while, on the other hand, certain bones present in the Fish appear to have no representatives in Man.

Thus, while the study of the cranial structure of the Man and the Pike reveals a fundamental identity of composition between the two, it demonstrates the existence of a no less marked diversity, each type exhibiting structures and combinations peculiar to itself.

The principal bones which surround the oral cavity in the Pike are disposed, as in Man, in pairs, some being in front of and above the oral aperture, while others are behind and below that aperture; and they inclose the buccal and pharyngeal chambers.

Fig. 71.

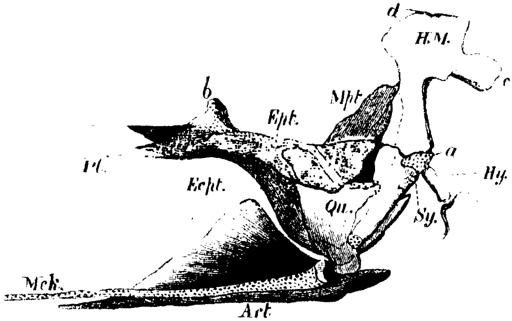


Fig. 71.—Palato-quadrate arch, with the hyomandibular and symplectic, the articular piece of the lower jaw, and Meckel's cartilage, of the Pike, seen from the inner side. *a*, the cartilage interposed between the hyomandibular and the symplectic; *b*, that which serves as a pedicle for the pterygo-palatine arch; *c*, process of the hyomandibular with which the operculum articulates; *d*, head of the hyomandibular which articulates with the side of the skull.

The anterior pair of pre-oral bones (*Pmx.* Fig. 65), small, and beset with teeth upon their under-surfaces, are connected with the vomer and the termination of the cartilaginous rostrum formed by the internasal septum. They obviously answer to the human pre-maxillæ. An elongated bone (*Mx.*), which bears no teeth, is connected anteriorly with the pre-maxilla, and, lying external to the other pre-oral bones, forms the boundary of the gape. Its homology with the maxilla of Man appears to be unquestionable. A second smaller bone is connected with the posterior part of the upper edge of the maxilla, and is usually regarded as a subdivision of it.

Behind the pre-maxillæ, and internal to the maxillæ, in the situation occupied by the palatine and pterygoid bones in Man, the Pike has an osseous arch of much greater complexity and somewhat different connections.

The summit of this "palato-quadrate" arch is moveably articulated, by a cartilaginous pedicle, with the outer surface of the pre-frontal process of the skull. The anterior crus of the arch stretches forwards, parallel with the vomer, to the premaxilla; its posterior crus extends backwards, and, spreading out, ends in an upper (*Mpt.*) and a lower (*Qu.*) prolongation.

Five bones enter into the composition of the arch—two median, two posterior, and one anterior. The median bones are so disposed that their anterior ends embrace the lower part of the cartilaginous pedicle (*b*), the one lying more external, and the other internal, to the latter. The more external has been called "*ectopterygoid.*"* It exhibits a short, ascending process, running up towards the pre-frontal, and strengthening the cartilaginous pedicle; an anterior process which articulates with the bone *Pl.*; and a posterior arched prolongation, which descends in front of the bone *Qu.*, and articulates with its anterior edge. The internal bone, called "*entopterygoid*" (*Ept.*), is a nearly straight, flat bone, the anterior half of which is applied, like a splint, to the inner face of the ectopterygoid, while its broader posterior face is similarly adjusted, above, to the bone *Mpt.*, and, below, to the bone *Qu.* The two last-mentioned "posterior" bones of the arch are termed respectively the "*metapterygoid*" and the "*quadrate*" bones. The former is a broad, four-sided bone, convex upon its inner surface, which presents a raised, curved ridge, beneath which the entopterygoid is received anteriorly and the hyomandibular posteriorly. It is connected below with the quadrate bone, and, behind, it overlaps the hyomandibular (*H.M.*) and the symplectic (*Sy.*).

The os quadratum (*Qu.*), so termed, not on account of its form, which is triangular, but by reason of its identity with a bone called by the same name in Birds and Reptiles, presents inferiorly an articular head, with an elongated articular surface, convex from before backwards, for the lower jaw. On the posterior part of its inner surface it has a deep groove, directed from above downwards, very nearly parallel to its posterior edge. Into this the symplectic is received.

The anterior bone (*Pa.*), lastly, is elongated and flattened, and bears teeth upon its lower surface. It is received ante-

* Not to multiply names unnecessarily, I adopt this term, which involves no theoretical implications. It must be carefully borne in mind, however, that this "ectopterygoid" has nothing to do with the "external pterygoid" process of Man.

riorly into the re-entering angle between the vomer and the pre-maxilla and maxilla. It is usually regarded as the palatine bone.

Before attempting to discuss the homologies of these several constituents of the palato-quadrate arch in the fish, it will be necessary to take into account the nature and arrangement of its post-oral facial bones.

In Man, the post-oral bones are arranged in two arches—the mandibular and the hyoidean; or, more strictly speaking, since the hyoidean arch is really composed of two, indicated by its lesser and greater cornua, there are three post-oral arches.

In the Pike, the lower jaw forms a mandibular arch, obviously corresponding in a general way with that of Man; behind this follows a second arch, answering to the styloid processes, stylohyoid ligaments, and cornua minora of the human hyoid, but with much greater masses of bone entering into its composition; and this is succeeded by no fewer than five other arches, the four anterior of which, supporting the gill filaments, are termed the "*branchial arches*," while the last pair, which carry no branchiæ, and are much smaller than the others, are called the "*inferior pharyngeal bones*."

The symphysis of the lower jaw is formed by the ligamentous union of two bones, which carry the inferior teeth of the Pike, and correspond respectively with the rami of the human mandible. But, besides these *dentary* bones (*D*, Fig. 65), each half of the lower jaw of the Pike has two other constituents, which are not represented in the human lower jaw. One of these is a small bone, which forms the lower part of the angular process of the jaw. It is termed the *os angulare*, or angular piece (*An*, Fig. 65). The other is a large triangular bone, which fits in between the dentary and the angular, and is termed the articular (*os articulare, Ar.*), because on its upper surface it bears a concave articular fossa, into which the condyle of the quadrate bone is received (Fig. 71). The cartilage which partially forms the walls of this fossa is continued into a long tapering rod, which lies upon the inner surface of the articular and of the dentary, and terminates in a point shortly before reaching the symphysis (*Mck.*, Fig. 71).

This rod of cartilage affords a safe basis upon which to found a homological argumentation. For it most certainly corresponds with Meckel's cartilage in the human fœtus, and the dentary bone lies outside it, in just the same way as the dentigerous ramus of the human mandible lies outside Meckel's cartilage. But the articular bone is an ossification in and around the proximal end of Meckel's cartilage in the Pike, just as the *malleus* is an ossification in and around the proximal end of Meckel's cartilage in the human fœtus; and the *os quadratum* is related to the *os articulare* of the fish in the same way as the *incus* is related to the *malleus*.

Hence it is to be concluded, in the absence of any evidence to the contrary, that the articular piece of the Pike's lower jaw answers to the *malleus*, and the quadrate bone to the *incus*.

I am not aware that any evidence can be adduced against this view; but, on the other hand, the relations of the parts thus identified to the *portio dura* of the seventh nerve, in Man and in the Fish, seem to me to afford it much support.

The *portio dura* in the former perforates the *pars petrosa*, and, after skirting the inner wall of the tympanum, external to the labyrinth, leaves the skull by the stylo-mastoid foramen. Before it does so, however, it gives off a recurrent branch, the *chorda tympani*, which takes a very singular course—passing between the pyramid, which is the upper end of the hyoidean arch, and the tympanic bone, entering the tympanum, crossing the auditory ossicles to make its way out at the front wall of the tympanum, between the tympanic and the squamosal, then uniting with the gustatory division of the trigeminal, and passing down along the inner side of the ramus of the mandible with it, until eventually it leaves it to become connected with the submaxillary ganglion.

The principal portion of the *portio dura*, on the other hand, makes its way out by the stylo-mastoid foramen, and is distributed to the facial muscles, some comparatively insignificant branches only, being furnished to the levators of the hyoidean apparatus and depressors of the lower jaw. But, as has been already stated, the facial muscles, so important and largely developed in Man, become insignificant in the lower Vertebrates, and are not represented at all in the Fish. Hence, in the latter, we might expect to find only mandibular and hyoidean branches of the *portio dura* corresponding with the *chorda tympani* on the one hand, and the stylo-hyoidean and digastric branches, on the other, in Man. And this is really the case. For the *portio dura* of the Pike, which leaves the skull by a special foramen in the pro-otic bone, traverses the hyomandibular bone, and then divides into two branches, one of which runs backwards to the hyoidean arch; while the other, directed forwards and downwards, passes to the inner side of the quadrate bone, and over its articulation with the *articulare* to the inner surface of the lower jaw, along which it runs to the extremity of the ramus. This last branch is obviously the representative of the *chorda tympani*, and its relations to the quadrate and articular bones are, it will be observed, very similar to those which the corresponding nerve has to the *incus* and *malleus* in Man.

Holding fast, then, by this determination of the homologies of the *articulare* and *quadratum*, what is the nature of the other bones entering into the palato-quadrate arch?

The *metapterygoid* may perhaps answer to the *os orbiculare*. The manner of its connection with the quadrate (*incus*) suggests this view, for which, however, I cannot pretend to offer any positive proof.

That the other three bones answer in a general way to the pterygo-palatine bones of Man is certain. The pterygoid of Man, it is true, is in no way connected with the incus, while both bones *Ecpt.* and *Ept.* are united with the quadratum. But this is in reality no difficulty, for we shall find that, in the higher oviparous *Vertebrata*, the *os quadratum* is very generally connected with a bone which is universally admitted to correspond with the pterygoid of Man.

Again, both the palatine and the pterygoid bones of Man are articulated with the base of the skull, while the palato-pterygoid arch of the Fish is not directly connected with any of the basi-cranial bones; but, in many of the higher *Vertebrata*, the pterygo-palatine arch is almost as free of the base of the skull as in the Fish.

No doubt, then, the palato-pterygoid bones of the Fish, taken together, answer to the palato-pterygoid bones of the Man; but it is a very difficult matter to identify the separate constituents of the two arches.

One of the most striking features of the palatine bone, not only in Man, but in the *Vertebrata* generally, is its articulation with the pre-frontal, or lateral mass of the ethmoid. If, guided by this character, we seek for the homologue of the palatine in the Fish, the so-called "ectopterygoid" alone satisfies the conditions. But if this bone be the homologue of the true palatine, the bone *Pl.* must be regarded as a dismemberment, or subdivision of the palatine,* and the entopterygoid will take the place of the true pterygoid.

The palato-quadrate arch, with the lower jaw, is immediately suspended to the skull only by the articulation of the cartilaginous pedicle *b* (Fig. 71) with the pre-frontal, none of the posterior elements of the arch being directly articulated with the skull. They are indirectly united with the latter, however, by two very remarkable bones, the *Hyomandibular* (*H.M.*) and the *Symplectic* (*Sy.*).

The *os hyomandibulare* is a broad flattened bone, somewhat constricted in the middle, and divided below into an anterior and a posterior process. The upper convex edge of the bone (*d*, Fig. 71) fits into an elongated, concave, glenoidal fossa bounded by the squamosal, opisthotic, and pro-otic bones, and swings freely therein, in a plane perpendicular to the longitudinal axis of the skull. The large anterior inferior process articulates by its anterior edge and outer face with the metapterygoid, while below it is united by a persistent synchondrosis with the irregular styliform bone, the *Symplectic*, which is firmly fitted into the groove already described upon the inner face of the quadrate bone.

The connection thus established between the hyomandibular and the symplectic, is strengthened externally by the firm apposition of a curved elongated bone, the *Pre-operculum*, to the hyomandibular above and to the quadrate bone below.

* Looking upon *Pa.* and *Ecpt.* as one bone homologous with the palatine of Man, it will be found that in osseous Fishes the separation between them takes place sometimes in front of the pre-frontal articulation, as in the Pike, sometimes behind it, as in the Cod and most bony fishes.

The hyoidean arch consists of two median bones,—an anterior, the "*entoglossal*," which supports the tongue; and a posterior, the "*urohyal*." Its lateral cornua are formed by four bones, two small (*basi-hyal*), and two large (*epi* and *cerato-hyals*) on each side, the latter supporting the "branchiostegal rays" on which the branchiostegal membrane is spread out; and the upper of the two larger bones is connected with the synchondrosis between the hyomandibular and symplectic by a styliform bone—the *stylo-hyal* (Fig. 71, *Hy.*). Thus, the hyomandibular may be regarded as common to the mandibular and the hyoidean arches, supporting the former, indirectly, by means of the symplectic, and the latter directly, by means of the stylo-hyal.

The stylo-hyal very probably corresponds with the styloid process and pyramid of Man, but it is difficult to find any very sure footing for our interpretations beyond this point.

The manner in which the symplectic is connected, on the one hand, with the representative of the *incus*, and, on the other hand, with that of the styloid process and pyramid, is strongly suggestive of a relation between this bone and the stapes. But it must no less be admitted that similar arguments might be used in favour of the stapedial character of the hyomandibular bone, the articulation of which with the pro-otic and opisthotic might be compared with the fitting in of the stapes into the *fenestra ovalis*, which is bounded by these two bones; or again, plausible arguments might be brought forward in favour of the view that the hyomandibular, at any rate, is a bone special to fishes. At present, it may be well merely to indicate these various possibilities, as the study of development has hardly been carried sufficiently far to enable us to decide in favour of one rather than of another.

Each of the four anterior branchial arches is composed of four bones, and the branchial arches of opposite sides are united by connecting cartilages and median ossifications. The anterior or first arch, which corresponds with the greater cornu of the hyoid of Man, is fixed to the pro-otic bone, between the exits of the trigeminal and the *portio dura*, by cartilage. The succeeding arches have no osseous or cartilaginous representatives in Man.

The branchiostegal rays attached to the epi-hyal and cerato-hyal are in like case.

Three bones, the *operculum* (*Op.*), *sub-operculum* (*S.Op.*), and *inter-operculum* (*I.Op.*), are developed within the membranous gill-cover, and serve to strengthen it (Fig. 65). The operculum is articulated with the posterior and inferior process of the hyomandibular bone; the inter-operculum is connected by ligament with the angular piece of the jaw, the sub-operculum lies between the two.

The gill-cover is developed from the outer surface of the second visceral arch, and corresponds with the concha of the ear in the human subject; and as the latter part contains no osseous elements, it is obviously in vain to seek for the homologues of these bones in Man.

The *pre-operculum*, which, as I have stated above, binds together the hyomandibular and the quadrate bone externally, has been compared with the tympanic bone of Man, and the position of the bone and its relations to the representatives of the *ossicula auditûs* are certainly not altogether unfavourable to this view.

These are the most important bones in the Pike's skull, but several yet remain for consideration.

Thus there is a small, oval, *supra-orbital* ossicle (*S.Or.*, Fig. 65) attached to the outer margin of the frontal, above the orbit, and an inverted arch of *sub-orbital* bones which bound the orbital cavity externally and inferiorly. The sub-orbital series consists of a large anterior bone, which lies beside the nasal, and of five or six smaller bones, the hindermost of which is connected with, or attached close to, the post-frontal.

Finally, in the Pike, a forked bone, the *supra-scapula*, suspends the scapular arch to the apices of the squamosal and epiotic bones. This bone, it need hardly be said, is without a distinct osseous representative in Man.

The merely anatomical comparison of the facial bones of the Pike with those of Man thus leads to a conclusion very similar to that attained by the examination of the bones of the skull proper. There is a certain identity of fundamental plan upon which special structural peculiarities are superadded in each case. Both types of skull exhibit many bones in common, but in each type, some of these bones acquire special arrangements and very different relative magnitudes; and each type exhibits bones peculiar to itself, the number of those present in the Fish and absent in the Man, being very much greater than of those present in the Man and absent in the Fish. As might be expected, the study of the development of the Fish's cranium brings out into still stronger light the fundamental resemblances of its structure with that of the higher Vertebrates. The primitive groove makes its appearance on the blastoderm, and becomes converted into a canal by the arching over and coalescence of the dorsal laminæ. The anterior part of the canal dilates and becomes subdivided into cerebral vesicles. The notochord appears and terminates, in front, in a point behind the pituitary body; while round its apex, that bend of the primitive cranium takes place which constitutes the cephalic flexure. The organs of sense make their appearance in the same regions, and the visceral arches and clefts are developed in the same way. But a greater number of them appear, and the posterior ones, instead of vanishing, give rise to the branchial skeleton and branchial clefts. The mandible is developed in the first visceral arch, and the hyoid apparatus in the second, as in Man; but the details of the mode of origin of the hyomandibular and symplectic, of the palatine and maxillary apparatus, and of the naso-frontal process, have not been as yet worked out with sufficient thoroughness to enable us to determine with certainty the homologies of all the resulting parts.

The cranium is at first wholly membranous, but after a time it becomes partially chondrified in the same way as in the higher Vertebrates (Fig. 72). Cartilage appears in the base of the skull upon each side of the notochord, and surrounds the great auditory capsules. Anteriorly it divides into two processes, the *trabeculæ cranii* (*Tr.*), which separate so as to inclose the pituitary fossa (*P*), and reunite, in front of it, to form the ethmo-vomerine rostrum. From the floor of the skull, at the front and lateral part of each auditory capsule, a cartilaginous process (*HM.*) is given off, and passing downwards and forwards ends in a free styliform process, which lies parallel with, and is bound by connective tissue to, the free hinder crus of an inverted arch of cartilage, the anterior crus of which passes into the pre-frontal region of the ethmo-vomerine cartilage. The centre of this

Fig. 72.

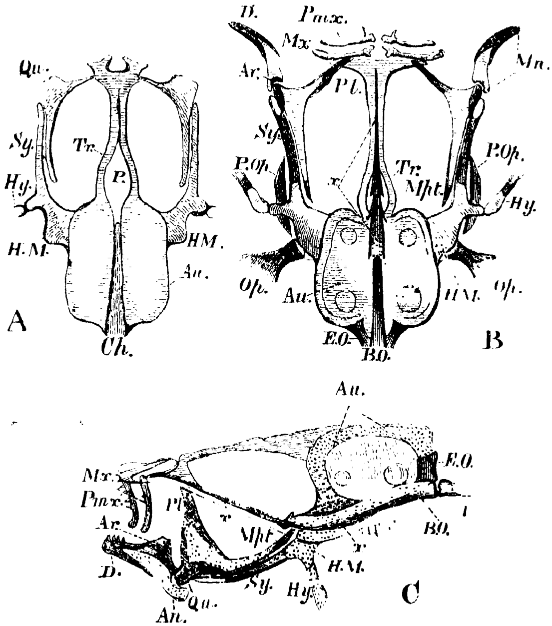


Fig. 72.—The cartilaginous and partially ossified crania of young Sticklebacks (*Gasterosteus*).—A, in a very early, B, in a more advanced condition, from above; C, viewed from the side; *Ch.*, notochord; *Au.*, auditory capsules; *P*, pituitary fossa; *Tr*, trabeculæ; *x*, parasphenoid; *H.M.*, *Sy.*, *Qu.*, indicate not only the bones, but the pre-existing cartilages.

palato-quadrate arch is prolonged into a process (*Qu.*), which articulates with the cartilaginous ramus of the mandible, while the upper part of the cartilage (*HM. Sy.*) gives attachment to the cartilaginous hyoid (*Hy.*).

This is the earliest condition of the cartilaginous cranium of the osseous fish that has yet been observed; but it can hardly be doubted that the hyomandibular and palato-quadrate cartilages have already deviated considerably from their primitive condition, and it would be a matter of great interest to ascertain whether these cartilages are primitively continuous; or whether, on the other hand, the hyomandibular altogether belongs to the second visceral arch, while the hinder crus of the palato-quadrate belongs to the first, but has become detached from its primitive connection with the *basis cranii.*

The basi-occipital originates as an ossification, which immediately surrounds and incloses the end of the notochord, and extends into the adjacent cartilage. The ex-occipital is developed within the substance of the cartilaginous cranium on each side of the basi-occipital. The parasphenoid, on the other hand, is developed as a superficial ossification in the perichondrium of the base of the skull, and extends in front of, and behind, the pituitary fossa in this membrane. The pre-maxillæ and maxillæ have no cartilaginous predecessors, nor have the dentary and angular pieces of the lower jaw. The palatine is developed around, if not in, the anterior crus of the palato-

Fig. 73.

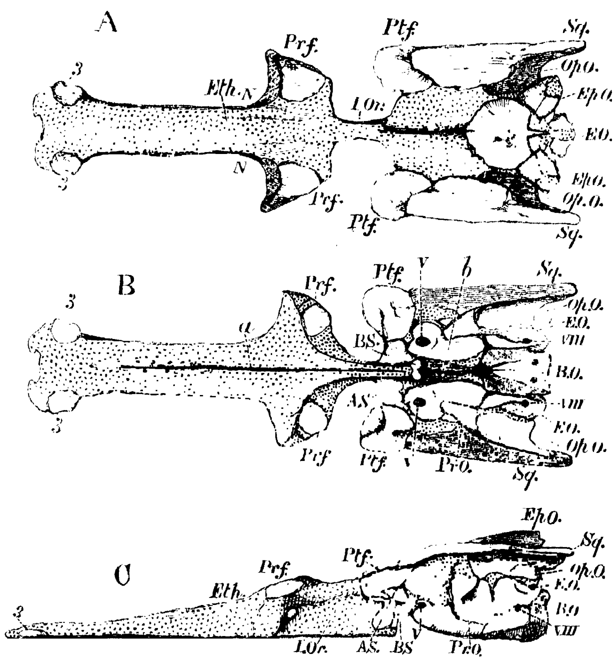


Fig. 73.—The cartilaginous cranium of a Pike, with its intrinsic ossifications viewed, A, from above; B, from below; C, from the left side. *N*, *N*, nasal fossæ; *I.Or*, inter-orbital septum; *a*, groove for a median ridge of the parasphenoid; *b*, canal for the orbital muscles.

quadrate arch; the metapterygoid in the same relation to its posterior crus; the quadrate bone, in its inferior process. The symplectic is a cortical ossification of the styliform part of the hyomandibular cartilage, the ossification of the rest of the latter giving rise to the hyomandibular bone itself (Fig. 72).

In many osseous fishes, such as the Carp, the cartilaginous cranium disappears, with age, as completely as it does in Man; but, in the Pike, it not only persists, but grows and enlarges with age, so that the relations of the cranial bones to cartilage, or to membrane, can be investigated at any period of life.

If the skull of an adult Pike be macerated, or, better, steeped for a short time in boiling water, a number of the cranial bones will separate with great ease from a sort of model of the skull chiefly composed of cartilage.

This "cartilaginous skull" forms a complete roof over the cranial cavity (Fig. 73, A), whence it is continued, without interruption, to the anterior end of the cranium, forming the narrow inter-orbital septum (*I. Or.*) and the broad internasal rostrum (*Eth.*), and giving rise to two antorbital processes (*Prf.*), which separate the orbits from the nasal chambers, and are perforated by the olfactory nerve, and by the nasal division of the fifth.

The inter-orbital cartilage is interrupted by an oval space filled with membrane, just in front of the basi-sphenoid, so that it is continued to the lower end of that bone only by a slender cartilaginous rod, which passes into the stem of the Y-shaped basi-sphenoid (Fig. 73, C).

The cartilaginous basis of the skull, therefore, is not continued back along the floor of the canal for the orbital muscles. The roof of the orbital canal contains cartilage in the middle line, which is almost completely hidden in front by the extension towards one another of the horizontal laminæ of the pro-otic bones. The under-surface of the inter-orbital septum and of the greater part of the cartilaginous rostrum is marked by a deep groove (*a*, Fig. 73, B), into which a median ridge of the parasphenoid is received.

The bones which, being developed in perichondrium, are easily removed from the macerated skull, are the parietals, the frontals, the bones 1.1. and 2.2. (Fig. 69), the squamosals (when these are not anchylosed with the opisthotic bones),* the vomer, and the parasphenoid.

The bones which, as ossifications of the substance of the cartilaginous cranium itself, are not thus separable, are the basi-, ex-, and supra-occipitals, the three periotic bones, the alisphenoids, the basi-sphenoid, the post-frontals, the pre-frontals, the bones 3.3 (Figs. 69 and 73).

Thus, in a certain sense, the adult skull of the Pike may be said to represent, in a persistent form, a condition of the skull which is transitory in Man.

Let the sides of the human fœtal cartilaginous cranium grow up and unite in the roof of the skull; let the pre-sphenoidal, ethmoidal, and internasal portions be greatly elongated; let no distinct ossification take place in the pre-sphenoidal and orbito-sphenoidal regions, or in the part answering to the lamina perpendicularis, while the basi-sphenoidal ossification remains very small, and that cranium would put on the most important and striking characters of that of the Pike.

* How far the bone which I have marked *Sq.* in the skulls of Fishes is really a membrane bone and the homologue of the squamosal of Reptiles, Birds, and Mammals, is a question which needs thorough re-investigation. Mr. Parker is of opinion that it is really a cartilage bone and the homologue, not of the squamosal, but of an independent ossification, which he finds well developed in the periotic capsule of the Mole and Shrew, and terms the "pterotic."

LECTURE X.

ON THE STRUCTURE OF THE SKULL.

THE SKULLS OF FISHES.

It has been seen that the skull of Man and that of the Pike agree in passing, in a similar order, through similar developmental stages. Each, at first, is a *membranous cranium*, its walls being composed of indifferent tissue, with the exception of that small part of its base which is occupied by the notochord. The greater part of the substance of each becomes chondrified, and thus that *cartilaginous cranium* is produced, which is a temporary structure in the Man, but a persistent one in the Fish. Neither in the membranous, nor in the cartilaginous state, does the cranium of either Man or Fish present any trace of that segmentation which becomes obvious in the third condition, when, by the deposit of calcareous salts around certain centres, either in the cartilaginous cranium or the adjacent membrane, the *bony cranium* is developed.

These three conditions of the skull are manifested, in the same order of succession, by all vertebrate skulls which become completely ossified; but the crania of many vertebrated animals remain throughout life in the second state, or in a condition intermediate between that and the third, while the skull of one of the *Vertebrata* persists in a state which can only be regarded as a modification of the membranous cranium. Hence I shall proceed to describe the leading modifications of the Vertebrate Skull under these heads:—A. The *membranous cranium*. B. The *cartilaginous cranium*. C. The *cartilaginous cranium, with* *superadded membrane bones, but no cartilage bones.* D. The *osseous cranium.*

The three first-mentioned kinds of skull are met with only among fishes; *Amphibia, Reptilia, Aves,* and *Mammalia* invariably possessing a larger or smaller number of cranial bones developed in cartilage.

A. *The membranous cranium.*

The only animal, at present known, which comes under this category is that singular fish, the lowest of all *Vertebrata, Amphioxus lanceolatus* (Fig. 74). The notochord (*Ch*), sur-

Fig. 74.

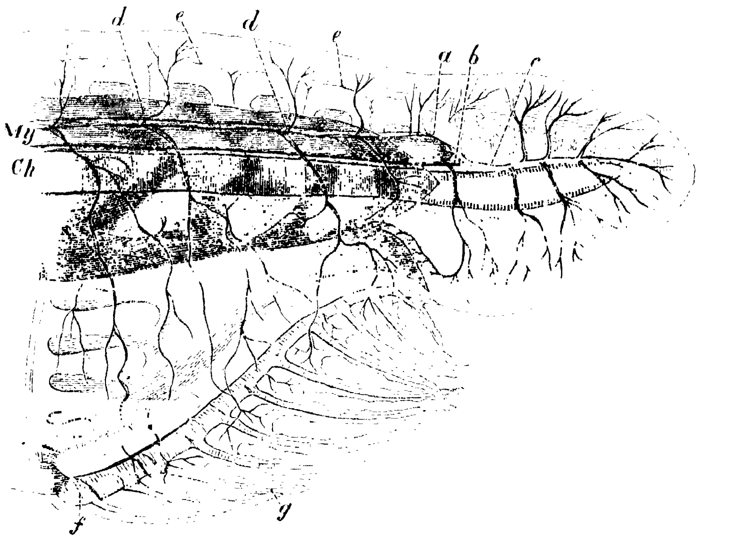


Fig. 74.—Skull of *Amphioxus lanceolatus* (after Quatrefages).—*a*, Position of olfactory (?) sac; *b*, optic nerves; *c*, fifth (?) pair; *d*, spinal nerves; *e*, representatives of neural spines; *f*, *g*, oral skeleton; *Ch*, notochord; *My*, spinal chord, or myelon.

rounded by a merely membranous sheath, extends very nearly to the anterior pointed extremity of the body. The myelon, or spinal chord (*My*), occupies the ordinary position above it, in a canal formed by upward processes of the membranous sheath, and gives off the spinal nerves, *d d*, on each side. Quadrate masses of somewhat denser tissue, *e e*, seem faintly to represent neural spines. Just above the anterior boundary of the mouth, but far behind the anterior end of the notochord, the myelon, dilating very slightly, suddenly terminates, and with it, the neural canal. The lateral muscles are divided into segments corresponding with the pairs of spinal nerves, and the most anterior of these segments is situated just behind the slightly dilated chamber of the neural canal which contains the correspondingly enlarged end of the nervous axis. The latter is all that represents the brain, and the chamber is the skull.

A ciliated sac placed at *b*, in connection with the upper surface of the brain, has been considered to be the olfactory organ of this fish, but it is possible the sac may simply represent the pineal body; optic nerves (*b*) are given off to the rudimentary eyes, and the branches (*c*) appear to be analogous in function to the fifth pair. But no pituitary body has been recognised, and, what is still more singular, there is no trace of auditory sacs. A cartilaginous ring, provided with tentacular prolongations (*f*, *g*), surrounds the mouth, and there is a singular branchial skeleton more like that of an Ascidian than any ordinary vertebrate structure; but neither of these structures probably have anything to do with the true cranial or facial skeleton.

It will be observed that this very remarkable skull, if it can be properly so called, is not strictly comparable to an arrest of development of a higher vertebrate skull; the notochord extending far beyond the end of the cranium, which it never does in any embryonic condition of a higher Vertebrate.

B. *The Cartilaginous Cranium.*

Of this there are three forms: in the first (*a*) there is no mandible; in the second (*b*) the mandible is present, and the suspensory apparatus by which it is connected with the skull forms one mass with the latter; in the third (*c*) the mandible is also present, but the suspensory apparatus by which it is connected with the skull is freely moveable.

a. The cartilaginous cranium without a mandible.

This kind of cartilaginous cranium is found only among the *Marsipobranchii*, or Lampreys and Hags, and a description of its characters in the former will suffice to illustrate its nature. Fig. 75 represents a vertical and longitudinal section

Fig. 75.

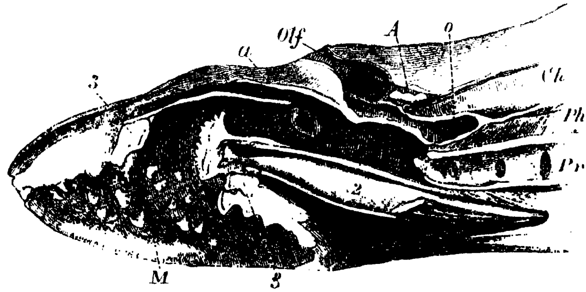


Fig. 75.—Vertical and longitudinal section of the anterior part of the body of a Lamprey (*Petromyzon marinus*).—*A*, the cranium, with its contained brain; *a*, section of the edge of the cartilage marked *a* in Fig. 76; *Olf*, the entrance to the olfactory chamber, which is prolonged into the cæcal pouch, *o*; *Ph*, the pharynx; *Br*, the branchial channel, with the inner apertures of the branchial sacs; *M*, the cavity of the mouth, with its horny teeth; 2, the cartilage which supports the tongue; 3, the oral ring.

of the anterior part of the body of the large Sea Lamprey (*Petromyzon marinus*), and gives a very good notion of the excessively minute proportions of the proper skull (A) to the rest of the body in this animal. A and B (Fig. 76) are lateral and superior views of the skull with its accessory cartilages, separated from the soft parts. The notochord (*Ch*) is, as in *Amphioxus*, exceedingly large, and is surrounded by a merely membranous sheath, from which prolongations are given off above to form the sides of the small neural canal. In the walls of this canal, cartilaginous rods, which represent neural arches, are developed, and it dilates more distinctly in the head than in *Amphioxus*, though the cranial cavity is still very minute. The myelon also undergoes a very distinct enlargement as it enters the cavity, and all the typical divisions of the vertebrate encephalon are recognisable in the brain thus formed.

The notochord terminates in a point immediately behind the pituitary body. As it approaches the cranium, a rod of cartilage (*l*, Fig. 76, A) is developed on each side in the lateral parts of its sheath, and gives attachment to the branchial skeleton (*m*); still more anteriorly two other cartilaginous filaments (k) appear, side by side, in the under region of the sheath. These pass into the hinder part of the proper cranium, which is a sort of cartilaginous box, closed in front, and through the greater part of its roof, only by membrane, but complete behind, where it arches over the myelon, and is perforated by the occipital foramen. The postero-lateral parts of this cranium are dilated to give rise to the two oval auditory capsules (c), and beneath these they are produced into two processes, h and f, which have a common base, but diverge from one another below. The process h gives attachment to a cartilage which is connected with that supporting the tongue (i). The process f, on the other hand, passing downwards and forwards, becomes

Fig. 76.

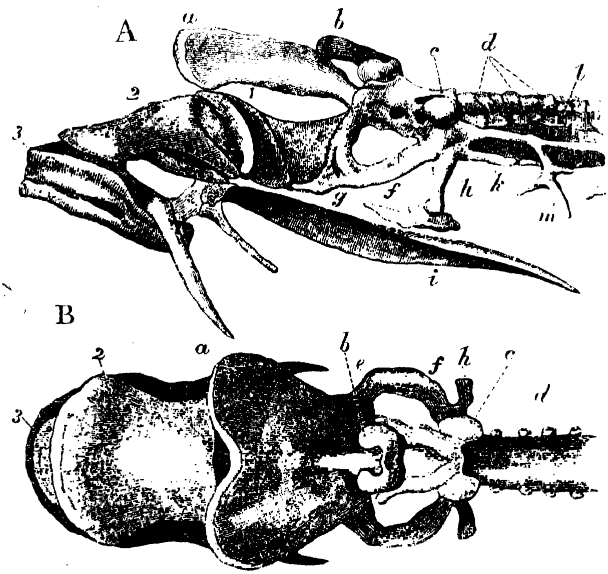


Fig. 76.—A, the skull of a Lamprey viewed from the side; B, from above (after Müller). —a, the ethmo-vomerine plate; b, the olfactory capsule; c, the auditory capsule; d, the neural arches of the spinal column; e, the palato-pterygoid portion; f, the hyomandibular and symplectic portion, and g, the quadrate portion of the sub-ocular arch; h, stylo-hyal process; i, lingual cartilage; k, inferior, l, lateral prolongation of the cranial cartilage; 1, 2, 3, accessory labial cartilages.

continuous at g, with another bar of cartilage e, which is connected with the antero-lateral part of the skull beneath the olfactory capsule. The eye lies over the triangular space inclosed between the sides of the skull and these two processes, so that *e*, *g*, *f* may be termed the *sub-ocular arch.*

If the skull is viewed from below, the processes *e* and *e* of opposite sides are seen to be continued into one another by a transverse band of cartilage, which forms the proper anterior boundary of the skull. The front edge of this band, which Müller calls the "hard palate," articulates with the broad and expanded cartilaginous plate (*a*). The common roots of the processes *f* and *h* are also continued into a "basi-occipital" plate of cartilage, but, between this plate and the "hard palate," there is an oval space through which the neck of the long olfactory cæcum (*o*, Fig. 75) passes. This cæcum, therefore, separates the front part of the floor of the cranial cavity, which is simply membranous, from the so-called "hard palate." On comparing this skull with that of the embryonic fish (see Fig. 72), *h* obviously answers to the stylo-hyal cartilage; *f*, to the ascending posterior crus of the palato-quadrate inverted arch and the hyomandibular cartilage; *e*, to the ascending and anterior crus of the same. It is true that no natural division of the arch into palato-quadrate and hyomandibular (and symplectic) portions occurs in the lamprey, but this is only one of several respects in which the Marsipobranchs resemble *Amphibia* rather than osseous fishes. The inverted cartilaginous arch which gives attachment to the hyoidean and mandibular apparatuses of a tadpole is strictly comparable to the arch (*e*, *g*, *f*) in the lamprey. The margins of the oval space upon the base of the skull answer to the divergent *trabeculæ cranii*, and the plate *a* to the ethmo-vomerine cartilage. The remarkable and apparently anomalous separation of the *basis cranii* into an upper membranous and a lower cartilaginous part, by the interposition of the back ward prolongation of the olfactory chamber, seems to me to be comparable to that separation of the upper and lower walls of the pre-sphenoid, basi-sphenoid, and even of the basi-occipital, by a backward extension of the olfactory cavities, which takes place in so many of the *Mammalia*. On the other hand, I doubt whether the accessory buccal cartilages, 1, 2, 3, &c., can be strictly compared with anything in other fishes, though some of them are doubtless, as Müller has suggested, the analogues of labial cartilages.

b. The cartilaginous cranium with a mandible and a fixed suspensorium.

The *Holocephali*, or Chimæroid fishes (*Chimæra* and *Callorhynchus*) present this type of cranial organization. In accordance with the large development of the brain, the skull of these fishes has attained a great advance in dimensions over the spinal

Fig. 77.

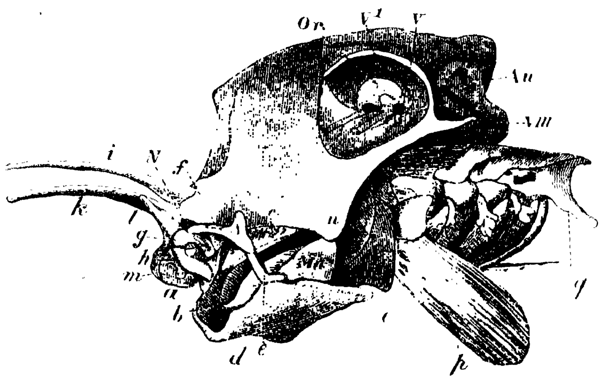


Fig. 77.—Skull of *Callorhynchus Antarcticus* (after Müller).—*a*, anterior tooth of the upper jaw; *c*, posterior tooth; *b*, mandibular tooth; *d, e, f, g, h, i, k, l, m*, accessory labial, nasal, and rostral cartilages; *n*, quadrate portion of the sub-ocular plate which supports the hyoid (*o*) and the mandible (*Mn*); *p*, the representatives of branchiostegal rays; *q*, the branchial arches; *Au*, auditory region; *Or.*, orbit; V^1, nasal division of the fifth nerve.

column, and presents a large internal chamber. It is a continuous cartilaginous mass, without any superior aperture of sufficient size to deserve the name of a fontanelle, in the base of which the notochord does not persist, and which is definitely articulated by two lateral convex facets and a median concave surface on the hinder margin of its floor (*A*, Fig. 78) with the anterior segment of the spinal column.

The skull is high and compressed from side to side; posteriorly, it exhibits, on each side, an enlargement (*Au*), which lodges the auditory organ. In front of these are the large orbits (*Or.*), separated by a thin membranous inter-orbital septum (*I.Or.*), which is unlike the inter-orbital septum usually met with, in that it lies above, and not below, the forward continuation of the cranial cavity (Fig. 78). Usually, an inter-orbital septum is formed by the compressed floor of the skull; here it is constituted by the compressed roof. Two chambers for the olfactory sacs (*N*, *Na*) terminate the skull anteriorly and inferiorly; and they, the lips and the anterior part of the snout, are protected and supported by a number of accessory cartilages (*d* to *m*).

Below the auditory and orbital regions, and in front of the latter as far as the nasal capsules, the base of the skull gives off a broad cartilaginous sub-ocular plate (*C*, *D*, Fig. 78), the two

Fig. 78.

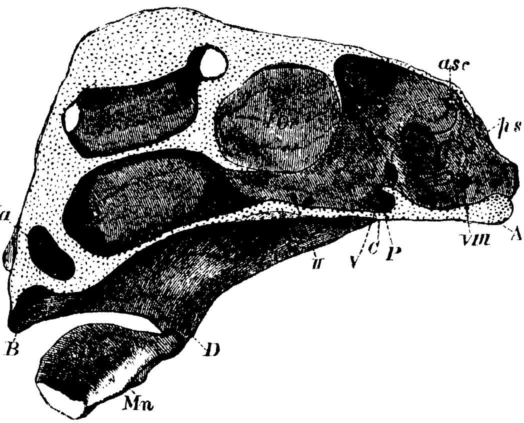


Fig. 78.—Vertical section of the skull of *Chimæra monstrosa* without the labial and nasal cartilages.—*A*, the basi-occipital region; *P*, the pituitary fossa; *Na*, the partition between the two olfactory sacs; *B*, the alveolus for the anterior upper jaw tooth; *I.Or.*, the inter-orbital septum; *asc*, *psc*, anterior and posterior vertical semicircular canals; *I.*, *II.*, *V.*, *VIII.*, exits of the olfactory, optic, fifth, and eighth pairs of cerebral nerves.

edges of which, sloping towards one another, bring it to a point at *n* (Fig. 77; *D*, Fig. 78). With this part of the plate the mandible (*Mn*) is articulated, while to the middle of its posterior margin (*D*, *C*, Fig. 78) the hyoidean apparatus (*o*, Fig. 77) is attached.

A vertical section of the skull (Fig. 78) shows that the proper cranial cavity consists of a large posterior chamber, divided by a long and comparatively narrow neck from a much smaller, but still large, anterior chamber. The latter contains the olfactory lobes, and presents on each side, in front, a sort of cribriform plate, through which the filaments of the olfactory nerve pass to the nasal sacs. The commencement of the narrow neck is perforated on each side by the optic foramina (*II.*). The hinder dilatation contains the mass of the brain, and, on each side, chambers for the auditory organs, which communicate with it, are situated. The posterior edge of the inter-orbital septum bounds this chamber in front, above the "neck." In front of the anterior boundary of the inter-orbital septum, and above the olfactory division of the skull cavity, there is a curious chamber filled with fatty matter, and open in front and behind, which is traversed by the nasal division of the fifth nerve.

Müller well says, "The skull of *Chimæra* is most like that of a tadpole; "* but if we interpret the former strictly by the latter, as I believe ought to be done, the results will be somewhat different from those at which Müller arrives. The plate *C, D* answers precisely to the sub-ocular arch of the lamprey and to the corresponding arch in the tadpole's skull, though it is chondrified throughout, and not perforated by a large aperture, as in the two latter animals. But, admitting this, the further development of the frog proves that the sub-ocular arch answers to the common suspensorium of the hyoid and mandible, and to the palatine, pterygoid, and quadrate bones; and that it has nothing to do with the maxilla or premaxilla. The large posterior upper jaw teeth of the Chimæroids (*c*), therefore, being attached to the under surface of the anterior part of the sub-ocular plate, must be palatine or palato-pterygoid teeth. The small anterior teeth (*a*), on the other hand, are fitted into fossæ, or alveoli (*B*), which are situated immediately under the floor of the nasal chambers, in the vomerine region of the skull, and must be regarded as vomerine teeth—as, indeed, Cuvier suggested. On the other hand, I think Müller's view that the cartilages (*d*, *e*, &c.) are accessory labial cartilages, and not, as Cuvier supposed, representatives of premaxillæ, maxillæ, &c., has everything in its favour.

c. The cartilaginous cranium, with a mandible and with a moveable suspensorium.

This form of cranium is met with in the sharks and rays, and may be illustrated by an account of that of *Squatina*, the

* Vergleichende Anatomie der Myxinoiden. Erster Theil, p. 159.

Fig. 79.

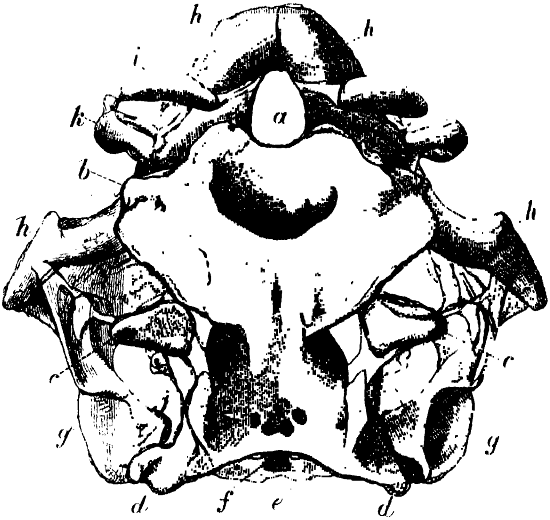
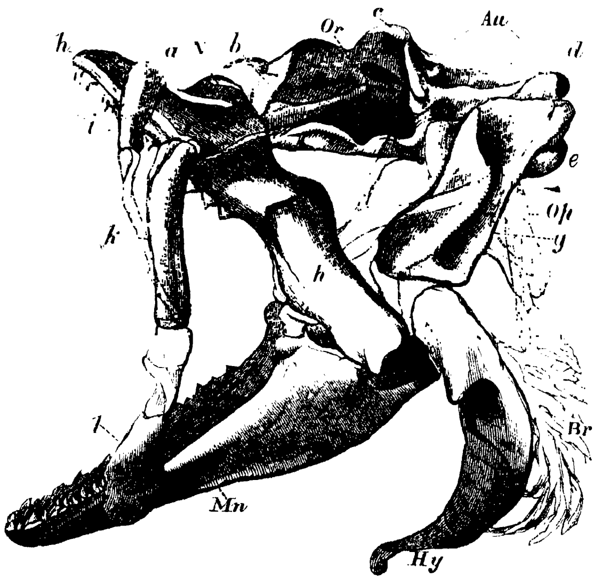


Fig. 80.



Figs. 79 and 80.—The skull of *Squatina* viewed from above (Fig. 79), and from the side (Fig. 80).—*a*, vomerine region; *b*, prefrontal; *c*, post-orbital; *d*, post-auditory processes; *e*, occipital condyles; *f*, occipital foramen; *g*, suspensorium; *h*, upper dentigerous arch; *i*, *k*, *l*, labial cartilages; *Mn*, mandible; *Au*, auditory chamber; *Or*, orbit; *N*, nasal chamber; *Op*, opercular cartilaginous filaments; *Br*, branchiostegal rays; *Hy*, hyoideau arch.

monk fish (Figs. 79 and 80). The form of the skull is here the exact converse of that observed in the Chimæroids, being exceedingly broad and depressed, instead of high and compressed. The surface of the cranium is encrusted with a pavement of minute ossicles, arising from the ossification of the superficial layer of the cartilage. Behind, the basilar region of the skull presents two lateral articular surfaces to the front part of the spinal column, and exhibits the wide lateral expansions for the auditory organs (*Au*); at the sides of the skull, in front of these, lie the orbits (*Or*) bounded behind by the post-orbital processes (*c*), and by the antorbital, or prefrontal, processes (*b*) anteriorly. The latter divide the orbits from the nasal chambers (*N*), the apertures of which look downwards. The prefrontal processes are continued, on the inner sides of the nasal chambers, into a broad plate, emarginate anteriorly, which terminates the floor of the skull, and corresponds with the ethmo-vomerine part of the cartilaginous skull of the human fœtus or of the pike. The anterior part of the roof of the skull is not directly continued into the upper surface of the plate, but ends in a deeply concave edge; the vacuity, or fontanelle, is occupied by fibrous tissue in the recent state. Small apertures upon the roof of the occipital region communicate with the auditory chambers. The upper end of a stout prismatic cartilage (*g*) is moveably articulated with the outer wall of the auditory prominence. The lower end of this cartilage is united by ligaments behind to the hyoidean arch (*Hy*), and in front to the upper and lower dentigerous arches (*h* and *Mn*). Each of these arches is composed of two pieces united in a median symphysis, and the under surfaces of the outer and posterior ends of the upper arch are articulated with the upper surfaces of the outer and posterior ends of the lower arch. The upper arch is, in addition, articulated with the under surface of the prefrontal region of the skull. Three cartilages (*i*, *k*, *l*), connected together by ligaments, lie outside the dentigerous arches, two, on each side, being superior and one inferior. Furthermore, cartilaginous filaments (*Op*) are attached to the hinder edge of the prismatic cartilage (*d*), and to the hyoidean arch (*Br*).

The interpretation of the cartilages (*i*, *k*, *l*) has been a matter of much controversy. In a remarkable essay published in the first volume of the "Mémoires du Museum," Cuvier proposed to consider the upper dentigerous arch (*h*) as the homologue of the palatine and pterygoid bones of osseous fishes, the cartilages (*i*, *k*) as the premaxilla and maxilla. The suspensorium (*g*) he considered to be the homologue of the hyomandibular, symplectic, and metapterygoid. The lower dentigerous arch (*Mn*) was obviously the mandible.

On this latter point all anatomists are agreed; but, in his famous "Comparative Anatomy of the Myxinoid Fishes," Johannes Müller—guided, like Cuvier, by purely anatomical considerations, and by what I have elsewhere termed the method of gradation—proposed a totally different interpretation of the other parts. According to this view, *i*, *k*, and *l* are merely labial cartilages, and therefore do not represent the premaxilla and maxilla. Again, Cuvier had greatly relied upon the absence of any parts on the inner side of *h* which could answer to palatine or pterygoid elements, in arguing that *h* itself represents them. But Müller adduced his own and Henle's observations to prove that in a great many Plagiostomes, particularly the Rays, such cartilages, situated on the inner side of the upper dentigerous arch, do occur, and thus arrived, by a line of argumentation precisely as legitimate as that of Cuvier, at the exactly opposite result,—that *h* represents the premaxilla and maxilla, and not the palatine or pterygoid.

The fact that these opposing views were entertained by men like Cuvier and Müller is evidence that each had much in its favour; but, in truth, neither was free from grave difficulties. Thus neither accounted for the articulation of the mandible with the upper dentigerous arch,—a relation into which the mandible never enters either with the palatine, or with the maxilla, in the vertebrate series; and as Müller himself is forced to admit that some of the cartilages on the inner side of the upper dentigerous arch are accessory, why should not all be so?

This is just one of those cases in which the study of development manifests its full importance, and decides, at once, problems which, without it, might be the subjects of interminable discussion. A comparison of the skull of the monk fish with that of the embryonic osseous fish (Fig. 72, C) seems to me to demonstrate beyond question, that the upper dentigerous arch (*h*) corresponds with the palato-quadrate cartilage of the embryo,* and that the suspensorium (*g*) equally corresponds with the hyomandibular and symplectic cartilage. But in this case Cuvier's view of the upper dentigerous arch must be regarded as a singularly near approximation to the truth, for it certainly answers to the palatine and pterygoid; though, in addition, it contains the representatives of the quadrate and metapterygoid bones of the osseous fish. And his opinion regarding the nature of the suspensorium was still nearer to what I believe to be right. On the other hand, I think it very probable, though not certain, that, as Müller supposed, the cartilages (*i*, *k*, *l*) are merely labial, and that these fishes have no representatives of the premaxilla and maxilla. But the so-called palatine and pterygoid cartilages of Müller, if the view I take is correct, are as much accessory parts as the spiracular cartilages, and, like them, have no representatives in osseous fishes.

* Rathke arrived at this conclusion also, on developmental grounds, in 1839. See his "Vierter Bericht," quoted in the last Lecture of this work.

LECTURE XI.

ON THE STRUCTURE OF THE SKULL.

THE SKULLS OF FISHES AND AMPHIBIA.

C. *The cranium, consisting chiefly of cartilage and without cartilage bones, but with superadded membrane bones.*

The skulls of the chondrosteous Ganoids, the Sturgeons, and *Spatulariæ* exemplify this type of structure, which forms a most interesting transitional link between the skull of Plagiostomes and the skull of ordinary osseous fishes.

Spatularia has a completely cartilaginous skull, produced in front into a great beak, flattened from above downwards. The cartilaginous representatives of, at fewest, seven of the anterior

Fig. 81.

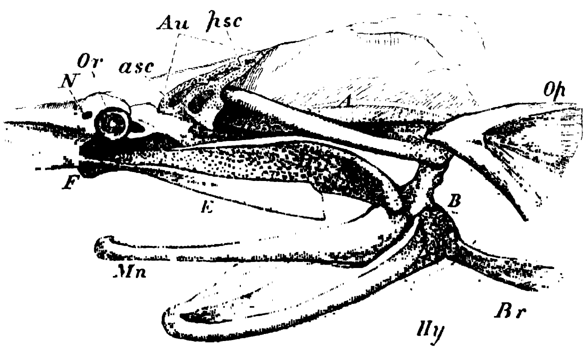


Fig. 81.—Side view of the skull of *Spatularia* with the anterior (*asc*) and posterior (*psc*) vertical semicircular canals exposed.—*Au*, the auditory chamber; *Or*, the orbit with the eye; *N*, the nasal sac; *Hy*, the hyoidean apparatus; *Br*, the representatives of the branchiostegal rays; *Op*, the operculum; *Mn*, the mandible.

vertebræ of the spinal column coalesce into one mass with one another and with the skull. The notochord, extremely large in the spinal column, rapidly diminishes in size as it enters the skull, and, becoming a mere thread, terminates behind the pituitary fossa. The auditory organs are contained in large postero-lateral projections of the cranial mass, with the outer sides of which the suspensoria are connected. The base of the skull is protected by a long parasphenoid, which extends back under the anterior part of the spinal column; in the dorsal region it presents an anterior and a posterior pair of perichondrial ossifications, separated by oblong laminæ from lateral bony plates of the same character, but the homology of these bones with those in the roof of the Teleostean skull is not, to my mind, satisfactorily made out.*

The suspensorial apparatus of *Spatularia* consists of a single bone (*A*), compressed from above downwards superiorly, and from side to side inferiorly, with a superior and an inferior cartilaginous epiphysis; to the lower cartilaginous epiphysis the operculum (*Op*) is attached, and a short thick prismatic cartilage (*B*) is united by ligament with, and can play freely upon, its anterior and inferior angle. Posteriorly the lower end of this cartilage (*B*) is connected by ligament with the hyoidean arch (*Hy*), which consists of two portions on each side; a small upper piece, with which the flat bone (*Br*), representing a branchiostegal ray, is connected; and a long lower ramus, the middle third of which is bony, while the two ends are cartilaginous.

Anteriorly, the lower end of the inferior suspensorial cartilage (*B*) is united by ligaments to two cartilaginous semi-arches (*D* and *Mn*), of which the upper (*D*) is articulated by a transversely convex head with a concavity of the lower (*Mn*). The upper semi-arch is ligamentously united to its fellow in the middle line, and is suspended by ligamentous fibres to the under part of the prefrontal region of the skull. A long flat bone (*E*), the hinder end of which is cut off in the specimen figured, lies on the outer side of the cartilage (*D*), and extends to the middle line. A second long flat bone is closely applied to the inner

* See "Spatulariarum Anatomiam descripsit Tabulaque illustravit Albertus Wagner." Berolini, 1848.

surface of the cartilage and follows its curves, from its hinder to its anterior extremity, overlapping and folding over the upper edge of the anterior three-fifths of the cartilage. Between the hinder part of *E*, here cut away, and *D*, is a space occupied by the levator muscle of the lower jaw.

The mandibular cartilage extends to the symphysis, and is coated externally, and partially embraced by, the flat bone (*Mn*), the greater part of the upper edge of which bears teeth.

On comparing these parts with those of the corresponding apparatus in the embryonic fish (Fig. 72), it becomes clear that the pieces *A* and *B* answer to the hyomandibular and symplectic, taken together. Indeed, at first sight, *A*, supporting as it does the operculum, seems to answer to the hyomandibular, and *B* to the symplectic itself; but then it may be suggested that the hyoidean apparatus is attached at the distal end of *B*, and not between it and *A*, as it would be if the two corresponded, respectively, to the hyomandibular and symplectic.

The cartilage *D* obviously answers to the palato-quadrate arch, and that of the lower jaw to Meckel's cartilage. The fact that a levator muscle of the lower jaw passes between *E* and *D* seems to prove the former to correspond with a maxilla; in which case the internal bone would be a sort of palato-pterygoid, similar to that we shall meet with in *Lepidosiren.*

The skull of the Sturgeon (*Accipenser*), like that of *Spatularia,* is greatly enlarged, posteriorly, by the coalescence with it, and with one another, of six or seven of the anterior vertebræ. In front, it is prolonged into a triangular snout or beak (*c*, Fig. 82; *a*, Fig. 83), the wide base of which is formed by the antorbital, or prefrontal, prominences which separate the olfactory chambers from the orbits. Behind the latter are the two great projections (*c*, Fig. 83) which contain the auditory organs; and behind these again, and separated from them by a deep lateral fossa, are two wing-like processes (*b*, Fig. 82), which are directed outwards and obliquely backwards, and proceed, not from the walls of the cranium proper, but from those of the spinal column, where it joins the skull. At this point there is, in the cranio-spinal cartilage of both the Sturgeon and the *Spatularia*, a great dilatation of the neural canal, which is closed above only by a membranous fontanelle. The skull proper has no such fontanelle. There is a well-marked pituitary fossa, and the notochord; very thick in the spinal column, tapers to a thread as it enters the base of the skull, and ends behind this fossa.

The bones which are developed in relation with this cartilaginous cranium in the base of the skull are,—a great parasphenoid which extends back under the coalesced anterior vertebræ, and forwards to the level of the nasal cavities; and a slender median bone in front of this, which underlies the rostral prolongation (*c*), and appears to represent the vomer.

No distinct ossifications protect the lateral walls of the skull, but the bones marked *F* (Fig. 82) send down processes for a short distance, and the parasphenoid gives off transverse prolongations upwards and outwards, from each side of the middle of its length, as in most fishes.

The roof of the skull presents a number of distinct flat ossifications, no one of which involves the subjacent cartilages, and which vary very much in contour and extent in different specimens. The general arrangement is, however, fairly represented by the accompanying figure (Fig. 82).

Fig. 82.

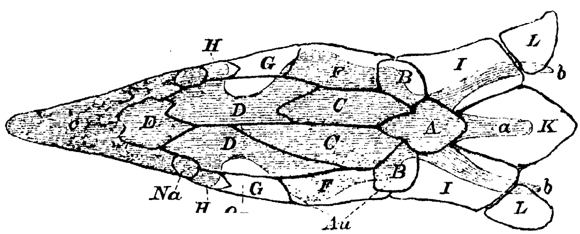


Fig. 82.—The cartilaginous skull of a Sturgeon, with the cranial bones. The former is shaded, and is supposed to be seen through the latter, which are left unshaded.—*a*, ridge formed by the spinous processes of the anterior vertebræ, which have coalesced with one another and with the skull; *b*, lateral wing-like processes; *c*, rostrum; *Au*, position of the auditory organs; *Na*, position of the nasal sacs.

Of these bones, the pairs *C, C* and *D, D* clearly represent, both in position and character, the parietal and frontal bones of the Pike, while *F, F* similarly correspond with the squamosals of that fish.

In position, again, *E* answers to the ethmoid, *H, H* to the prefrontals, *G*, *G* to the post-frontal, *B*, *B* to the epiotics, and *A* to the supra-occipital of the Pike. But every one of these is a membrane bone, and not, as are the corresponding elements of the Pike's skull, a cartilage bone.

These bones are therefore, strictly speaking, the analogues, and not the homologues, of the bones to which they appear to answer in the Pike, though hitherto no distinction has been drawn between the two.

K and *I*, *I* are bones which do not properly belong to the skull, but which, as happens among many Siluroid *Teleostei*, are anchylosed with the cranium. *K* is the most anterior of the median dermal scutes, and *I*, *I* are the supra-scapular bones. The letters *L*, *L* indicate the scapular bones moveably united with these last.

The suspensorium of the Sturgeon consists of a large, irregularly-prismatic body, composed of a bony central piece (*f*, Fig. 83) with two cartilaginous epiphyses, the lower of which (*g*) is much the longer, and is connected by ligament with another cylindrical cartilage (*h*), while the upper articulates with the outer and under part of the auditory capsule. Rather above the letter *h*, the lower cartilage gives attachment to a cartilaginous nodule with which the principal piece of the hyoidean arch is connected.

At its distal end the cylindrical cartilage (*h*) is united by ligaments to the two apparatuses *k* and *Mn*. Of these, *k* may be described as a rhomboid, composed partly of cartilage and partly of bone, and so bent as to assume a transversely arched form. Its outer angles present convex articular facets to concavities on the lower arch (*Mn*), which last, composed of a single bony ramus on each side, is undoubtedly the mandible.

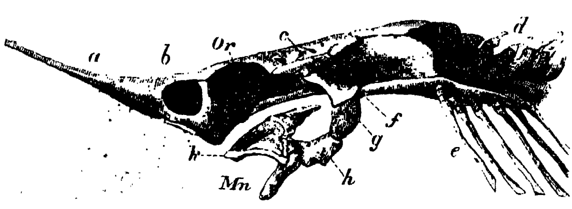


Fig. 83.—Side view of the cartilaginous cranium of *Accipenser* (after Müller).—*a*, rostrum; *b*, nasal chamber; *Or*, orbit; *c*, region of the auditory organ; *f*, *g*, *h*, suspensorium; *k*, maxillo-palatine apparatus; *Mn*, mandible.

The cartilaginous basis of *k* is strengthened by eight bones, four on each side. Of these, two lie altogether external to the cartilage, and leave between themselves and it an interspace, in which the levator muscle of the lower jaw lies.

The other pair consist, firstly, of a large bone, which lies, for the most part, internal and inferior to the cartilage, and extends from the inner side of the articular process for the lower jaw, upwards and inwards, to meet its fellow, posteriorly; forwards, to articulate with the anterior of the external bones. And, secondly, of a small bone fitted on to the anterior and external edge of this, and to the inferior surface of the anterior external bone. The whole apparatus, *k*, is very loosely connected with the skull, so that it is capable of being protracted and retracted with great freedom.

The general relations of this singular mechanism to the manducatory organs of ordinary Teleostean fishes appears to be rendered evident by the same method as that which has been employed to demonstrate the nature of the jaws of the Plagiostomes. The osseo-cartilaginous structure, *k*, answers to the palato-quadrate arch of the Sharks and Rays, or to the palato-quadrate cartilage of the embryonic fish; and *f*, *g*, *h* correspond with the undivided suspensorium of the Sharks and Rays, and with the hyomandibular and symplectic cartilages of the embryo Teleostean. Furthermore, on comparing *k* with the maxillary apparatus of *Spatularia*, the cartilaginous basis appears to answer to the cartilages (*D*, *D*) of that fish joined together; while the anterior outer bone in the Sturgeon is the equivalent of the bone *E*, and may be regarded as a maxilla. The two internal bones correspond with the inner bone of the Spatularia's jaw. The Sturgeon, however, more nearly approaches ordinary fishes in the development of an anterior or palatine element, distinct from the posterior or pterygoid element. As for the small external bone, which passes obliquely from the end of the maxilla to the outer surface of the cartilage, it is possibly a quadrato-jugal.

D. *The cranium consisting of cartilage to a greater or less extent, but with cartilage bones as well as membrane bones.*—

The class *Pisces* presents us with a complete series of these crania, from the least ossified forms, which possess only one or two pairs of cartilage bones in the walls of the cranium, to the

Fig. 84.

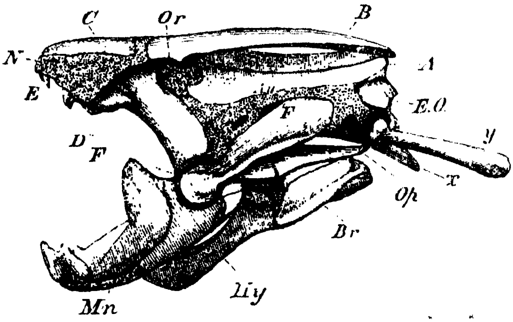


Fig. 84.—*Lepidosiren.* *A*, the parieto-frontal bone; *B*, the supra-orbital; *C*, the nasal; *D*, the palato-pterygoid; *E*, the vomerine teeth; *E.O.*, the ex-occipital; *Mn*, the mandible; *Hy*, the hyoid; *Br*, the branchiostegal ray; *Op*, the opercular plate; *x*, the parasphenoid; *y*, the bone which gives attachment to the scapular arch; *Or*, the orbit; *Au*, the auditory chamber; *N*, the nasal sac.

completely ossified skulls of the Cyprinoids and Siluroids. And again, just as among the preceding groups we found that the Chimæroids differed widely from the rest in having the sub-ocular process, or arch of the skull, to which the mandible is attached, formed of one piece of cartilage, which is continuous with, and immoveable upon, the skull; so, in this series, *Lepidosiren* is at once distinguished from all the rest by a similar character.

The skull of the Mudfish (Fig. 84) is composed of a framework of cartilage, which sends down a broad triangular process, on each side, to articulate with the mandible, and expands, posteriorly and laterally, into chambers for the auditory organs. Between these, the roof and the floor of the skull are both constituted by cartilage; but anterior to them, as far as the extremity of the parasphenoid (*x*), this tissue becomes very thin or disappears (Fig. 85). In front of the anterior end of the parasphenoid, it makes its appearance again on both the roof and the floor of the cranial cavity, beyond which it is continued as a thin lamella to the end of the snout. A fibrous septum with a free concave, posterior margin, divides this region of the cranium into two lateral chambers, one for each olfactory lobe.

Behind the auditory chambers the cartilage is almost excluded from the walls of the skull by two lateral ossifications of its substance—the ex-occipitals (*E.O.*). As in the *Amphibia*, there is no ossified supra- or basi-occipital. The rest of the lateral parietes of the skull would be devoid of bony walls were it not that the parasphenoid (x) and the great bone (A), which roofs in the whole length of the skull, and answers to the frontals and parietals, send upwards and downwards, respectively, lateral processes, which unite together, and so replace the alisphenoid (Fig. 85). The ethmo-vomerine cartilage (*Eth. Vo.*) bears, superiorly, the nasal bones (C), and inferiorly it carries teeth (E). A long flat bone, pointed posteriorly (B, B), is attached to the hinder edge of the nasals, and roofs over the orbit and temporal fossa.

Fig. 85.

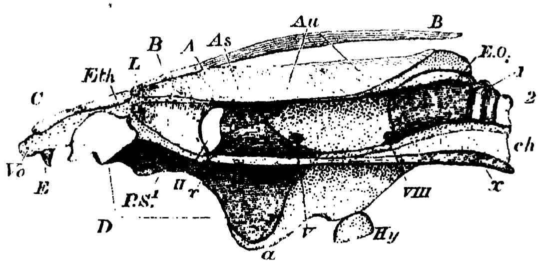


Fig. 85.—Longitudinal and vertical section of the Skull of *Lepidosiren*. The cartilage is dotted; the membranous and bony constituents are shaded with lines. *A*, *B*, *C*, *D*, as in the preceding figure; *x*, *x*, the parasphenoid; 1, 2, the first and second vertebral arches; *Ch*, the notochord; *Au*, the situation of the auditory organ.

The notochord, which forms the chief axis of the spinal column of this fish, is continued into the base of the skull, and ends in a point about the level of the exit of the trigeminal nerves (V). There is neither basi-occipital nor basi-sphenoid, and the presphenoid is represented only by the cartilaginous floor at ($P.S^1$). The pterygo-palatine apparatus is represented, on each side, by the great dentigerous curved plate (D), which is applied to the inner surface of the cartilaginous sub-ocular process, abuts against the parasphenoid by its inner edge, and descends to the inner side of the articular condyle for the mandible (a). The hyoidean arch (Hy) is attached to the middle of the posterior and inferior edge of the sub-ocular cartilage, to the posterior part of the outer surface of which is applied the bone (*F*, Fig. 84) with which the opercular bone (*Op*) is moveably united by ligament.

The bone (*F*) has, like most of the bones of the *Lepidosiren*, a green colour. Through the greater part of its length it is so easily separated from the cartilage that it is clearly a membrane bone. Towards the condyle, however, it adheres firmly to, though, on the application of a certain force, it springs away from, a nodule of whitish bone, which lies in the very substance of the articular end of the cartilage, and repeats its pulley-like form. I suspect that this nodule, which represents the *os quadratum*, is primitively distinct from the bone (*F*). The latter, under these circumstances, would have much analogy with the pre-operculum of osseous fishes, and *Op* would correspond with the sub- or inter-operculum.

All other fishes, comprising such *Ganoidei* as have not been already mentioned, and the *Teleostei*, have, so far as is at present known, the palato-quadrate arch primitively distinct from the hyomandibular suspensor; the latter is, primitively, moveable upon the skull; and, in the walls of the cranium, the pro-otic bones, at least, are ossified as well as the ex-occipitals; that is to say, they are constructed essentially upon the plan of the Pike. The modifications they exhibit in detail are almost infinite, but a few of the most important may be enumerated:—

1. The cartilaginous cranium persists throughout life in such fishes as the Pike and the Salmon; in very many, as the Perch and the Carp, it disappears almost entirely.

2. In most fishes the *basis cranii* is compressed from side to side in the orbital region, and vertically enlarged, so as to form an inter-orbital septum, which, as it were, encroaches upon the cranial cavity and narrows it anteriorly. But in others—such as the Cyprinoids and the Siluroids—no inter-orbital septum is developed, the *basis cranii* remaining flat, and the cranial cavity of nearly equal size throughout.

3. The last-mentioned fishes have the cranial walls completely occupied by bone, distinct ossifications representing the alisphenoids and orbito-sphenoids.

4. The opisthotic bone, occasionally absent as a distinct ossification, is very small in some fishes, such as the Perch (where it is Cuvier's "*rocher*" or "*petrosal*"), but becomes very well developed in such genera as *Ephippus,* and attains an immense size in the *Gadidæ.*

5. The canal for the orbital muscles is absent in many fishes, such as the Cod tribe.

6. The most remarkable modification of the fish's cranium proper, however, is the want of symmetry produced in the flat fishes, or *Pleuronectidæ,* by a sort of twist, which affects the anterior and upper, but not the hinder and inferior, part of the skull. Thus, if the skull of a Turbot be examined, the supra-occipital will be found in its ordinary place; while the epiotics and squamosals are symmetrically disposed on each side of it, so that the skull, viewed from behind, is like that of any other ordinary osseous fish. The basi-occipital, parasphenoid, and vomer are likewise arranged, as usual, along the median basal axis of the skull. The pro-otics and post-frontals are also nearly symmetrical, but the alisphenoids are thrown over to the left side, so that the anterior aperture of the cranial cavity, between the alisphenoids, lies no longer immediately over the parasphenoid, but to the left of it. The left frontal sends down a long curved process, which joins with one from the prefrontal of the same side, and the two eyes come to lie in the secondary orbit, developed between the curved bony boundary thus formed and the median frontal crest.

7. An addition takes place to the posterior extremity of the skull, in many fishes, by the anchylosis with it, and with one another, of a variable number of vertebræ. Cartilaginous vertebræ, as I have already pointed out, coalesce with the cartilaginous skull in both *Accipenser* and *Spatularia,* and two or three bony vertebræ are anchylosed with the osseous skull in *Lepidosteus* and *Polypterus.* Whether a similar addition takes place in the other living ganoid, *Amia,* or not, I cannot say. In many Siluroids a great number of vertebræ become thus anchylosed with one another and with the skull.

8. In both Siluroids and Ganoids, again, an addition to the roof of the skull is effected by the coalescence therewith of the

suprascapular bones, as well as, in some cases, of dorsal dermal bones.

9. But certain of the most striking modifications of the physiognomy of osseous fishes are the result of the prolongation of the region in front of the orbit, which may be effected in two very different ways. For example, it is chiefly the elongation of the premaxillæ and mandible which gives rise to the remarkable beak of the "sword-fish" (*Xiphias*); while, in *Fistularia*, the premaxillæ and mandible remain very short, but are thrust out to a great distance from the orbit, by the production of the nasal and vomerine regions, on the one hand, and of the bones of the suspensorium on the other.

10. In such fishes as *Syngnathus* and *Fistularia*, a line joining the articular socket of the hyomandibular with the condyle of the *os quadratum*, makes a very acute angle with the base of the skull. In most fishes this angle is more or less acute; but in *Polypterus*, and still more in *Muræna*, it becomes a right or an obtuse angle, the corner of the gape being thus thrown behind the eye, instead of being, as in most bony fishes, in front of it. We shall find a similar rotation of the distal end of the suspensorium to take place in the series of the *Amphibia*, and in the passage from the tadpole to the adult state of the highest of these animals.

11. The connection of the palato-quadrate arcade with the hyomandibular and symplectic suspensor varies, from the firm sutural union which is observed in the Pike and most osseous fishes, to a bond which is hardly closer than that which obtains in the Plagiostomes and Sturgeons, in *Polypterus*. In *Lepidosteus*, except for the inter- and pre-operculum, the tie between the symplectic and the palato-quadrate bones would be very loose, the palato-quadrate arcade and the suspensor being, as it were, naturally dissected from one another.

In some *Plectognathi* and Siluroids, on the other hand, all these parts become firmly anchylosed together, and with the side walls of the cranium.

12. Finally, the multiplication of the bony constituents of the maxilla and the mandible in *Lepidosteus*—the conversion of the maxilla into a mere support for a tentacle in many Siluroids

—the absence of branchiostegal rays, and the presence of two "jugular" plates between the mandibular rami in *Polypterus*, must not be overlooked even in this brief enumeration of a few of the most salient modifications of the skulls of osseous fishes.

THE SKULLS OF AMPHIBIA.

In cranial structure, as in all the other more important features of their organization, the *Amphibia* are closely allied to Fishes, and widely separated from the abranchiate *Vertebrata*.

As in Fishes, a single median membrane bone, or parasphenoid, is developed under the base of the skull, while no such median bone is found in the higher *Vertebrata*. Like *Lepidosiren*, the *Amphibia* have no ossified basi-occipital or supra-occipital, whereas all the abranchiate *Vertebrata* possess these bones.

Again, like *Lepidosiren* and many other Fishes, the *Amphibia* have no true basi-sphenoid, developed in the cartilage of the *basis cranii;* while all the abranchiate *Vertebrata* have that bone well developed.

The hyoidean apparatus is, in *Amphibia*, as in Fishes,* connected with a suspensorium common to it and the mandibular apparatus. In all the higher *Vertebrata* the hyoidean apparatus, if it is attached directly to the skull at all, is united therewith separately and distinctly.

In all *Amphibia* which have ossified ex-occipitals, a condyle is developed on each, for articulation with the first vertebra of the spinal column; and the basi-occipital, remaining unossified, takes no share in the formation of these condyles. In all the higher *Vertebrata*, on the other hand, the bony basi-occipital takes a greater or less share in the formation of the occipital condyle, or condyles.

The skull of *Amphibia* resembles that of the Chimæroids and *Lepidosiren*, and differs from that of Teleostean, Ganoid, and Plagiostome fishes, in the absence of any natural division between the palato-quadrate and suspensorial cartilages.

* According to Stannius, however, the hyoidean arch is attached directly and independently to the skull in many Rays. See that author's admirable "Handbuch der Anatomie der Wirbelthiere," Erster Buch, p. 46.

Like the Carp and the Siluroids, the *Amphibia* are devoid of any inter-orbital septum, the cranial cavity remaining of tolerably even size from the occipital foramen to its anterior termination.

In the Frog (Fig. 86) the skull is roofed in by two long flat membrane bones (*Pa*, *Fr*), which correspond with the parietals and frontals, and, in fact, each originate in two distinct centres,

Fig. 86.

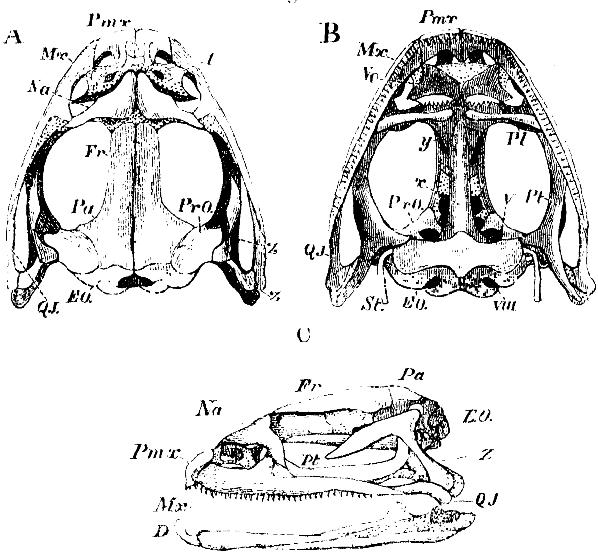


Fig. 86.—Skull of *Rana esculenta*. Seen A, from above; B, from below; C, from the side (after Dugès).—*x*, the parasphenoid; *y*, the girdle bone; *z*, the "temporo-mastoid" of Dugès.

one in front and one behind. In front of these are two other membrane bones (*Na*, *Na*), which have been variously interpreted, but which probably answer to the nasals. On the base of the skull is the long single parasphenoid (*x*), the hinder part of which is produced into two broad lateral processes, which underlie the auditory capsules.

When these membrane bones have been stripped off, a subjacent cartilaginous cranium becomes apparent, produced behind into two lateral enlargements, or tuberosities, for the auditory organs, and having certain fontanelles or membranous spaces in its upper wall (Fig. 87). In the substance of this cartilaginous cranium, posteriorly, are two ossifications, one on each side of the occipital foramen, which nearly meet in the middle line above and below. These, the ex-occipitals, bear the condyles for articulation with the atlas, and partly shelter the posterior portion of the auditory organ. The front and upper wall of each auditory tuberosity is also largely ossified, the resulting bone protecting the anterior part of the organ of hearing, and being perforated, or notched, for the transmission of the third division of the trigeminal. This therefore is, without a question, the homologue of the pro-otic bone of the fish and of Man.

A fifth ossification of the cartilage is the very singular bone (*y*) which Cuvier termed the *os en ceinture*, or "girdle bone," from its encircling the anterior part of the cranial cavity. This bone has somewhat the form of a dice-box, with one end divided by a longitudinal partition. The latter—the front part of the bone—extends into the prefrontal processes in some frogs, protects the hinder ends of the olfactory sacs, and is perforated by the nasal division of the fifth. The median partition therefore must answer to some extent to the ethmoidal septum, while the lateral parts of the anterior division of the bone correspond with the prefrontals. On the other hand, the hinder division of the bone is an ossification of each wall of the cranium, in front of the exit of the optic nerves; so that I conceive this part of the bone can only answer to the orbito-sphenoids, united above and below. Upon this view of its nature, the girdle bone answers to at least five bones, viz., the ethmoid, prefrontals, and orbito-sphenoids.

No alisphenoid is developed in any Amphibian. There is no separate opisthotic in the adult state, and I am not fully satisfied as to the existence of any distinct epiotic, though such a bone has been affirmed to exist (under the name of "mastoid") in the axolotl and the *Menobranchus*.*

The anterior part of the ex-occipital, in front of the foramen for the eighth nerve, which perforates that bone, probably represents the opisthotic, as between it and the posterior external margin of the pro-otic is placed the *fenestra ovalis*, a structure not met with in the class *Pisces*.

The facial bones are, for the most part, readily determinable;

* Mr. Parker informs me that the common Toad has a thin bony crest answering to the epiotic.

thus there can be no doubt about the premaxillæ (*Pmx*), the maxilla (*Mx*), and the two large-toothed vomers (*Vo*). The position of the posterior nares between the last-named bones and the bones (*Pl*) taken in connection with the relations of the latter to the prefrontal region of the skull, sufficiently defines the palatine character of *Pl;* while *Pt*, connected with the palatines on the one hand, and terminating on the inner side of the mandibular suspensorium on the other, corresponds as distinctly with the pterygoids of the higher *Vertebrata.*

Fig. 87.

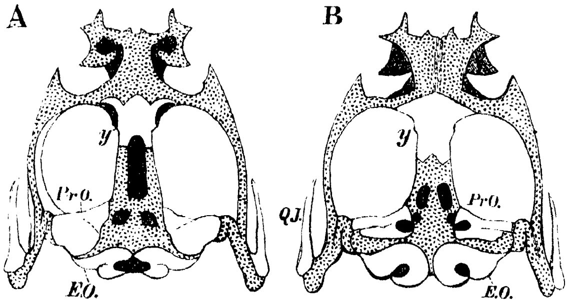


Fig. 87.—The Cartilaginous Cranium of *Rana esculenta*. A, from above; B, from below (after Dugès).—*y*, the girdle bone.

The bone (*QJ*), which connects the end of the maxilla with the outer side of the suspensorium, appears to correspond with the quadrato-jugal of abranchiate *Vertebrata.*

It is more difficult to determine the nature of the bone *z*, the "temporo-mastoid" of Dugès, which is a long, hammer-shaped membrane bone, extending from the skull to the articular surface for the lower jaw, and sending a long process forwards over the temporal region.

When this bone, the pterygoids, palatine, quadrato-jugal, &c., have been removed, the cartilaginous cranium of the Frog (Fig. 87) is seen to give off from the outer ends of the prefrontal region and the auditory protuberances, two prolongations, the anterior of which curves round the orbit, and eventually unites with the posterior in the cartilaginous process which articulates below with the mandible, and unites by its upper or cranial end with the suspensor of the hyoidean apparatus (*St.*, Fig. 86).

This arch clearly answers to the sub-ocular arch of the Lampreys and to the sub-ocular cartilage of the Chimæroids and *Lepidosiren*, and corresponds with the palato-quadrate, hyomandibular, and symplectic cartilages of the embryonic osseous fish taken together. The distal end of this cartilaginous pedicle commonly presents a larger or smaller ossification of its substance, which represents the quadrate bone. Now, the problematical bone (*z*) lies on the outer side of the pedicle, and I was at one time inclined to think that it represented the hyomandibular bone of osseous fish—being largely led to that impression by the great size of the hyomandibular and the comparative minuteness of the quadrate in the Conger and the Murœnoid fishes. But the hyomandibular is an ossification in the cartilage of the suspensorium, not a membrane bone. The bone has been compared with the tympanic, but the tympanic membrane has a special and distinct supporting ring in the Frogs. It has been identified, again, with the squamosal, but it lies too far down on the outer side of the pedicle for that bone. Tracing the changes of form in this bone (which is very constant in the *Amphibia*) downwards to the *Menobranchus* and *Siren*, its resemblance in these perennibranchiates to the bone (*F*) of *Lepidosiren* becomes very striking; and I am disposed to identify it with that bone, which, as I have stated above, has much resemblance to the pre-operculum of osseous fishes.

The mandible of *Amphibia* is commonly composed of three pieces—a dentary, an angular, and an articular. The latter, always continuous with Meckel's cartilage, may itself remain persistently cartilaginous.

The skull of the tadpole, before ossification has commenced, presents a cartilaginous base, in which the notochord terminates in a point, immediately behind the pituitary fossa. At the sides, the basal cartilage expands into two oval auditory capsules, and in front passes into the *trabeculæ cranii*, which embrace the membranous floor of the pituitary fossa, and reunite in the broad ethmo-vomerine cartilage. The apex of a sub-ocular arch, connected, behind, with the auditory region of the *basis cranii*, and, in front, with the prefrontal region, furnishes an articular surface to the axial, or "Meckel's cartilage," of the mandible. In the young Tadpole, a line drawn from the mandibular articulation to the auditory capsule makes an acute angle with the *basis cranii;* but, as age advances, the angle becomes more and more open, until, in the adult Frog, it is obtuse (Fig. 86), the articular surface for the mandible having passed far behind the auditory capsule. Of course the width of the gape increases *pari passu* with this rotation of the mandibular suspensor.

A survey of the series of the *Amphibia* from the perennibranchiates upwards, shows, in a persistent form, those inclinations of the suspensor which are transitory in the Frog. Thus in the perennibranchiate *Siren, Siredon, Proteus,* and *Menobranchus,* the angle is acute; in the Salamander and Salamandroid *Menopoma,* it is nearly a right angle; while, in the Frogs and Toads, and the ancient Labyrinthodonts, the angle is obtuse.

In the lower *Amphibia* there is no girdle bone, the orbitosphenoid and the prefrontals being usually represented by distinct bones. The frontals are distinct from the parietals, and the maxillary and pterygo-palatine arcades become imperfect.

Some of the Frogs and the *Cœciliæ*—the snake-like apodal *Amphibia*—have the cranial bones expanded and anchylosed into a sort of shield, presenting apertures only for the orbits and the nostrils; a process which is carried still further, by the addition of bones not known to existing *Amphibia,* in the extinct salamandroid members of the class, called Labyrinthodonts.

LECTURE XII.

ON THE STRUCTURE OF THE SKULL.

THE SKULLS OF REPTILIA AND AVES.

THE skulls of those abranchiate *Vertebrata* which do not suckle their young, and are oviparous, or ovo-viviparous, present certain peculiarities of construction in which they all agree with one another, and differ from the branchiate *Vertebrata* on the one hand, and from the *Mammalia* on the other.

Thus, the basi-occipital and the basi-sphenoid are always well developed, and the former furnishes a large part of the occipital condyle, which is single and central.

There is no parasphenoid, or median membrane bone, underlying the base of the skull.

The lower jaw, each ramus of which is composed of several pieces, articulates with the quadrate bone, as in the branchiate *Vertebrata*; but the quadrate bone articulates directly with the cranial wall, and is not separated from it by any structure representing the hyomandibular bone.

It may probably be added that the basi-sphenoid is formed by the union of three ossifications of cartilage—one supero-median and two infero-lateral (the basi-temporals of Mr. Parker); but further research is required before this generalization can be regarded as firmly established.*

* The caution expressed in the text seems to be no longer necessary, as my friend Mr. Parker, who possesses a remarkably extensive knowledge of the details of the structure and development of the vertebrate cranium, informs me that he has now found "the median basi-sphenoid and the symmetrical basi-temporals in Ophidians, Anguians, Scincoids, Iguanians, Geckos, Chamæleons, Cyclodonts, Lacer-

The combination of peculiarities just mentioned at once characterises the skulls of Birds and Reptiles, and distinguishes them from all others.

In all these animals, the basi-occipital bone gives attachment to a pair of ex-occipitals, which articulate, above, with a distinct supra-occipital. The homology of these bones with those which have received similar names in the Man's and in the Pike's skull is not doubted; and, indeed, their relations to one another, and to the exits of the eighth pair, are so similar as to allow of no discussion on this point.

Furthermore, the skulls of all Reptiles and Birds are roofed in by membrane bones, the correspondence of which with the parietals and frontals of Man is universally admitted; and, in all, there is a single or a double vomer, clearly identifiable with that of the Man and that of the Fish. So, again, there is no doubt about the homology of the premaxillæ and the maxillæ, the palatine and the pterygoid bones with the parts so named in Man. Nor is it questioned that the mandible and the hyoidean arches, in a general way, correspond with his. But there has been, and is, very great divergence of opinion as to the true nature of certain bones in the side walls of the skull, and of some of those which enter into the composition of the maxillary apparatus. I shall address myself chiefly to the discussion of these debatable ossifications.

The bone of most importance among these (the misinterpretation of which must needs, indeed, completely vitiate and render worthless any theory of the vertebrate skull) is that which lies in the side wall of the cranium, in front of the ex-occipital; while it is connected below with the basi-sphenoid, and above with the supra-occipital and parietal. In all Birds

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tians, Monitors, Chelonians, Crocodiles, and in all kinds of Birds." Mr. Parker agrees with my suggestion (suprà, p. 170), that the basi-temporals of the *Sauropsida* (or Birds and Reptiles) are the homologues of the *lingulæ sphenoidales* of Man. He has found similar bones in numerous Mammals, and they are of especially large size in the Mole and in the Shrew. He informs me that the Sheep has no bony centre for the basi-sphenoid, the alisphenoids meeting in the middle line. Nevertheless its *lingulæ* are well developed at the commencement of the last third of intra-uterine life.

Fig. 88.

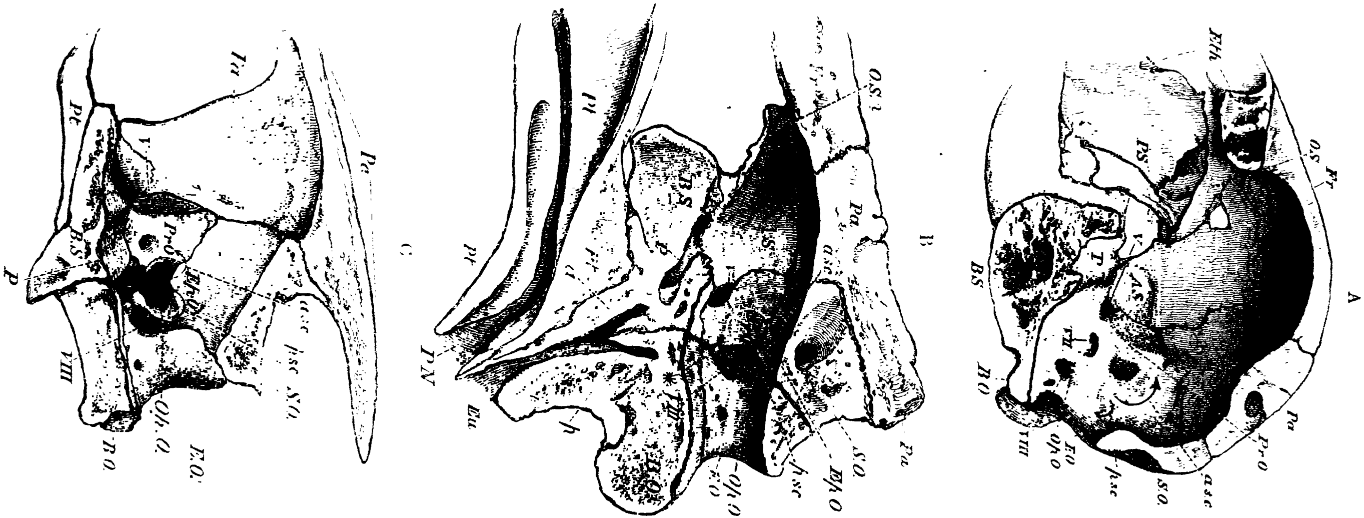


Fig. 88.—Vertical and longitudinal sections of the cranial chambers of (A) an Ostrich (*Struthio camelus*), (B) a Crocodile (*C. biporcatus*), and (C) a Turtle (*Chelone midas*), to show the interior of the cranial cavity in each. In B, * indicates the end of the cochlear plate of the opisthotic of the Crocodile; *Eu*, the common Eustachian tube, with *a* and *p* its anterior and posterior affluents; *P N*, the posterior nares. The arrows denote the position of the anterior and posterior vertical semicircular canals. In all the figures *P* indicates the pituitary fossa.

and Reptiles the relations of this bone are essentially such as are shown in the accompanying figures of sections of the skulls of an Ostrich, a Crocodile, and a Turtle (Fig. 88, A, B, C). In all these it will be observed, that the aperture for the exit of the third division of the trigeminal (*V*) lies in front of a bone, which is notched, or perforated, by apertures for the *portio dura* and *portio mollis*, and that the anterior part of the organ of hearing is lodged within this bone. Furthermore, an external view of this region of the skull (Fig. 89, A and B) shows that the bone in question contributes, in each case, the anterior half of the boundary of the *fenestra ovalis*. In other words, the bone in question has every essential relation of that ossification which, in Man and in the Pike, I have termed *pro-otic*.*

The other elements of the periotic capsule are not far to seek. In the Turtle one of them retains its independence throughout life, and occupies a considerable space on the exterior of the skull, though, internally, only a small strip of it is seen in front of the foramen for the eighth pair (Fig. 88, C). This bone furnishes the posterior half of the frame for the *fenestra ovalis*, with so much of that of the *fenestra rotunda* as is osseous, and it lodges the posterior and outer part of the auditory organ. It answers precisely, therefore, to the *opisthotic*.†

The corresponding ossification in most other Reptiles and in Birds early coalesces with the ex-occipital.

The third periotic bone, the *epiotic*, does not remain distinct throughout life in any Reptile or Bird, and its place appears to be taken by a triangular process of the supra-occipital, which

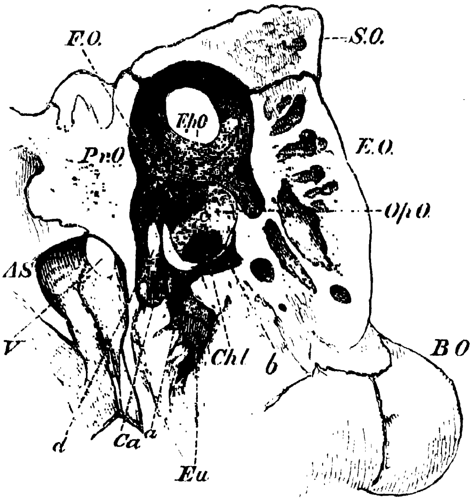
* This is the bone called by Cuvier "rocher," and regarded by him and by most of the German anatomists as the homologue of the *pars petrosa* of the human temporal bone. I took the same view myself when I delivered the Croonian Lecture in 1858, and I do not now *substantially* depart from it. For that part of the *pars petrosa* which is most obvious and visible in the interior of the skull is its pro-otic portion; and so long as the complex nature of the *pars petrosa* was unknown, the identification of the bone *Pr.O* in the Bird and Reptile with the petrosal of the Mammal was the nearest approximation that could be made to the truth. Cuvier's identification would have been absolutely correct if he had termed the ornithic and reptilian bone not "petrosal," but "anterior part of the petrosal."

† Cuvier termed this bone the "*occipital externe*." Hallmann regarded it as the equivalent of the "mastoid," and I followed him in my Croonian Lecture. In the absence of a full knowledge of the development of the human *pars petrosa*, it was difficult, if not impossible, to see one's way to any better conclusion.

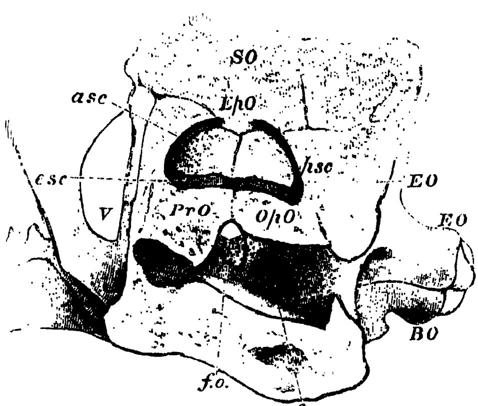
shelters the summits of the vertical semicircular canals. But the study of development has shown that this part of the supra-occipital is, in many, if not all, Reptiles and Birds, developed from

Fig. 89.

A



B



. 89.—External view of the auditory region of the skull in (A) a Crocodile (*C. biporcatus*), and (B) a Turtle (*Chelone midas*). The walls of the tympanic cavity have been cut away in each case so far as is necessary to show the auditory *fenestræ*; and, in the Turtle's skull, the semicircular canals are also partially displayed. In the Crocodile's skull (A) *F.O.* is the *fenestra ovalis*, separated by the cochlear process of the opisthotic, *c*, from the *fenestra rotunda*; *Chl* is the hook formed by the curved process (*b*) of the opisthotic, which supports the cochlea externally. The lower end of the a separate centre, which subsequently coalesces with the supra-occipital; so that, just as the opisthotic in these animals ordinarily coalesces with the ex-occipital, the epiotic anchyloses with the supra-occipital.

In many Reptiles, though two of the three periotic bones coalesce with their neighbours, the suture between the three persists on the inner surface of the skull, and is always shaped like a Y (Fig. 88, B); the stem of the Y answering to that part of the suture which separates the pro-otic from the opisthotic ossifications, while the diverging branches of the Y correspond with the suture between the opiotic and pro-otic in front, and that between the epiotic and opisthotic behind. In the Turtle an interspace filled with cartilage takes the place of the stem of the Y (Fig. 88, C).

In the adult Crocodile the epiotic is united with the supra-occipital, and the opisthotic with the ex-occipital; but that process of the opisthotic (*c*, Fig. 89, A) which separates the *fenestra ovalis* from the *fenestra rotunda* (the anterior and inner edge of which, only, is completed by bone) where it meets the pro-otic below and anteriorly (at *d*, Fig. 89, A), sends downwards and backwards a process, which curves round the cochlea, and, expanding to a broad plate, adjusts itself by harmonia (at *b*) to the outer and lower edge of the opisthotic, and to part of the posterior edge of the pro-otic. The anterior and inferior angle of the broad plate is thicker than the rest, and is seen in the interior of the dry skull, at the bottom of the stem of the Y-shaped suture (*, Fig. 88, B). If, as has been remarked, this part of the curved cochlear plate of the opisthotic be pressed

cochlea rests in the fossa *a*, formed by the basi-sphenoid and basi-occipital. The upper end, bounded externally only by cartilage, has disappeared in the dry skull and, with it, the outer lip of the *fenestra rotunda*, the plane of which is horizontal, and nearly on the level of the dotted line leading from *Op.O* in the figure. *d* is a small process of the pro-otic, against which the bend of the curved cochlear process (*b*) rests. The dotted line from *b* indicates the position of the suture between the hinder end of that process and the remainder of the opisthotic bone. *Ca*, the carotid canal; *Eu*, the upper opening of the posterior of the two canals by which each tympanum communicates with the common Eustachian tube. The narrow anterior tympanic canal opens just in front of *Ca*, the cleft-like aperture being traversed by the dotted line from *d*. In the Turtle's skull (B) *Op.O* is a distinct bone from *E.O*, and sends down a process between *f.o.*, the *fenestra ovalis*, and *f.r.*, the *fenestra rotunda*, which terminates in no recurrent hook, but otherwise corresponds exactly with the cochlear process (*c*) in the Crocodile.

upon with a point, it gives way; but this is not because it is merely suturally connected with the periotic bones, as has been supposed, but because the lamina of bone by which the cochlear plate is fixed to the opisthotic is very thin and elastic.

Among the many singular speculations which the historian of the theory of the skull will have to record, perhaps the strangest is that which identifies this cochlear loop, imagined to be a distinct bone, with the entire "petrosal" bone of the *Mammalia*.

In Birds, the three periotic bones anchylose with one another, as well as with the adjacent supra-occipital and ex-occipital, so completely, that even the Y-shaped suture becomes obliterated (Fig. 88, A).

The determination of the homologues of the periotic bones in the skulls of Birds and Reptiles, and more especially of the pro-otic, is not only a matter of first-rate importance in itself,

Fig. 90.

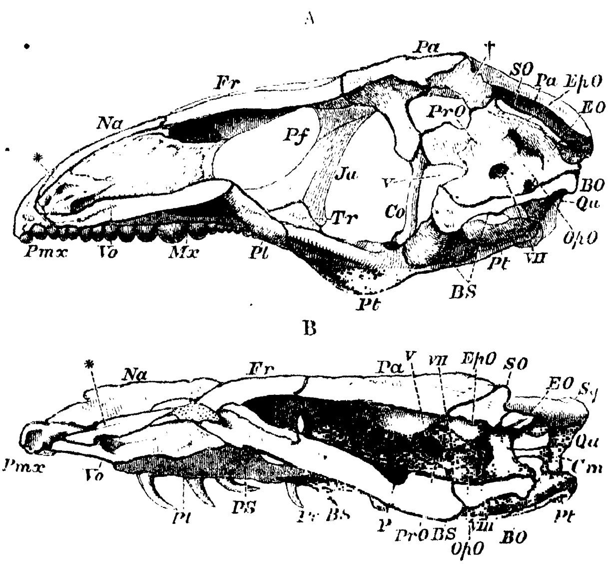


Fig. 90.—A, a vertical and longitudinal section of the skull of a Lizard (*Cyclodus*). B, a similar section of the skull of a Snake (*Python*). †, membranous space in the roof of the Lizard's skull; * *, ossifications in the internasal cartilage; *Co*, the *columella* of the Lizard; *Cm*, the bone also called "*columella*," which corresponds with the stapes.

but it involves that of certain other bones of the side walls of the skull.

In the *Chelonia*, and in many Lizards, the lateral walls of the cranium, between the pro-otics and the prefrontals, are entirely occupied by cartilage, or by membrane. In the dry skull of the Turtle (Fig. 88, C) it is true that there is an apparent bony wall in front of the pro-otic, but this is only a process sent down from the parietal, which becomes connected with the pterygoid, and with a small, distinct lamella of bone.

In Lizards a distinct, rod-like bone (*Co*, Fig. 90, A, and Fig. 91), occupies a corresponding position, articulating above with the parietal, and below with the pterygoid, and receives the name of the *columella*.

Fig. 91.

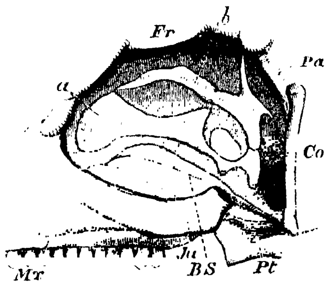


Fig. 91.—The inter-orbital septum of a Lizard (*Iguana*). *BS*, the anterior prolongation or beak of the basi-sphenoid; *a*, the inferior median ossification; *b*, the superior paired ossification of the left side of the inter-orbital septum; *Co*, the columella.

In both Chelonians and Lizards the basi-cranial axis is laterally compressed in the presphenoidal region, and is converted into a vertical inter-orbital septum, as in the Pike. In the Chelonians, neither the septum, nor the membranous, or cartilaginous, alisphenoidal and orbito-sphenoidal regions connected with it, present any ossifications, but, in many Lizards, delicate laminæ of bone are developed in this region. In the *Iguana tuberculata*, for example (Fig. 91), the inter-orbital septum is supported below by the prolonged beak of the basi-sphenoid. Above this, it presents a long median presphenoidal ossification (*a*) forked posteriorly. The forks are connected with two bones, one on each side (*b*), which appear to represent orbito-sphenoids.

The Crocodiles, on the other hand, possess a large and distinct lateral ossification in front of each pro-otic (*A S*, Fig. 88, B). This ossification bounds the foramen for the third division of the fifth nerve in front, and unites with the basisphenoid below and with the parietal above, so far agreeing with the alisphenoid. Since it extends so much further forward than the alisphenoid ordinarily does, Cuvier has suggested that it probably represents both the ali- and the orbito-sphenoids; but Stannius has pointed out the existence of two small ossifications close to the optic foramina, with an insignificant descending median stem at their bases. The former he considers to be the orbito-sphenoids and the latter the presphenoid.

In these Reptiles, in the *Lacertilia* and in the *Chelonia*, the *basis cranii*, as has been already stated, is modified anteriorly into an inter-orbital septum, as in the Pike; but in the *Ophidia*, the Cyprinoid, or Batrachian, type of skull reappears, and the cavity of the cranium is continued without any sudden narrowing, from above downwards, from its posterior to its anterior end. In the Ophidian skull (Fig. 90, B) the side walls of the cranium, in front of the pro-otics, are completely closed in by bones, which might readily be taken for alisphenoids and orbito-sphenoids; but, according to Rathke, they are merely downward growths of the parietals and frontals, and therefore can have nothing to do with the true lateral cranial elements.

The anterior part of the *basis cranii* in Birds is always vertically elongated into an inter-orbital septum, as in the *Crocodilia*, *Lacertilia*, and *Chelonia*. In the Ostrich (Fig. 88, A) the presphenoid is completely ossified, but, in other members of the class, the nature and extent of the presphenoidal ossifications may vary greatly. The alisphenoid is always well ossified, and occupies its characteristic position in front of the pro-otic and of the exit of the third division of the trigeminal nerve (Fig. 88, A). The orbito-sphenoids, on the other hand, may or may not be represented by bone. In the Ostrich they are present, and are continuous with the presphenoid.

Reptiles possess prefrontal and post-frontal bones, which usually remain distinct throughout life, and are admitted to be homologous with those of Fishes, and therefore the line of argument which identified the prefrontals of the Pike with the lateral masses of the ethmoid in the Man is equally applicable to the same bones in Reptiles. In Birds, the post-frontals have only a doubtful and exceptional distinctness, and in them the true prefrontals seem early to coalesce with the ethmoid. The last-mentioned cranial element is usually ossified and appears upon the upper surface of the skull, in Birds; while, in *Reptilia*, it almost always remains cartilaginous. In the extinct *Dicynodon*, however, it and the presphenoidal region were completely ossified.

In Birds, in consequence of the prolongation of the snout

Fig. 92.

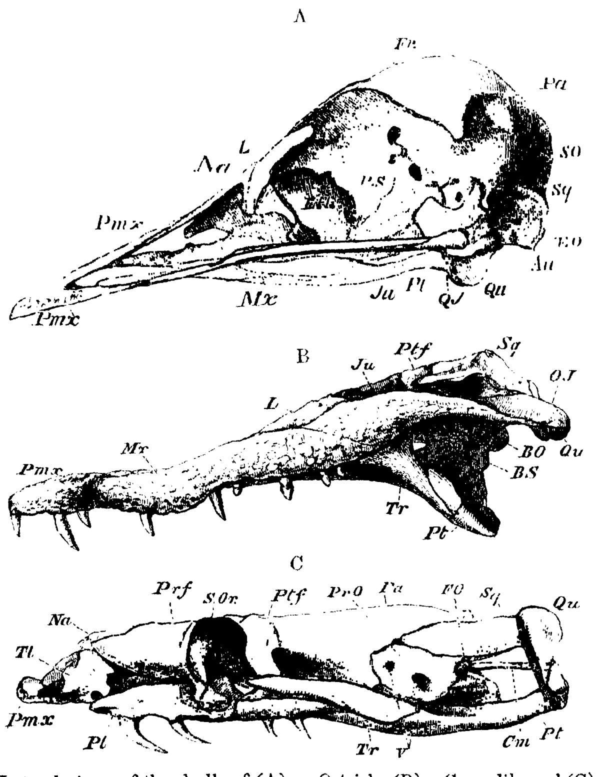


Fig. 92.—Lateral views of the skulls of (A) an Ostrich, (B) a Crocodile, and (C) a Python, without the mandible. In the Python's skull the maxilla has also been removed. *Tl*, turbinal bone of the Ophidian.

into a beak, the internasal part of the basi-facial axis acquires a considerable size, and becomes the subject of a great variety of ossifications, which, in many Birds, are so arranged as to allow the anterior part of the cranio-facial axis to be moveable on its posterior part. In many Lizards, on the other hand, the anterior part of the cranium is rendered moveable upon the posterior in another way. The cranio-facial axis in front of the basisphenoid is cartilaginous, and consequently slightly flexible, while the roof of the skull between the parietals, the supra-occipital and the periotic bones is merely membranous (†, Fig. 90, A); hence, the front part of the skull is capable of being slightly raised or depressed, in a vertical plane, upon the posterior part.

Next to the pro-otic, the squamosal and the quadrate bones of Birds and Reptiles have been the subject of the greatest amount of controversy among morphologists.

The bone which was originally called "*os quadratum*" is that moveable facial bone of the Bird (*Qu*, Fig. 92, A) which is articulated, above, with the outer side of the periotic capsule, and especially with the pro-otic bone, and below with the *os articulare* of the mandible, while, internally and anteriorly, it is connected with the pterygoid. In the *Crocodilia* (Fig. 92, B) and *Chelonia*, a bone, admitted by all to be the homologue of this, is attached immoveably in the same region: in most *Lacertilia* (Fig. 93) it is moveable, and remains connected with the produced extremity of the pro-otic bone; but, in most *Ophidia* (Fig. 92, C) its proximal end is thrust out from the skull upon the extremity of another bone. However, its homology with the quadrate of the Bird is not affected by this circumstance.

With what bone in the human skull does this correspond? Cuvier identified it with the tympanic of Man, and his interpretation has been generally accepted; but the tympanic is always a membrane bone, whereas this is always a cartilage bone. The tympanic directly supports the tympanic membrane, while this bone sometimes gives no direct attachment to the tympanic membrane at all. The tympanic of Mammals again becomes smallest in those *Mammalia* which most nearly approach Birds and Reptiles, and is never known to articulate, by a moveable joint, with the *malleus*, which, as we have seen, is the representative of the *os articulare* of the mandible of the lower *Vertebrata*.

It is impossible, therefore, that the quadrate bone should be the homologue of the tympanic of *Mammalia*. On the other hand, it corresponds altogether with the quadrate bone of Fishes, which is united in like manner with the pterygoid arcade, and is similarly connected by a moveable joint with the articular piece of the mandible; and this quadrate bone of Fishes is, I have endeavoured to show, the homologue of the incus of the *Mammalia*. I make no question that, as Reichert long ago asserted, the Bird's *os quadratum* and, therefore, that of the Reptile, is the equivalent of the Mammalian *incus*.

It is difficult to understand how any doubt can be entertained as to the bone which is the homologue of the Mammalian squamosal in Birds. Lying above the tympanic cavity, between the parietal, frontal, and periotic bones, is a membrane bone (*Sq*, Fig. 92, A) which corresponds with the Mammalian squamosal, and with no other bone in the Mammalian skull.

But if this be the Bird's squamosal, there is no difficulty in determining that of any Reptile, the *Crocodilia*, *Lacertilia*, *Chelonia*, and *Ophidia* all presenting a bone in a similar position. It is this bone which, in most *Ophidia* (Fig. 92, C),

Fig. 93.

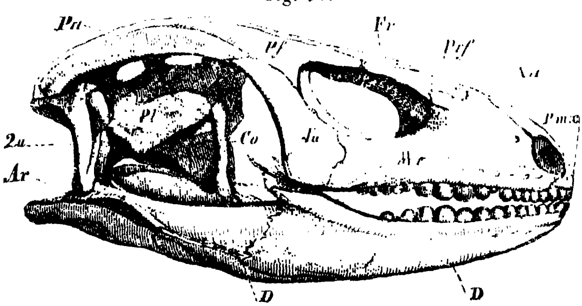


Fig. 93.—The skull of a Lizard (*Cyclodus*).—*D D*, Dentary piece of the lower jaw; *Qu*, Os quadratum; *Sq*, Squamosal.

carries the *quadratum* as on a lever; but, as Rathke has well shown, the final position of the *quadratum* is a result of developmental modification, the proximal end of that bone being originally in *Ophidia*, as in other Reptiles, applied to the periotic capsule.

The palato-maxillary apparatus presents a considerable diversity of structure in Reptiles and Birds. In all Birds, and in most Reptiles, the pterygoid and the quadrate bones are more or less closely connected, but in the Crocodiles and Chamæleons they are separated. In *Crocodiles* and *Chelonia*, and in the extinct *Plesiosauria*, the quadrate bone is immoveably united with the skull, and the other facial bones are firmly and fixedly united with one another and with the cranium. In most Birds and *Lacertilia*, on the contrary, the quadrate bone is moveably

Fig. 94.

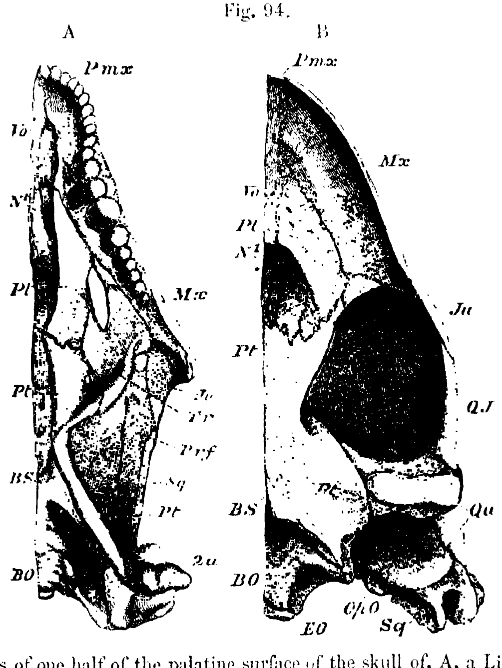


Fig. 94.—Views of one half of the palatine surface of the skull of, A, a Lizard (*Cyclodus*), and B, a Turtle (*Chelone midas*). N^1, the posterior nasal aperture.

articulated with the skull, and its motion may be communicated by the pterygoid, the quadrato-jugal and the jugal bones to the fore-part of the face. This mobility reaches its maximum, on the one hand, in such birds as the Parrots, in which the beak and fore-part of the basi-facial axis are united by a sort of hinge with the rest of the skull; and, on the other, in the Serpents, in which, as has been already stated, the quadrate bone is shifted to the end of the squamosal, and the palatine, pterygoid, and maxillary bones are bound only by ligaments to the skull, so that the utmost possible amount of play is allowed to the bones which surround the mouth.

In many Reptiles a bone makes its appearance which cannot, at present, be identified with any bone of Fishes or of Mammals. This is the *transverse* bone of Cuvier (*Tr*), which unites together the maxilla with the palatine and the pterygoid.

Remarkable differences are noticeable in the degree to which the premaxilla is developed in the various orders of Reptiles and in Birds. In the Snakes it is very small, or rudimentary; in the *Lacertilia*, *Chelonia*, and *Crocodilia* it has a moderate size; while in the extinct *Ichthyosauria*, and still more in Birds, the premaxilla attains vast dimensions, completely surpassing the maxillary element, which in Birds is reduced to a mere bar of bone, connected by similar slender rods, which represent the jugal and quadrato-jugal, with the outer part of the distal end of the quadrate bone.

In the *Ophidia*, most *Lacertilia*, and Birds, the nasal sacs open below and behind into the cavity of the mouth, by apertures placed between the vomer and palatine bones, which correspond with what I have termed the "median nares" in Man; or there is, at most, an indication of a separation between the oral cavity and the nasal passage, produced by the sending downwards and inwards of a process by the maxillary and palatine bones on each side. But, in the *Crocodilia* (Fig. 95, B), not only the maxillary and palatine bones, as in Man, but the pterygoid bones, in addition, send such prolongations downwards and inwards; and these, meeting in the median line, shut off from the cavity of the mouth a nasal passage, which opens into the fauces by the posterior nares (N^1, Fig. 95). The arrangement of the palatine bones is such that, in most *Crocodilia*, the vomers are completely excluded from the roof of the mouth.

When a tympanic cavity exists in the branchiate *Vertebrata*, it is little more than a diverticulum of the buccal cavity, connected by so wide an aperture with the latter, that an Eustachian tube can hardly be said to exist. In the *Ophidia* and in certain *Lacertilia* the tympanic cavities and Eustachian tubes are altogether absent, and, even in the higher *Lacertilia*, the tympanum can hardly be said to have definite bony walls. In the *Chelonia*,

Fig. 95.

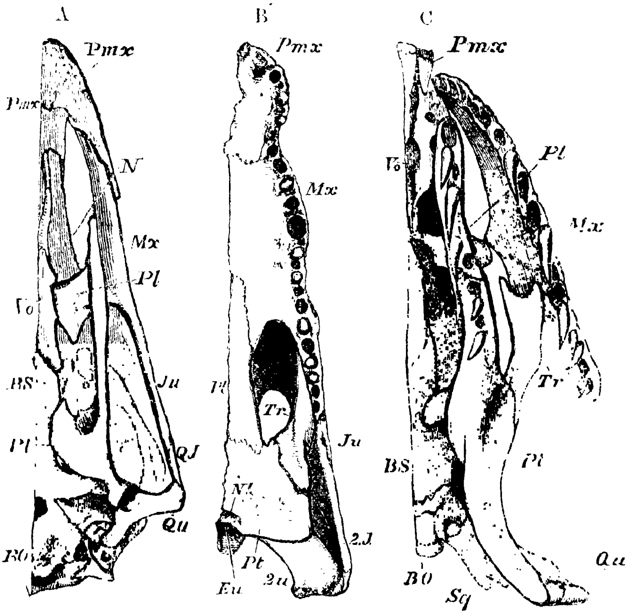


Fig. 95.—Views of one half of the palatine surface of the skull in (A) an Ostrich, (B) a Crocodile, (C) a Python. *N*, the posterior nasal aperture (median nares of Man) in the Bird. The dotted line traverses the posterior nasal aperture, situated between the palatine, the vomer, and the maxillary. The corresponding opening is placed between *Vo* and *Pl* in the Snake. N^1, the posterior nasal aperture, or posterior nares, of the Crocodile.

on the other hand, the opisthotic and the pro-otic bones are produced outwards so as to form the anterior and posterior boundaries of a cavity, the *antivestibulum Bojani*—which is bounded externally by the great quadrate bone. The latter is funnel-shaped, and deeply notched posteriorly and inferiorly. The tympanic membrane is fixed to the margins of the funnel, and the so-called "*columella*," which answers to the *stapes*, is fastened by one end to this tympanic membrane, and traversing the notch and entering the *antivestibulum*, passes to its other insertion into the membrane of the *fenestra ovalis*. The

Eustachian tubes have separate openings into the pharyngeal cavity, and curve upwards and backwards from the latter round the inferior and posterior edges of the quadrate bones to open into the tympana.

In Birds the tympanic cavity is roofed over by the squamosal, while a more or less complete floor is furnished to it by the basi-sphenoid, and a back wall by the produced ex-occipital (and opisthotic ?). It may be completed in front by fibro-cartilage or even by bone, and the *membrana tympani* is fastened to the outer margin of these boundaries of the tympanum and not to the quadrate bone.

The Eustachian passages ordinarily traverse the basi-sphenoid, and when they reach the base of the skull unite into a single, cartilaginous, common Eustachian tube, which opens in the middle line, on the roof of the mouth.

Fig. 96.

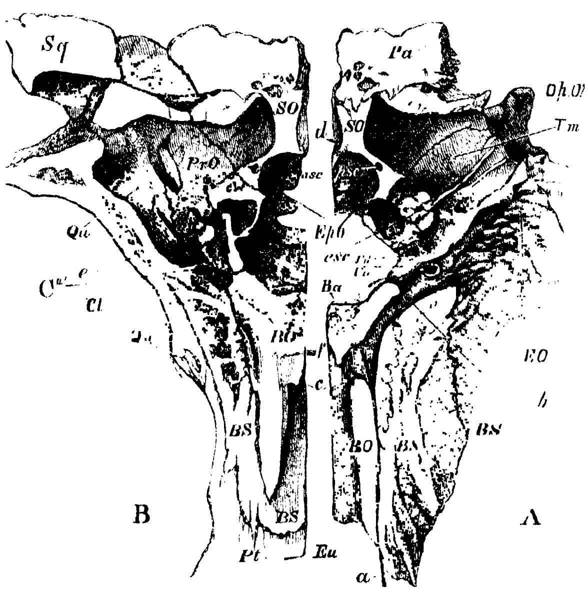


Fig. 96.—Vertical and transverse sections of the left tympanic cavity of *Crocodilus biporcatus*. A, posterior, B, anterior segment; *a*, bristle passed into the small lateral Eustach in passage leading from *b*, the posterior tympanic passage, which opens into *c*, the common Eustachian passage; *d*, a bristle thrust into the air-passage which traverses the supra-occipital; *f*, bristle passed into the anterior tympanic passage; *Ca*, *Ca'*, carotid canal; *Cl*, fossa for the extremity of the cochlea; *Tm*, inner division of the tympanic cavity.

In the *Crocodilia* the tympanic cavities and Eustachian passages are still more remarkably disposed.*

The tympanic cavity of *Crocodilus biporcatus* (Fig. 89, A; Fig. 96) is distinguishable into an inner and an outer part. The latter is bounded by the squamosal bone, above and behind, by the quadrate bone, below and in front. Into the former the supra-occipital enters, above; the quadrate, and, to a slight extent, the basi-occipital and basi-sphenoid below. To the posterior wall of the inner division, that outward and backward prolongation of the ex-occipital, which answers to the opisthotic of the turtle, contributes, while the front wall is formed partly by the quadrate and partly by the pro-otic bones.

Externally the tympanum opens by the external auditory meatus—its internal wall is formed chiefly by the pro-otic, opisthotic, and epiotic. The two latter are, as I have already stated, anchylosed, respectively, with the ex-occipital and the supra-occipital.

Each tympanic cavity communicates with its fellow of the opposite side, superiorly, by a wide passage, which perforates the supra-occipital bone and has a secondary diverticulum traversing the ex-occipital. Below, the tympana communicate with one another indirectly, by means of the common median Eustachian tube, the aperture of which, formed, half by the basi-sphenoid and half by the basi-occipital, is seen on the base of the skull behind the posterior nares (*e*). Each tympanum communicates with the common Eustachian tube by two passages: one, wide, from the posterior and inferior part of the tympanum (*b*); and one, very narrow, from its anterior and inferior region (*f*).

The two exits are separated by that part of the floor of the tympanum which is formed by the basi-sphenoid and basi-occipital. This presents, behind, a hemispherical fossa (*Cl*) into which both the basi-sphenoid and basi-occipital enter, and, in front, a round aperture with raised edges, situated altogether in the basi-sphenoid (C^a). The fossa lodges the distal blind end of the cochlea. The aperture leads into a canal, which, passing

* These were first carefully described by Professor Owen in a memoir published in the *Philosophical Transactions* for 1850. Windischmann, "De Penitiori auris in Amphibiis Structura" (1831), has given but a very imperfect account of them.

downwards and forwards in the basi-sphenoid, opens into the pituitary fossa, and lodges the internal carotid.

The upper aperture of the anterior, narrow, passage from the tympanum (*f*) is situated in front of the lip of the carotid canal, and, at first, lies between the basi-sphenoid and the pro-otic; but, soon turning inwards, it enters the basi-sphenoid, and passes beneath the carotid canal, to open into a much wider median channel. The latter ends blindly in front and above, behind and below the pituitary fossa; but, inferiorly, it traverses the substance of the basi-sphenoid, to open into the upper and front part of the common Eustachian tube (Fig. 96, B).

The posterior, wide, passage (*b*) leads downwards and inwards through the substance of the basi-occipital, and the two passages of the opposite tympana unite to form a short median canal, which opens, on the front face of the basi-occipital, into the common Eustachian tube (Fig. 96, A).

The posterior tympanic passage has, however, another means of communication with the exterior; for, just before it joins with its fellow, it gives off, downwards, a narrow canal, which traverses the basi-occipital, and opens on its inferior face to the outer side of, and a little behind, the aperture of the common Eustachian tube (*a*, Fig. 96, A). There might, then, be said to be three Eustachian tubes in the Crocodile,—two small and lateral, one for each tympanum, and one large and median, common to both tympana.

Where the posterior tympanic passage passes into the tympanum, the ex-occipital presents a round aperture with raised edges, which is the anterior termination of the posterior division of the canal for the internal carotid (*C'*, Fig. 96, B). In the interval between this aperture of entrance and that of exit already described, the internal carotid is unprotected by bone, and is closely adherent to the outer surface of the cochlea; which, held by the cochlear hook already described, rests inferiorly upon the fossa afforded by the basi-sphenoid and basi-occipital (*Cl*).

The posterior wall of the tympanum also exhibits, internally, the aperture by which the eighth pair of nerves reaches the exterior; externally, those by which the portio dura leaves, and the external carotid enters; superiorly, between the supra-occipital and the squamosal, is a cleft which leads to the occipital surface in the dry skull.

The early stages of the development of the skull of a Bird have already been described. The process of formation of the Reptilian skull has been admirably worked out by Rathke in the Common Snake, *Coluber natrix*, and I conclude this Lecture by an abstract of his researches on this subject.*

The differences between the basis of the skull and the vertebral column in the earliest embryonic condition are,—

1. That round that part of the notochord which belongs to the head, more of the blastema, that is to be applied, in the spinal column, to the formation of the vertebræ and their different ligaments, is aggregated than around the rest of its extent, and—

2. That this mass grows out beyond the notochord to form the cranial trabeculæ.

The lateral trabeculæ, at their first appearance, formed two narrow and not very thick bands, which consisted of the same gelatinous substance as that which constituted the whole investment of the notochord, and were not sharply defined from the substance which lay between them and at their sides, but seemed only to be two thickened and somewhat more solid, or denser, parts of that half of the basis of the cranium, which lies under the anterior cerebral vesicle.

Posteriorly, at their origin, they were separated by only a small interval, equivalent to the breadth of the median trabecula, and thence swept in an arch to about the middle of their length, separating as they passed forwards; afterwards they converged, so that, at their extremities, they were separated by a very small space, or even came into contact. Altogether they formed, as it were, two horns, into which the investing mass of the notochord was continued forwards. The elongated space between them, moderately wide in the middle, was occupied by a layer of softer formative substance, which was very thin posteriorly, but somewhat thicker anteriorly. Upon this layer rested the infundibulum; and in front of it, partly on this layer, partly on the trabeculæ, that division of the brain whence the optic nerves

* Entwickelungsgeschichte der Natter, 1839.

proceed; and, further forwards, the hemispheres of the cerebrum. Anteriorly, both trabeculæ reached as far as the anterior end of the head, and here bent slightly upwards, so that they projected a little into the frontal wall of the head, their ends lying in front of the cerebrum. Almost at the end of each horn, however, I saw a small process, its immediate prolongation, pass outwards and form, as it were, the nucleus for a small lateral projection of the nasal process of the frontal wall.

The middle trabecula grows, with the brain, further and further into the cranial cavity; and as the dura mater begins to be now distinguishable, it becomes more readily obvious than before, that the middle trabecula raises up a transverse fold of it, which traverses the cranial cavity transversely.* The fold itself passes laterally into the cranial wall; it is highest in the middle, where it encloses the median trabecula, and becomes lower externally, where it forms, as it were, a short ala proceeding from the trabecula. With increasing elongation, the trabecula becomes broader and broader towards its free end, and, for a short time, its thickness increases. After this, however, it gradually becomes thinner, without any change in its tissue, till, at the end of the second period, it is only a thin lamella, and after a short time (in the third period) entirely disappears.

In Mammals, Birds, and Lizards, that is, in those animals in general in which the middle cerebral vesicle is very strongly bent up and forms a protuberance, while the base of the brain exhibits a deep fold between the infundibulum and the posterior cerebral vesicle, a similar part to this median trabecula of the skull is found.

In these animals, also, at a certain very early period of embryonic life, it elevates a fold of the dura mater which passes from one future petrous bone to the other, and after a certain time projects strongly into the cranial cavity. Somewhat later, however, it diminishes in height and thickness, as I have especially observed in embryos of the Pig and Fowl, until at last it disappears entirely in these higher animals also, the two layers of the fold which it had raised up coming into contact. When

* What Rathke terms the "middle trabecula," appears to be only very indistinctly developed in Fishes and *Amphibia*.

this has happened, the fold diminishes in height and eventually vanishes, almost completely.

The two lateral trabeculæ, which in the Snake help to form the anterior half of the basis of the skull, attain a greater solidity in the second period, acquire a greater distinctness from the surrounding parts, and assume a more determinate form, becoming, in fact, filiform; so that the further forward, the thinner they appear. They increase only very little in thickness, but far more in length, during the growth of the head. Altogether anteriorly, they coalesce with one another, forming a part which lies between the two olfactory organs and constitutes a septum. As soon as these organs increase markedly in size, this part is moderately elongated and thickened, without, however, becoming so dense as the hinder, longer part of the trabeculæ. The prolongations into the lateral projections of the nasal processes, which now proceed from the coalesced part in question, also become but little denser in texture for the present, though they elongate considerably.

The lateral parts and the upper wall of the cranium, with the exception of the auditory capsules, or of the subsequent bony labyrinth, remain merely membranous up to the end of the second period; consisting, in fact, only of the cutaneous covering, the dura mater, and a little interposed blastema, which is hardly perceptible in the upper part, but increases in the lateral walls, towards the base of the skull.

The notochord reaches, in very young embryos of the Snake, to between the auditory capsules; and further than this point it can be traced neither in the Snake nor in other *Vertebrata*, at any period of life, as manifold investigations, conducted with especial reference to this point, have convinced me.

At the beginning of the third period, the basal plate chondrifies, at first leaving the space beneath the middle of the cerebellum membranous; but this also eventually chondrifies, and is distinguished from the rest of the skull only by its thinness.

Lateral processes grow out from the basal cartilage just in front of the occipital foramen, and eventually almost meet above. They are the ex-occipitals.

The two lateral trabeculæ—parts which I have also seen in Frogs, Lizards, Birds, and Mammals—chondrify at the beginning of the third period. At first, they pass, distinct from one another throughout their whole length, as far as the frontal wall, on entering which they come into contact; they are more separate posteriorly than anteriorly, and they present, in their relative position and form, some similarity with the sides of a lyre. But as the eyes increase, become rounder, and project, opposite the middle of the trabeculæ, downwards towards the oral cavity, the latter are more and more pressed together, so that, even in the third period, they come to be almost parallel for the greater part of their length. Anteriorly, where they were already, at an earlier period, nearest to one another, they are also pressed together by the olfactory organs (which have developed at their sides to a considerable size), to such a degree, that they come into contact for a great distance and then completely coalesce; they are now most remote posteriorly, where the pituitary body has passed between them,* so that they seem still to embrace it. Anteriorly, between the most anterior regions of the two nasal cavities, they diverge from their coalesced part, as two very short, thin, processes or cornua, directed upwards, and simply bent outwards.

It has been seen above that the median trabecula does not chondrify, but eventually disappears; in its place, a truly cartilaginous short thick band grows into the fold of dura mater from the cartilaginous basal plate.

Where the pituitary gland lies, there remains between the lateral trabeculæ of the skull a considerable gap, which is only closed by the mucous membrane of the mouth and the dura mater. But there arises in front of this gap, between the two trabeculæ, as far as the point where they have already coalesced, a very narrow, moderately thick, and anteriorly pointed streak of blastema, which, shortly before the end of the third period, acquires a cartilaginous character and subsequently becomes the body of the presphenoid.

* The pituitary body, however, as Rathke has since admitted, does not pass between the trabeculæ, and is developed in quite a different manner from that supposed in the memoir on *Coluber*.

Altogether anteriorly, however, where the two trabeculæ have coalesced, there grows out of this part, from the two cornua in which it ends, a pair of very delicate cartilaginous plates. At the end of the third period both plates acquire a not inconsiderable size, take the form of two irregularly-formed triangles, and are moderately convex above, concave below, so as to be, on the whole, shell-shaped. The nasal bones are developed upon these, while below them are the nasal cavities, and the nasal glands with their bony capsules.

The alæ, or lateral parts, of the two sphenoids do not grow, like the lateral parts of the occipital bone, out of the *basis cranii*, the foundation of which is formed by the cephalic part of the chorda, but are formed separately from it, although close to it, in the, until then, membranous part of the walls of the cranium.

The alæ of the presphenoid (orbito-sphenoids), which are observable not very long before the termination of the third period, appear as two truly cartilaginous (though they never redden), irregular, oblong, plates of moderate thickness; lie in front of the optic foramina, at the sides of the lateral trabeculæ of the skull; ascend from them upwards and outwards, and are somewhat convex on the side turned to the brain, somewhat concave on the other. The alæ magnæ (alisphenoids) are perceptible a little earlier than these. They are formed between the eye and the ear, and also originally consist of a colourless cartilaginous substance: they appear, at the end of the third period, as irregular four-sided plates; lie at both sides of the anterior half of the investing plate of the chorda; ascend less abruptly than the alæ orbitales, and are externally convex, internally concave.

The upper posterior angle of each elongates, very early, into a process, which grows for a certain distance backwards, along the upper edge of the auditory capsule, and applies itself closely thereto.

The auditory capsules, or the future petrous bones, chondrify, as it would appear, the earliest of all parts of the skull: the *fenestra ovalis* arises in them by resorption.

The *ossification* of the Snake's skull commences in the basi-occipital, or, at any rate, this is one of the first parts to ossify. At a little distance from the occipital foramen, there arises a very small semilunar bony plate, the concave edge or excavation of which is directed forwards; thereupon, the bony substance shoots from this edge further and further forwards, until at length the bony plate has the form of the ace of hearts. Its base borders the fontanelle in the base of the skull, which lies under the anterior half of the third cerebral vesicle, while its point is contiguous to the occipital foramen; for the most part it is very thin, and only its axis (and next to this its whole posterior margin) is distinguished by a greater thickness. The cephalic part of the notochord can be recognised in the axis of this bony plate up to the following period. It passes from the posterior to the anterior end of the bony plate, where it is lost, and is so invested by the osseous substance of the plate, that a smaller portion of the latter lies on the upper side of the notochord, a larger portion beneath it. On this account it forms, on the upper side of the plate, a longitudinal ridge, which subsequently becomes imperceptible by the aggregation of matter at the sides. On one occasion, however, I saw, in an embryo which had almost reached its full term, a similarly formed and sized bony cone, which, through almost its entire length, appeared merely to lie *on* the body of the basi-occipital, since it had only coalesced with it below.

The nucleus and sheath of the cephalic part of the notochord become gradually broken up and the last trace of them eradicated, as the ossification of the basi-occipital proceeds, like the nucleus and sheath of the rest of the notochord wherever a vertebral body is developed.*

The articular condyle is not yet formed. The ex-occipitals ossify through their whole length and breadth.

The body of the basi-sphenoid is formed between the above-mentioned posterior fontanelle of the *basis cranii* and the pituitary space, therefore far from the cephalic part of the notochord. It ossifies by two lateral centres, each of which forms

* In the Stickleback it has appeared to me that the wall of the anterior conical termination of the notochord in the *basis cranii* becomes ossified, or, at any rate, invested by an inseparable sheath of bony matter, just in the same way as the "urostyle" is developed in the tail.

a ring round the carotid canal.* The alisphenoids ossify in their whole length and breadth; the orbito-sphenoid only slightly, and the presphenoid not at all. The premaxillary bone arises as an azygos triangular cartilage between the cornua of the anterior ethmo-vomerine plate. It ossifies from a single centre.

The auditory capsule, or the future petrosal [= periotic] bone, may, even at the end of this period, be readily separated from the other part of the cranial wall, and still consists, for the most part, of cartilage. On the other hand, the triangular form, which it had before, is not inconsiderably altered, since it greatly elongates forwards, and thus, as it were, thrusts its anterior angle further and further forwards, and becomes more unequal-sided. At the lower edge, or the longer side of it, about opposite to the upper angle, at the beginning of this (third) period, or indeed somewhat earlier, a diverticulum of the auditory capsule begins to be formed (the rudimentary cochlea), and develops into a moderately long, blunt, and hollow appendage, the end of which is directed downwards, inwards and backwards, and also consists of cartilage. Close above, and somewhat behind this appendage, however, there appears, at about the same time, a small rounded depression, in which the upper end of the auditory ossicle eventually rests; and, somewhat later, an opening appears in this depression which corresponds with the fenestra rotunda of man. Very much later, namely, towards the end of this period, the auditory capsule begins to ossify. Ossification commences in a thin and moderately long, hook-like process, which is sent forwards and inwards from the lower hollow diverticulum of the cartilage, and unites with the basisphenoid. From this point it passes upwards and backwards, and, for the present, extends so far that, at the end of this period, besides that process, the diverticulum in question, and about the anterior third of the auditory capsule itself, are ossified.† Later than at the point indicated, an ossific centre appears at the posterior edge of the auditory capsule, where it abuts against the supra- and ex-occipitals, but extends from hence by no means so far forward as to meet that from the

* These are the "basi-temporals" of Mr. Parker.

† This is the pro-otic ossification.

other point.* The middle, larger part of the auditory capsule, therefore, for the present, remains cartilaginous.

In the beginning of the fourth period, a third ossific centre † arises in the upper angle of the capsule, whereupon all three grow towards one another. But the mode of enlargement and coalescence of these bony nuclei is very remarkable. They do not unite with one another in such a manner as to form a continuous bony capsule for the membranous part of the labyrinth, but are permanently separated by cartilagino-membranous and very narrow symphyses. On the other hand, one [the epiotic] coalesces, in the most intimate manner, with that edge of the supra-occipital which is nearest to it; so that, even in the more advanced embryos, this bone and it form a moderately long oblong plate, each end of which constitutes a small, tolerably deep, and irregularly-formed shell, containing a part of the anterior, or upper, semicircular canal. The second bony centre [the opisthotic] becomes anchylosed with the anterior edge of the lateral part of the occipital bone, and also forms a small, irregularly-shaped, but longish scale, which contains the deeper, or lower part, of the posterior crus of that semicircular canal, and besides this, the lower sac, or representative of the cochlea. The remaining bony mass developed in the auditory cartilage [the pro-otic], however, includes the greater part of the membranous portion of the labyrinth, and is the largest. The same phenomenon, viz. that the petrosal bone breaks up, as it were, into three pieces, of which two coalesce with the occipital bone, occurs also in *Lacerta agilis*, and probably takes place in like manner, if we may conclude from the later condition of the petrous bone to the earlier, in *Crocodilia* and *Chelonia*.

It has been seen that subsequent observers have fully justified the conviction here expressed by Rathke.

* The opisthotic ossification. † The epiotic ossification.

LECTURE XIII.

ON THE STRUCTURE OF THE SKULL.

THE SKULLS OF MAMMALIA.

We have met with no important difficulties in the way of identifying the bones of the Bird's skull with those found in the skulls of the *Reptilia* and still lower *Vertebrata*; and hence, if the cranium of a Mammal be compared with that of a Bird, the bones which correspond in the two will obviously be homologous throughout the series.

The accompanying figure represents a longitudinal and

Fig. 97.

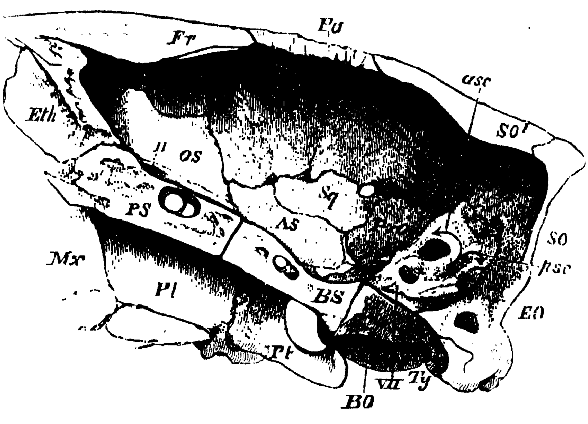


Fig. 97.—Longitudinal and vertical section of the cranial cavity of a Beaver.

vertical section of the skull of a Beaver (*Castor fiber*), drawn of the same absolute length as the section of the Ostrich's skull

(Fig. 88, A), and exhibiting a corresponding extent of the cranium. The three segments of the basi-cranial axis are at once recognisable and identifiable with the basi-occipital, basi-sphenoid, and presphenoid of the Bird; but the basi-sphenoid is truncated at its anterior end, as in the Crocodile, not produced into a long beak, as in Birds and many Lizards. The ex-occipital and supra-occipital bones, again, have all the relations of those of the Ostrich, and are universally admitted to be the homologues of the latter.

In the Ostrich, as we have seen (Fig. 88, A), there lies in front of the ex-occipitals a large bony mass, composed of the confluent opisthotic, epiotic, and pro-otic bones. The inner face of the single periotic bone thus formed is divided into two surfaces, one anterior and one posterior, by a ridge which runs somewhat obliquely from above downwards and forwards. The anterior surface is concave, looks somewhat forwards, articulates in front with the alisphenoid, and contains no part of the organ of hearing; the third division of the trigeminal nerve passes out in front of it. The posterior surface presents, inferiorly, the apertures for the *portio dura* and the *portio mollis*; superiorly and in front, a fossa arched over by the anterior vertical semicircular canal; while, superiorly and behind, it contains the posterior vertical semicircular canal. Between the posterior edge of this division of the bone and the ex-occipital the eighth pair of nerves leaves the skull.

In the Beaver (Fig. 97), there is a single mass of bone not dissimilar in form and proportional size, which has always been admitted to be the homologue of the *pars petrosa* and *pars mastoidea* of Man, and the general relations and characters of which may be described in exactly the same terms. The inner face is divided into two surfaces, one anterior and one posterior, by a ridge which runs, somewhat obliquely, from above downwards and forwards. The anterior surface is concave, and looks slightly forwards; it articulates in front with a bone which, as all agree, corresponds with the alisphenoid of Man, and lies behind the exit of the third division of the trigeminal. The posterior division presents, inferiorly, the apertures for the *portio dura* and *portio mollis*; superiorly and in front, a fossa arched over by the anterior vertical semicircular canal; while superiorly and behind it contains the posterior vertical semicircular canal. Between the hinder edge of this division and the ex-occipital, the eighth pair of nerves leaves the skull.

The inferior, or internal, edge of the periotic bone in the Bird, and that of the *pars petrosa* in the Beaver, comes into relation with the basi-occipital and basi-sphenoid; externally, each exhibits the *fenestra ovalis* and *rotunda*, and is related, above, to the squamosal.

In fact, the only noteworthy differences between the ornithic periotic, and the Mammalian *pars petrosa* and *mastoidea*, are that the former becomes anchylosed with the adjacent bones of the cranial wall, while the latter remain separate from them; and that, while the periotic articulates, above, with the parietal in the Bird, the corresponding ossification in the Mammal is separated from that bone by the squamosal.

On the former distinction it would of course be absurd to lay any weight; as regards the latter, it is deprived of all significance by the circumstances that in some Birds—as, *e.g.*, the common Fowl—the squamosal interposes between the periotic and the parietal in the wall of the skull; and that in some Mammals—as, *e.g.*, the Sheep—the squamosal is completely excluded from the skull, and the *pars petrosa* unites with the parietal.

The simple anatomical comparison of the parts appears, then, to be amply sufficient to demonstrate, that the *pars petrosa* and *mastoidea* of the Beaver correspond in every essential respect with the periotic mass of the Bird, and therefore with the pro-otic, opisthotic, and epiotic bones of Reptiles and Fishes. On the other hand, no one has ever doubted that the petrosal and mastoid of the Beaver answer to the petrosal and mastoid of Man; and therefore we are led by the comparison of adult structure, merely, to exactly the same conclusion as that at which we arrived by the study of development, to wit, that the *pars petrosa* and *pars mastoidea* of Man answer to the periotic bones of the lower Vertebrates.

In front of the periotic, the side wall of the cranium is formed by an alisphenoid, anchylosed below with the basi-sphenoid; and, still more anteriorly, by a large orbito-sphenoid, united inferiorly with the presphenoid, which is distinct from the basi-sphenoid behind, and from the ethmoid in front.

In the roof of the skull (Fig. 98) a large inter-parietal, SO^1, which corresponds with the upper part of the *squama occipitis* of Man, occupies an interval left, posteriorly, between the two

Fig. 98.

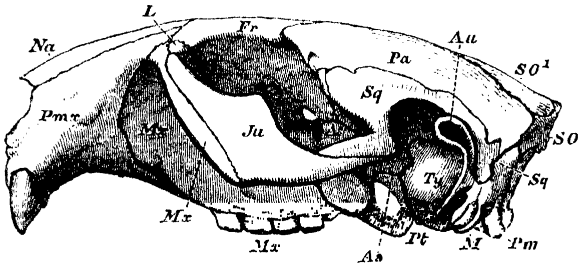


Fig. 98.—Side view of the skull of a Beaver. *Ty*, tympanic bone; *M*, *pars mastoidea*; *Pm*, the downward process of the ex-occipital, called "paramastoid."

parietals; otherwise, the bones correspond with those found in the roof of the skull of the Bird. The ethmoid, the vomer, the nasal bones, the premaxillæ, maxillæ, lachrymal, jugal, and squamosal bones, the palatines, and the pterygoids of the Rodent, present no difficulties to the student acquainted with the structure of the Bird's and Reptile's skull; but he will miss the pre-frontals, the post-frontals, the quadrato-jugal, the transverse, and the quadrate bones, together with all the pieces of the lower jaw, save the dentary.

The post-frontals, the quadrato-jugal, the transverse, and four out of the five missing pieces of each ramus of the lower jaw, appear to have no representatives in the Mammalian skull.

The pre-frontals, on the other hand, are represented by the so-called "lateral masses of the ethmoid," with their developments, the superior and middle ethmoidal turbinal bones, which answer precisely to those of Man. A third turbinal, developed from the primitive cartilaginous wall of the olfactory chamber, eventually becomes united with the maxilla, and answers to the inferior or maxillary turbinal of Man; while, in the Beaver, there is a fourth turbinal, connected with the superior turbinal and with the nasal bones, which may be termed the "nasal turbinal."

How far these well-defined turbinals of the Mammal answer to the cartilaginous and osseous turbinals of Birds and Reptiles, is a question which has yet to be elucidated.

I have already endeavoured to show that the quadrate and articular bones of the oviparous *Vertebrata* are represented by the *incus* and *malleus* of Man, and consequently by the corresponding bones in all *Mammalia*; and that, as a consequence of the appropriation of two bones of the mandibular series to the uses of the organ of hearing, the dentary bone develops its own condyle, and articulates with the squamosal.

Another bone which appears to have no distinct representative in most oviparous Vertebrates* is very conspicuous in most Mammals, and far more so in the Beaver than in Man. This is the tympanic element, and it will be useful to study with especial attention the characters of this bone, its relations to the periotic, and the manner in which both are connected with the other bones of the skull.

In a transverse section of the conjoined tympanic and periotic bones, taken through the canal which is common to the anterior and posterior vertical semicircular canals (Fig. 99), the periotic mass is seen to be prolonged, external to and below the horizontal semicircular canal and that for the passage of the *portio dura*, into a stout "mastoid process" (*M*), which appears upon the outer surface of the skull, between the ex-occipital, the squamosal, and the tympanic, as a production downwards and outwards of the "*pars mastoidea*," which is doubtless, as in Man, composed partly of the pro-otic and partly of the epiotic and opisthotic bones.

Fig. 99.

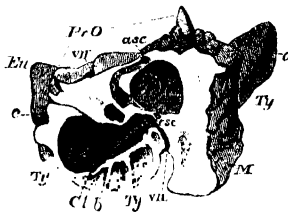


Fig. 99.—A vertical section of the conjoined tympanic and periotic bones of the Beaver (*Castor fiber*). *a*, external auditory meatus; *b*, groove for the tympanic membrane; *c*, the inner lip of the tympanic; *Eu*, Eustachian tube; *Cl*, cochlea; *M*, *pars mastoidea*.

The tympanic bone is produced, externally, into a spout-like tube, directed forwards and upwards, which is the external auditory meatus (*Au*, Fig. 98); below and internally the tube dilates into a thin walled hemispherical *bulla* (*b*, *c*, Fig. 99), open superiorly, and produced in front and anteriorly into a perforated process, which contains the osseous part of the Eustachian tube.

* I learn from Mr. Parker that all Birds above the *Struthionidæ* have a more or less perfect chain of tympanic bones, of which there are six in *Corvus corone*.

The outer lip of the *bulla* and the auditory meatus are anchylosed with that region of the pro-otic which corresponds with the *tegmen tympani* in Man. The inner lip of the tympanic *bulla* is, as is the case with the corresponding edge of the tympanic bone of Man, applied against the opisthotic, but it does not anchylose with this bone in the Beaver; at any rate, for the greater part of its extent. Consequently, a very narrow cleft or fissure, leading into the tympanum, is opened up, if the inner lip of the *bulla* is gently prized away from the periotic mass in this region. I shall term this the "*tympano-periotic fissure*." The great difference between the tympanic bone of Man and that of the Beaver arises from the circumstance, that, in Man, by far the greater part of the bone is occupied by the external auditory meatus; the interval between the groove for the attachment of the tympanic membrane and the inner edge of the tympanic bone—which forms the floor of the tympanum—being quite insignificant, except in the region of the Eustachian tube. In the Beaver, on the other hand, this part of the tympanic bone is greatly enlarged, and constitutes more than the inner half of the *bulla tympani.*

The tympanic bone and the periotic being thus anchylosed together externally (though only coadjusted internally), form one bone in the adult Beaver. But this "*tympano-periotic bone*" is not anchylosed with any of the adjacent bones, even the squamosal remaining perfectly distinct. Nor, indeed, is it fixed to them by very firmly interlocking sutures, so that in the dry skull it may be pushed out without difficulty. It is held in place, in fact, only by the descending post-auditory process of the squamosal (answering to the posterior part of the *margo tympanicus*), which curves behind the external auditory passage; and by the fitting in of the "*pars mastoidea*" between the ex-occipital and supra-occipital.

Of the vast multitude of modifications undergone by the Mammalian skull, I select for comment, in this place, only a few of the most important, such as, 1stly, those which are the result of unusual forms or combinations of bones in skulls not otherwise abnormal. 2ndly. Those which are exhibited by the skulls of the higher Mammals as compared with the lower. 3rdly.

Those which are presented by what may be termed aberrant Mammalian skulls, *e.g.*, the crania of the *Monotremata* and *Proboscidia*, and of the aquatic *Mammalia*—the *Sirenia*, *Phocidæ*, and *Cetacea*.

I am not aware that there is any example among the *Mammalia* of the bones of the roof, or lateral walls, of the two posterior segments of the skull taking a share in the formation of the floor of the cranial cavity. On the other hand, a careful study of development will probably show that it is no uncommon circumstance for the orbito-sphenoids to unite together in the middle line, so as to exclude the presphenoid from the cranial floor, or even to supply its place entirely.

A still more remarkable deviation from the typical arrangement than this occurs in certain Mammals, and has been thus noted by Cuvier (Leçons ii., p. 319):—"La lame cribleuse de l'ethmoide dans tous les *Makis*, dans les *Loris*, et les *Galagos*, vient toucher comme dans l'homme, au sphénoide antérieur; tandisque, dans les Singes, elle en reste éloignée en arrière par le rapprochement des deux côtés du frontal."

I find the union of the frontals to which Cuvier refers in this passage to take place in *Cynocephalus*, *Macacus*, *Cercopithecus*, and *Semnopithecus*. The frontals, however, do not really separate the presphenoid and ethmoid, but only form, above the junction of these two bones, the front part of a thick osseous bridge, the hinder part of which is contributed by the orbito-sphenoids.

The Gorilla agrees with the Monkeys and Baboons in these respects. Thus, in the adult male Gorilla in the Museum of the Royal College of Surgeons, the distance from the anterior boundary of the *sella turcica* to the anterior end of the cribriform plate of the ethmoid is 1·4 in. Of this extent of the base of the skull, 0·35 in. is occupied by the conjoined orbito-sphenoids, 0·42 in. by the coalesced frontals, and 0·6 in. by the *lamina perpendicularis* of the ethmoid. But, in a vertical section, the ethmoid is seen to extend back under the basi-cranial processes of the frontals (which are not more than one-fifth of an inch thick) as far as the suture between the orbito-sphenoids and these processes, which end anteriorly in a free rounded, transversely concave ridge, constituting the posterior boundary of the olfactory fossa. Laterally, the basi-cranial processes of the frontals arch downwards for a short distance and unite with the lateral masses of the ethmoid.

In the Gorilla, the frontal bridge is much smaller than in the lower Catarhines. The Chimpanzee approaches Man still more nearly; a triangular process of the presphenoid interposing itself between the frontals and joining the ethmoid. Sometimes, however, very small processes of the frontals just unite over this junction. In the Orang, the frontals are widely separated, as in Man.

The epiotic, pro-otic, and opisthotic bones are always anchylosed into a single periotic bone in the *Mammalia;* but they unite with the other elements of the temporal bone, and with the adjacent cranial bones, in very various modes, and the tympanic cavity presents very different boundary walls in different Mammals.

In the Beaver, as we have seen, the tympanic and periotic bones are anchylosed into a single "*tympano-periotic*," which remains unanchylosed with the squamosal, and is easily detached. In the *Sirenia* and in *Cetacea* (sooner or later) the same anchylosis takes place, but the tympano-periotic is still less firmly fixed in its place, and, in some *Cetacea*, does not appear at all in the interior of the skull, in consequence of the growth of the adjacent bones towards one another over it.

The tympano-periotic of the Rhinoceros, Horse, and Sheep, long remains unanchylosed to the surrounding bones, but is so wedged in between them as to be practically fixed within the walls of the skull.

In *Echidna* and in *Orycteropus* the periotic, the squamosal, and the tympanic remain perfectly distinct for a long time, if not throughout life.

The squamosal and tympanic of the Pig anchylose into a single "*squamoso-tympanic*," which is firmly fixed to the adjacent bones; but the periotic remains free, and consequently readily falls not *out of*, but *into* the skull.

In the nine-banded Armadillo (*Praopus*) it is the periotic and squamosal which are anchylosed, the tympanic remaining rudimentary and free; and the Opossums and the Tapir exhibit a similar arrangement.

Other *Mammalia*, such as the *Carnivora* and *Primates*, have the squamosal, tympanic, and periotic all anchylosed together into one "*temporal bone.*"

Even in one and the same order the constitution of the tympanic cavity exhibits the most remarkable differences. To take the *Edentata* as an example:—

In the *Orycteropus* the walls of the tympanic cavity have a wonderfully reptilian arrangement; the periotic is very large in proportion to the other bones of the skull, and its plane presents comparatively little inclination, so that its exterior face looks more outwards than downwards. A large part of its posterior and outer face is seen, as a *pars mastoidea*, upon the exterior of the skull, between the supra-occipital, the ex-occipital, and the squamosal, but there is no distinct "mastoid process;" below, the periotic comes into contact with the basi-occipital and basi-sphenoid; in front, with the alisphenoid. The latter bone is strongly convex outwards, so as to present a posterior, as well as an external, face; the posterior face forms the front wall of the tympanum, and exhibits a somewhat deep excavation, or alisphenoidal air-cell.

The squamosal, a very large bone, is divided by a well-marked ridge into an upper face, which constitutes part of the roof, and an outer face, which forms a portion of the lateral wall, of the skull. The latter enters into the outer and upper wall of the tympanum; the former, very thin, constitutes the roof of that cavity, abutting internally upon the supra-occipital and parietal. The Fallopian canal is open for the greater part of its extent, and a hook-like osseous process, which overhangs its outer and posterior part, gives attachment to the hyoid.

The tympanic is a strong hoop of bone, incomplete above, and much shorter anteriorly than posteriorly. By its expanded anterior end it articulates by an interlocking suture with the squamosal. The thin posterior end is free.

In *Myrmecophaga tetradactyla* (and essentially the same arrangement obtains in the great Ant-eater), the squamosal, as in *Orycteropus*, enters largely into the wall of the cranial cavity; but the tympanic, which is large and bullate, is anchylosed with *it.* The tympanic, however, forms only the outer part of the posterior wall of the tympanum, the inner and posterior walls of that cavity being furnished by a downward process of the basi-occipital, while its inner and anterior wall is formed partly by the pterygoid and partly by the alisphenoid. These two bones enclose a great air-cell, which communicates freely with the tympanic cavity behind. In front, it is closed by a thin bony partition, which separates it from a second large air-chamber, enclosed, partly by the alisphenoid and pterygoid, and partly by the palatine.

In the genus *Manis* there is a large *bulla*, formed altogether by the tympanic, which, in moderately young skulls, at any rate, is not anchylosed with the adjacent bones.

The squamosal is an immense bone, extending from the ex-occipital to the orbito-sphenoid, and entering into the lateral walls of the skull for that extent. Its posterior part, dilated and convex outwards, contains a large air-cell, which opens into the roof of the tympanum by a wide aperture. The plane of the periotic is nearly horizontal. It is a relatively small bone, and only a small part of it appears on the base of the skull, behind the tympanic *bulla*, the squamosal completely hiding it externally.

Of the Armadillos, some, like *Euphractus*, have a tympanic *bulla* of the ordinary construction, with, occasionally, a very long external auditory meatus; while others, such as the nine-banded Armadillos (*Praopus* of Burmeister), have a mere hoop of bone open above, almost as rudimentary as that of *Echidna*.

Or, if we turn to the perissodactyle *Ungulata* :—

In the *Rhinoceros*, the periotic and tympanic early anchylose together, but remain distinct from the surrounding bones, the compound tympano-periotic being only wedged in between the squamosal, ex-occipital, and other adjacent cranial bones, in such a manner that it cannot fall out. The "*pars mastoidea*" is completely hidden, externally, by the union of the squamosal and the paramastoid process of the ex-occipital over it. The region itself, however, is very well developed, and is continuous, internally and below, with a very strong, conical, somewhat curved, styloid process, to the flattened, free base of which the hyoidean apparatus is attached.

The tympanic element is very singularly formed. It has the shape of a very irregular hoop, open above and behind, and much thicker at its anterior superior than at its posterior superior end. The former, irregular and prismatic, is anchylosed with the periotic, just behind and above the auditory labyrinth; it then splits into two divisions, an anterior and inner and a posterior and outer. The anterior, acquiring a thick and spongy texture, curves round to form the front part of the wall of the tympanum, and then ends in a free, backwardly-directed apex, without becoming in any way connected with the periotic, or with the posterior division. The latter, much thinner and denser, curves downwards and backwards in the same way, and also remains perfectly free, but its hinder end is prolonged into a flat process, which bends for a short way round the base of the styloid process. The outer wall of the tympanum is therefore very incomplete in the dry skull, opening forwards and downwards, first, by the fissure between the anterior branch of the tympanic and the periotic; and, secondly, by the cleft between the two divisions of the tympanic.

Posteriorly, there is a large irregular aperture between the hinder end of the anterior branch of the tympanic and the periotic. Externally, there is no bony auditory meatus—or rather the merest rudiment of one.

The Horse presents a very different structure. There is a tympano-periotic bone which is wedged in between the squamosal and adjacent bones, and not anchylosed therewith; but the *pars mastoidea* appears largely on the outside of the skull between the post-auditory process of the squamosal and the paramastoid, and the tympanic element consists of a complete *bulla*, with a long external auditory meatus. The styloid process is almost completely infolded by a vaginal process furnished by the auditory meatus, and the tympanic is altogether anchylosed to the periotic, posteriorly.

No Tapir's skull which I have examined has presented any trace of an ossified tympanic bone.*

In the Horse, most *Primates*, Carnivores and Rodents, the

* According to Cuvier, "L'os de la caisse ne paroit jamais bien se souder avec les os voisins et tombe aisément, comme dans l'hérisson, le sarigue," &c.

tympano-periotic fissure is closed, either by the close apposition, or by the actual anchylosis, of the inner lip of the tympanic to the periotic.

But, in the Sheep and Pig, this fissure is replaced by a wide elongated aperture, the inner edge of the tympanic *bulla* being rolled in like a scroll. In the Seals and *Cetacea* the scroll-like form of the immensely thick tympanic *bulla* becomes still more marked, and the tympano-periotic fissure wider; while the latter is converted into a great gap in the floor of the tympanum in *Orycteropus* and in the *Sirenia*, the tympanic being reduced to a mere thick hoop.

In many *Marsupialia* the alisphenoid dilates posteriorly and inferiorly into a funnel-shaped, thin-walled, bony chamber, which closes the tympanic cavity anteriorly, uniting by its edges with the tympanic bone. In certain *Insectivora*, such as the Hedgehog and Tenrec, the tympanic cavity is partly walled in by a process of the basi-sphenoid.

In *Hyrax*, and in many *Marsupialia* and Rodents, the jugal enters into the composition of the glenoid facet for the lower jaw. In the Marsupials the alisphenoid may also contribute towards the formation of this articular surface. In almost all Marsupials the angle of the mandible is continued inwards into a horizontal plate of bone. This "inflexion of the angle of the jaw" is peculiar to these Mammals.

The palatine and pterygoid bones present very considerable differences in their connections among *Mammalia*.

Thus, in the *Ornithorhynchus*, in the larger *Myrmecophagæ*, and in some *Cetacea*, the pterygoids unite in the middle line below, so as to prolong the bony palate beyond the palatines, as in the Crocodiles. In the Marsupials, on the other hand, the bony palate, formed only by the maxillæ and palatines, is often defectively ossified, so that large open spaces are left therein on the dry skull.

In order to understand the changes which the normal type of skull undergoes in the Mammalian series, it is necessary to define a few lines and planes by the help of certain well-marked organic fixed points.

A line drawn from the hinder extremity of the basi-occipital to the uppermost part of the junction between the presphenoid and the ethmoid, may be called the line of the axis of the *basis cranii*, or the "*basi-cranial line.*"

A second line, drawn from the premaxilla to the *basis cranii* through the junction of the vomer with the ethmoid, traverses the axis of the facial part of the skull, and may be termed the line of the axis of the *basis faciei*, or "*basi-facial line.*" This line, if produced upwards and backwards, will cut the foregoing so as to form an angle open downwards, which I shall term the "*cranio-facial angle.*"

A third line, drawn from the end of the basi-occipital bone to the posterior edge of the supra-occipital in the median line, will give the general direction of the plane of the occipital foramen, or the *occipital plane.* The angle it forms with the basi-cranial line is the "*occipital angle.*"

A fourth line, drawn from the *torcular Herophili*, or junction of the lateral and longitudinal sinuses, through the middle of a plane joining the tentorial edges of the pro-otic bones, will give the general direction of the tentorium, or, in other words, of the demarcation between cerebrum and cerebellum.* This line, therefore, may be taken to indicate the "*tentorial plane.*" The angle it forms with the basi-cranial line is the "*tentorial angle.*"

A fifth line, drawn through the median junctions of the cribriform plate of the ethmoid, with the frontal above and anteriorly, and with the presphenoid below and posteriorly, will give, in the same general way, the "*olfactory plane.*" The angle it forms with the basi-cranial line is the "*olfactory angle.*"

Lastly, the longest antero-posterior measurement of the cavity which lodges the cerebrum will give the "*cerebral length.*"

Having defined these lines and planes, the following general rules may be laid down :—

1. The lower *Mammalia* have the *basi-cranial line* longer in proportion to the *cerebral length* than the higher. Taking the length of the *basi-cranial line* as 100, I have observed the *cerebral*

* Of course no straight line can give this boundary with exactness, as the co-adapted surfaces of the cerebrum and cerebellum, and consequently of the interposed tentorium, are curved in all directions.

length to be, in a well-developed European skull, 266; in a Negro, 236; in an adult female Chimpanzee, 180; in an adult male Gorilla, 170; in a Baboon, 144; in a Lemur, 119; in a Dog, 87; in a Beaver, 70; in a *Thylacinus*, 60; in an Opossum, 93; in *Echidna*, 100.

2. In the lower *Mammalia* the olfactory, tentorial, and occipital angles nearly approach right angles; or, in other words, the corresponding planes are nearly vertical, while they become more and more obtuse in the higher Mammals, until, in Man, these planes are nearly horizontal, in the ordinary position of the skull.

3. In the lower *Mammalia* (Fig. 100) the cranio-facial angle is so open as to reach 150° or more, but, in the higher *Mammalia*, it becomes smaller and smaller, until, in Man, it may be as little as 90°.

4. In many of the lower *Mammalia*, a sudden narrowing of the front part of the cranial cavity indicates the boundary between the chamber which lodges the cerebral hemispheres and that which contains the olfactory lobes of the brain (Fig. 100), and the latter cavity forms a large and distinct *olfactory fossa*. In the higher Mammals this cavity becomes absolutely and relatively smaller, until in Man it is so shallow and insignificant as to be hardly noticeable.

5. In many lower *Mammalia* the olfactory fossa is altogether in front of the cerebral cavity, and the cerebellar fossa is altogether behind it, the three being separated by marked constrictions (Fig. 100).

Fig. 100.

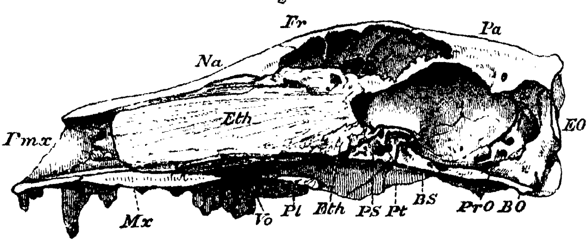


Fig. 100.—Longitudinal and vertical section of the skull of *Thylacinus cynocephalus*.

In the higher Mammals, on the other hand, the excessive development of the cerebral hemispheres causes the cerebral chamber to overlap the olfactory fossa in front and the cerebellar fossa behind; so that these come to be placed respectively under, instead of in front of and behind, the cerebral chamber.

Thus it may be said, that in passing from the lower to the higher forms of Mammalian skull, we find the cavity for the cerebrum enlarging in proportion to the basi-cranial axis, and thrusting the olfactory plane downwards and forwards, the tentorial and occipital planes downwards and backwards, in such a manner that these may be said to rotate on the ends of the basi-cranial axis; at the same time, the basi-facial line rotates on the basi-cranial line, being more and more bent downwards and backwards.

It must be clearly understood that I by no means intend to suggest that all Mammalian skulls can be arranged in a series, the lower members of which shall be distinguished from the higher by always exhibiting smaller olfactory and occipital angles, larger cranio-facial angles, less proportional cerebral lengths, &c. On the contrary, the various angles and measurements show a considerable range of irrelative variation; as, for example, in the *Cetacea*, a relatively large cerebral length is associated with small occipital and olfactory angles, and a very large cranio-facial angle; in the *Edentata* and *Monotremata* a somewhat large olfactory angle is associated with a small tentorial and occipital angle; and in the Opossum and *Echidna* the cerebral length is anomalously great. All that can be said is, that the crania of the higher orders of Mammals, as a whole, are distinguished from those of the lower orders by the characters I have mentioned.

The skull of *Echidna* (Figs. 101 and 102) may be taken as an example of the "aberrant" monotreme type of skull. It is composed of a pyriform cranium proper, and a produced, beak-like maxillary portion. The lower jaw is remarkable for its length and slenderness, and the very small vertical height of its rami (Fig. 101).

The basi-occipital (*B.O.*) is very wide, and so much depressed as to be quite a thin lamella of bone; it contributes, to a small extent, to each occipital condyle, which, like the ex-occipital bone itself, is very large. The ex-occipitals are connected above by a wide supra-occipital, which extends so far upon the roof of the skull that the lambdoidal suture is not very distant from its summit. The plane of the roof of the skull slopes upwards and forwards, from the occipital foramen to this point.

Fig. 101.

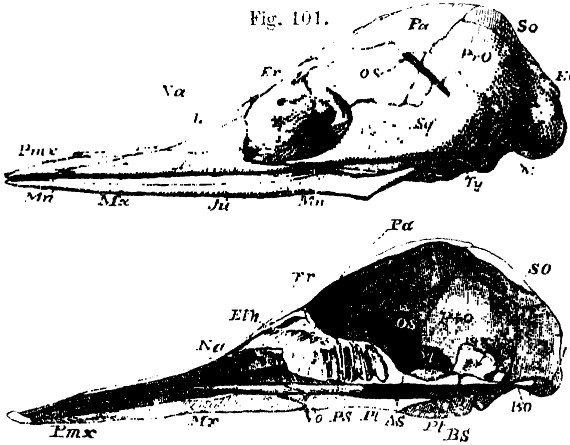


Fig. 101.—The skull of a young *Echidna* viewed from without, and in longitudinal and vertical section.

The large parietals, anchylosed together in the middle line, form all but a very small portion of the rest of the roof of the skull, and are succeeded by the small frontals. These are met in the middle line, inferiorly, by the *lamina perpendicularis* of the ethmoid, which separates one olfactory chamber from the other, and are united by sutures, anteriorly, with the long nasals. These stop short of the anterior nasal aperture, being excluded therefrom by the premaxillaries.

In the base of the skull the basi-sphenoid, presphenoid, and ethmoid are anchylosed together. The basi-sphenoid is a wide, flattened bone, somewhat deflexed at the sides. Its long, thin, postero-lateral margins articulate externally with the broad, flat bones (*Pt*) which contribute above to form the floor of the cranial cavity by filling up a vacuity which would otherwise exist between the basi-sphenoid, periotic, and alisphenoid. The thick posterior and external edges of these bones are excavated by a deep groove, which forms the front wall of the tympanum and of the Eustachian tubes. The palatine bones are completely anchylosed with the sphenoid, and pass abruptly inwards from the outer edges of that bone (Fig. 102). The anterior and internal edges of the bones (*Pt*), which obviously represent the pterygoids, articulate with them as well as with the basi-sphenoid. The anterior and external edges of the pterygoids are united with an antero-lateral prolongation of the pro-otic part of the periotic; and, rather above the cleft between the latter and the pterygoid, is fixed the large process of the malleus (*m*, Fig. 102), to which the tympanic ring closely adheres.

The periotic bone is remarkable for the lamellar prolongations which it sends forwards from its pro-otic, epiotic, and opisthotic regions, beyond the space required for the auditory organ, and which enter more largely into the side walls of the skull than any of its ordinary constituents. The periotic contributes towards the floor of the skull by a triangular process, which it sends in between the basi-occipital and the basi-sphenoid. Posteriorly, it articulates largely with the ex-occipital, the foramen for the eighth pair being situated between it and the latter. By its wide superior prolongation it unites behind with the ex-occipital, posteriorly and superiorly with the supra-occipital; anteriorly and superiorly, first with the parietal, and then with a large bone (*OS*, Fig. 101) which stretches outwards, upwards, and backwards from the presphenoid and ethmoid, articulating partly with the frontal, and more extensively with the parietal. Except in its unusual articulation with the periotic, this bone corresponds with the orbito-sphenoid. Between the superior prolongation of the periotic, and its thin and imperfectly-ossified anterior and inferior prolongation, there is an interspace filled up by the squamosal. The lower edge of this prolongation articulates with the pterygoid, and, in front of this, forms the upper boundary of the foramen for the third division of the fifth nerve. Between its front edge and a small process, sent up by the palatine towards the orbito-sphenoid, is a small plate of bone, which alone seems to represent the alisphenoid.

Fig. 102.

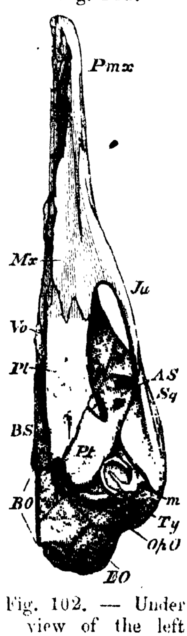


Fig. 102. — Under view of the left half of the skull of *Echidna*.

The premaxillæ enter largely into the composition of both the upper and under regions of the snout. As has been already stated, they unite in front of the nasal bones, so as to exclude the latter from the anterior nares, as is the case in some *Crocodilia.* The maxillary bones send horizontally inwards a broad and long palatine process. This, like the corresponding process of the palatine bone, is separated from its fellow in the middle line, for some distance, by the vomer. On the left side of the specimen from which this description is taken there is a distinct large triangular lachrymal (Fig. 101); it is imperforate, and situated altogether upon the side of the face. An oblique suture extends downwards and forwards from that which separates this lachrymal, inferiorly, from the adjacent bones, and seems to mark off the jugal from the maxillary bone. On the right side neither this suture exists, nor any indication of a distinct lachrymal.

The essential characters of the Proboscidean cranium are best displayed in the fœtal Elephant, as the sutures become obliterated, and the true form of the skull is disguised by the enormous development of the air-chambers between the tables of the skull, in the adult.

Fig. 103 represents the longitudinally and vertically bisected skull of such an Elephant. The whole basi-cranial axis is slightly concave upwards. The basi-occipital and the basi-sphenoid, the presphenoid, and the ethmoid are already so completely anchylosed that the traces of their primitive distinctness have almost disappeared. On the other hand, the presphenoid and the basi-sphenoid are widely separated by the remains of a synchondrosis. The occipital angle is about 90°, the olfactory angle 160° to 170°.

The frontals enter as much into the front wall as into the roof of the skull, and extend largely down upon its sides. Anteriorly and externally they are prolonged into great arched supra-orbital processes, which form the roofs of the orbits.

The parietals are narrower in the middle line of the vertex than anywhere else, being encroached upon by the frontals, anteriorly, and by the supra-occipital behind. Infero-laterally, the parietals widen out very much and extend far down into the temporal fossæ, where they unite, in front, with the apices of the tolerably large orbito-sphenoids, and behind, with the periotic and supra-occipital. Below the inferior margin of the parietals the squamosals appear largely in the lateral wall of the skull.

The alisphenoids are very small, and are directed horizontally outwards. The foramen for the exit of the third division of the trigeminal is between the hinder margin of the bone and the periotic.

The latter bone has a considerable proportional size, and is devoid of any cerebellar fossa.

Fig. 103.

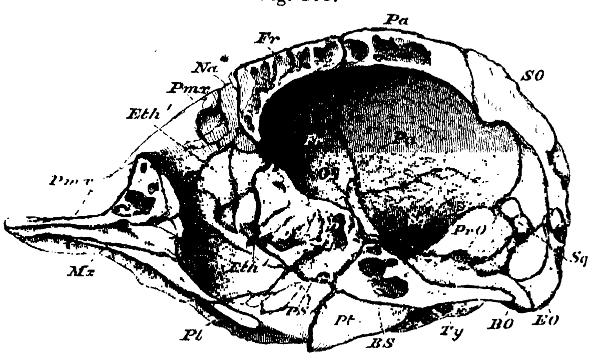


Fig. 103.—Longitudinally and vertically bisected cranium of a fœtal Elephant (*Elephas Indicus*).

On the exterior of the skull the squamosal joins the ex-occipital, so that no "*pars mastoidea*" appears upon the surface. The post-glenoidal and post-auditory processes of the squamosal are very large, and bend towards one another inferiorly, so as to meet (in the adult skull) and form a spurious external auditory meatus.

But besides this, there is a true external auditory meatus which is, as usual, an outgrowth from the tympanic. The latter bone is very large and bullate. It is grooved anteriorly by the carotid, and the short styloid process appears between it, the squamosal, and the ex-occipital.

The tympanic and the periotic are anchylosed together and wedged into the space left between the ex-occipital, squamosal, parietal, alisphenoid, and the basi-cranial axis.

The very short nasal bones (absent in the specimen figured) are adjusted by a broad posterior face to the frontals at *Na**. The large premaxillaries ascend along the sides of the anterior nasal aperture to the nasal bones, but are almost excluded from the palate, inferiorly, by the maxillaries; their alveolar portion, however, is very large and long, and this circumstance, together with the shortness of the nasal bones, throws the anterior nares, in the dry skull, almost to the top of the head. As the palatine processes of the maxillaries and palatines are, at the same time, relatively short, the posterior nares are situated but little behind the anterior nares, and thus the axis of the nasal passage forms a large angle with the basi-cranial axis. The lachrymal is a very small, though distinct, bone.

In the fœtal Elephant here described the space between the two tables of the skull is moderate, and is filled with a spongy diplöe; but, with advancing age, the interspace between the tables in the frontal, parietal, and supra-occipital increases until it equals or exceeds the depth of the cranial cavity, and the diplöe is replaced by vertical plates and pillars of bone, between which air-cavities extend back from the frontal sinuses and nasal passages. The skull of the Elephant resembles that of the Pig in many of its most important and characteristic features, and, through the Pig, its affinities are traceable to the other *Ungulata*. Of these, the skull of the Tapir resembles it most in some respects, such as the shortness of the nasal bones and of the palate; the consequent large angle which the axis of the nasal passages makes with the basi-cranial axis; and the prolongation downwards and forwards of the frontal bones.

Fig. 104.

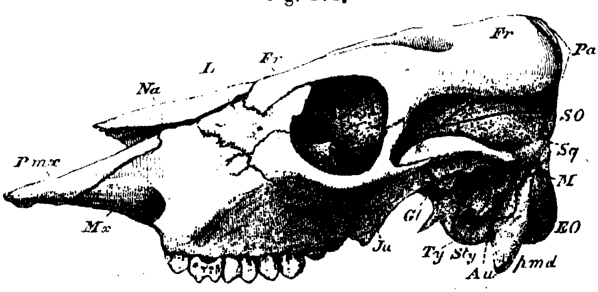


Fig. 104.—Side view of the skull of a Calf.—*pmd*, the paramastoid process of the ex-occipital.

On the other hand, some Ruminants carry to an extreme the development of the frontal into a great supra-orbital arch, its extension backwards in the middle line, and the concomitant expansion of the supra-occipital forwards; so that the parietals of the Ox, for example, are reduced to a comparatively narrow band in the middle line, while they expand widely in the temporal fossæ (Fig. 104).

The crania of the purely aquatic Mammals, such as the typical Seals, the *Sirenia* and the *Cetacea*, exhibit a certain similarity of character in the midst of very wide and important differences.

The basi-cranial axis is either flat or slightly curved upwards at its anterior and posterior extremities. The olfactory and occipital planes are vertical, or nearly so. The *squama occipitis*, alone, or united with large inter-parietal elements, extends upon the vertex of the skull between the parietals, and approaches, or even reaches, the frontals, so that the parietals are very much shorter antero-posteriorly than at the sides and below.

The frontals take but a small share in the formation of the roof of the cranial cavity; the nasals are relatively short, the anterior nasal aperture relatively large, and the posterior often situated far forwards. The prefontals, or lateral masses of the ethmoid, are small or rudimentary. The tympanic and periotic are always anchylosed together, and, whether connected or not with the squamosal, are more easily detachable from the skull than usual.

The Seals are extreme aquatic modifications of the carnivorous type of cranial structure; the *Sirenia*, of the ungulate type. The *Cetacea* present resemblances to both.

In the common Seal (*Phoca vitulina*) (Fig. 105) the cranial cavity is exceedingly broad and spacious, and the cerebral extends far further back over the cerebellar chamber, and is much larger in proportion to it, than is usual in *Carnivora*. There is a strong bony tentorium, and an osseous falx is more or less developed. The basi-cranial axis, very thin and broad, is curved, so as to be concave from before backwards. The synchondrosis between the presphenoid and basi-sphenoid persists.

The superior and middle turbinal bones are greatly flattened from side to side, and unite below and internally with the *lamina*

Fig. 105.

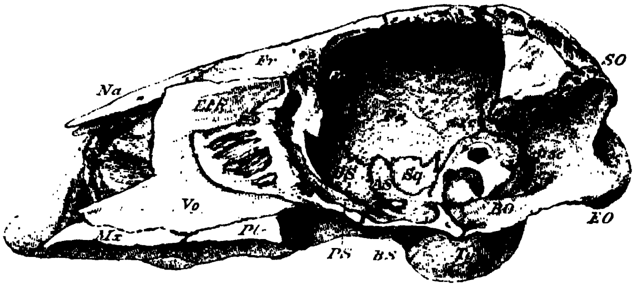


Fig. 105.—Longitudinal and vertical section of the skull of a Seal (*Phoca vitulina*). The premaxilla is absent.

perpendicularis, or proper ethmoid, so that all direct communication with the superior and middle meatuses of the nose is shut off below. The inferior turbinal, on the other hand, is exceedingly large and complex in its structure. The orbito-sphenoids are large and, ascending upon the front wall of the skull, unite anteriorly behind and below the cribriform plate, so as to hide nearly the half of the ethmoid when the base of the skull is regarded from above. The presphenoid is relatively small.

Less than half the length of the frontal bones enters into the upper wall of the cranial cavity, the rest being devoted to the roof of the nasal chambers. This part of the frontals is very much narrower than the other, and is bent down at the sides, so as to form two broad thin plates, which wall in the superior and middle spongy bones, articulate below with the vomer and with the palatine, and take the place of the *os planum*.

The lower edge of the parietal unites with the front part of the alisphenoid and with the ex-occipital, leaving a great infero-lateral space, which is filled up in front and above by the squamosal, and behind and below by the periotic. The squamosal is relatively a small bone, but the periotic and the tympanic, which are anchylosed with it, are very large. A swollen *pars mastoidea* appears on the exterior of the skull, and is hollowed internally by a cavity which opens into the cranium, and extends under the anterior and posterior vertical semi-circular canals.

The tympanic forms a very thick *bulla*, prolonged externally into an auditory meatus. It is firmly anchylosed with the pro-otic regions of the periotic and with the squamosal, but for the rest of its extent it is only applied to, and not anchylosed with, the periotic. It is pierced by the carotid canal.

The anchylosed squamosal, periotic, and tympanic are very easily detached from the walls of the skull, as is the premaxilla from the upper jaw.

The skull of the Dugong (*Halicore*, Fig. 106) presents the peculiarities of the cranial conformation of Mammals of the order *Sirenia* in a very marked form. The basi-cranial axis is almost flat above, but very thick. The suture between the basi-occipital and the basi-sphenoid persists, but that between the basi-sphenoid and the presphenoid is completely obliterated, as is that between the presphenoid and the ethmoid, which last

Fig. 106.

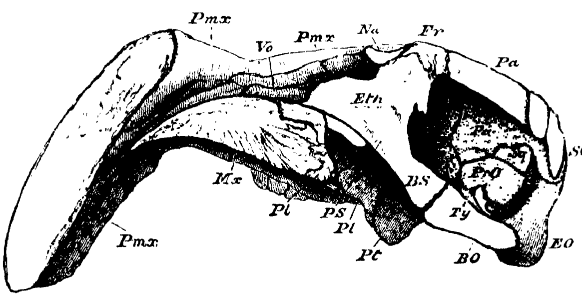


Fig. 106.—Longitudinal and vertical section of the skull of a Dugong (*Halicore Indicus*).

has the form of a stout bony plate, with an almost vertical posterior edge, or *crista galli*. The upper median part of the frontals is very narrow from before backwards, so that they cover not more than the posterior half of the upper edge of the ethmoid, and appear but very little on the roof of the cranial cavity; laterally and below, they are much expanded, and produced forwards and outwards. The greater part of the roof of the skull is furnished by the parietals, the longest antero-posterior diameter of which bones is in the middle line, as they are not separated, posteriorly, by the supra-occipital, or, anteriorly, by the frontals.

The orbito-sphenoids are large, and enter into the composition of the front wall of the skull. The alisphenoids are also large, and contribute to the formation of the side walls, as well as of the base, of the skull.

The squamosal appears in the interior of the cranium between the parietal, supra-occipital, and periotic, with which last it is not anchylosed.

The periotic, a large and dense ossification, has a very peculiar form, being divided into an inner portion, corresponding with the *pars petrosa*, and an outer thick mass which answers to the *tegmen tympani* and *pars mastoidea*.

The tympanic is a mere ring of bone, open above, and having a thicker anterior than posterior crus. It is by the former that it is more especially attached to the periotic, though the hinder thinner crus also becomes anchylosed with that bone.

The squamosal unites behind and below with the ex-occipital, but leaves a space, superiorly, in which the *pars mastoidea* appears on the exterior of the skull. The malar process of the squamosal is exceedingly thick, and extends far forwards as well as transversely outwards. The frontals send very large processes downwards and forwards, as in the Elephant and Tapir, which are not only met by the maxillæ, as in the latter animal, but also meet, and indeed are covered by, the nasal processes of the premaxillæ. The lachrymals are large, but imperforate. The jugals, thick and curved, are connected with them.

The very small nasal bones are fixed by the greater part of their under surfaces to the anterior half of the ethmoid, beyond which they project but little, so that almost the whole of the vast anterior nasal aperture is, in the skeleton, uncovered. The premaxillæ are enormous, and constitute a large proportion of the lateral margins of the upper jaw as well as the whole of its anterior region. Their ascending, or nasal, processes are produced forwards instead of downwards, so that the point which corresponds with the *spina nasalis anterior* in Man is nearly on a level with the top of the head. The alveolar process is even more largely developed, to contain the incisor tusks of the animal.

The maxillæ, also large and prolonged forwards, have very thick and long palatine processes, separated by a wide incisive foramen from the premaxilla. The palatine process of the palatine is also very thick, but it is shorter than deep, so that the posterior nares, which open behind it, are placed vertically under the hinder part of the anterior nares, in the dry skull. The vomer, thick and stout behind, thin and ridge-like in front and above, embraces the lower edge of the ethmoid, and is suturally united to both the palatines and the maxillaries.

The skulls of the *Sirenia* have resemblances on the one side with those of the ungulate Mammals and *Proboscidea;* on the other, with those of the *Cetacea,* but yet differ in many and most important respects from all.

The skulls of the *Cetacea* present more singular modifications than those of any other *Mammalia.* In all these animals, the basi-cranial axis is concave superiorly, and the primitive separation between the basi-sphenoid and presphenoid persists for a long time.

The vomer is very long, and extends backwards on the base of the skull at least as far as the basi-sphenoid, and sometimes covers the whole length of that bone.

The ethmoid has its posterior edge perpendicular, or nearly so, to the basi-cranial axis, and the foramina for the exit of the olfactory nerve are small or obliterated.

The frontals enter but very little into the roof of the skull, largely into its anterior and lateral walls. They are prolonged outwards and forwards into the long and broad supra-orbital processes, which are concave inferiorly, where they form the roof of the orbital cavity.

The parietals hardly appear at all, externally, upon the top of the skull, their median parts being obscured or interrupted by the inter-parietal and supra-occipital. They occupy a large space, however, in the temporal fossæ.

The ex-occipitals and supra-occipitals are enormous. The latter, usually increased by coalescence with the large inter-parietal, extend up to, or beyond, the vertex to meet the frontals. The orbito-sphenoid and alisphenoid vary in size. The squamosal is large, and is firmly fixed to the side of the skull, forming part of the wall of the cranial cavity. The periotic, usually anchylosed into one bone with the bullate tympanic, sometimes enters largely into the wall of the cranium, sometimes is almost altogether excluded therefrom by the parietal, alisphenoid, and other adjacent bones, which send prolongations over it.

The maxillary apparatus is greatly elongated, so as to form

Fig. 107.

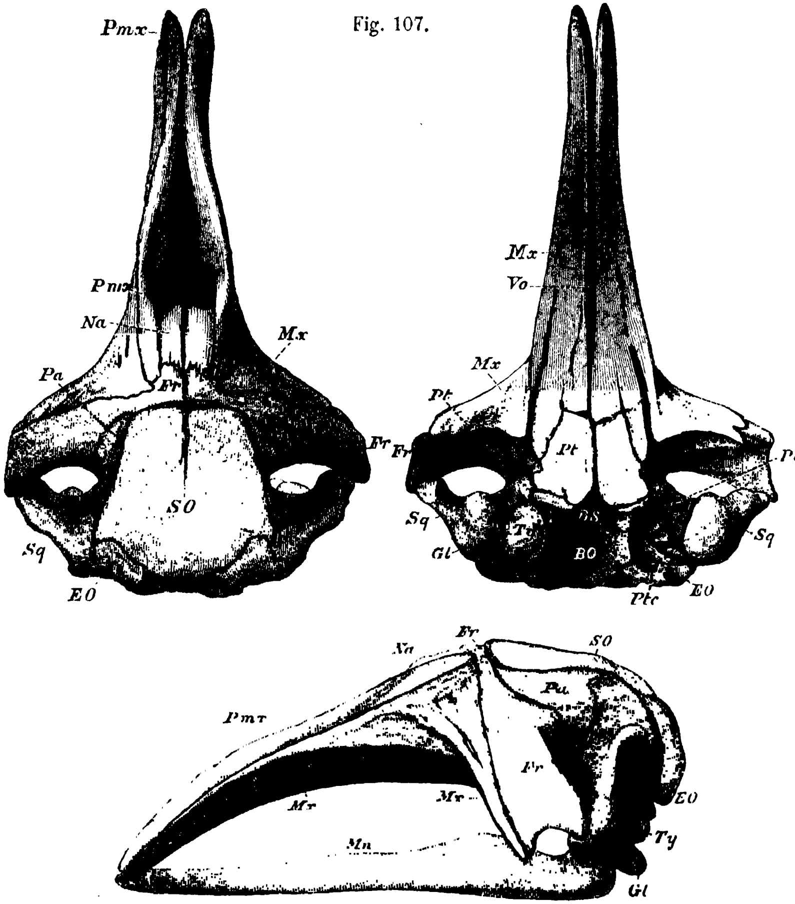


Fig. 107.—Upper, under, and side views of the skull of a fœtal Whalebone Whale (*Balæna australis*). The jugal bones are absent. In the under view the palatine bone is accidentally marked *Pt* instead of *Pl*.

a kind of beak. The premaxillæ enter into the upper and inner part of the whole length of this maxillary beak, but contribute little or nothing to its palatine surface and lateral boundaries, which are formed mainly by the maxillæ. The latter bones are always prolonged over, or in front of, the supra-orbital processes of the frontals.

The imperforate lachrymal is small, and sometimes coalesces with the jugal.

The nasal bones are always short, sometimes rudimentary; and the palatine bones are so disposed that the posterior nares are situated almost vertically under the anterior nares.

The squamosal bones are produced outwards, and the processes thus formed approach, or come into contact with, the posterior part of the supra-orbital processes of the frontals, which they separate from the jugal. Inferiorly, these processes support the glenoidal facets for the condyle of the lower jaw.

The sides of the broad basi-occipital are always prolonged downwards into free plates, which are concave outwards. These plates join the pterygoids in front, and the ex-occipitals behind, and so constitute the inner and posterior walls of an auditory chamber, the anterior and outer boundaries of which are furnished by the alisphenoid and the squamosal. In this chamber the tympano-periotic is lodged, sometimes quite loosely, at others fixed firmly in by interlocking sutures.

In the *Balænoidea*, or "Whalebone Whales," the symmetry of the skull is undisturbed, though there may be a slight inequality of the maxillæ. The skull of the fœtal *Balæna australis*, represented in Fig. 107, is perfectly symmetrical. Each lateral edge of the broad and flat basi-occipital is prolonged downwards and outwards into a broad process, concave outwards and convex inwards, the inferior edge of which is free, while the hinder edge unites with the ex-occipital, and the front edge with the pterygoid, to form the inner wall of the funnel-shaped chamber which lodges the tympano-periotic bone.

In front, this chamber is bounded by the pterygoid and the squamosal, and between and above them, for a small space, by the alisphenoid; behind, it is constituted almost entirely by the ex-occipital, while, externally and above, it is bounded and roofed in by the squamosal. Between these bones there is left, at the apex of the chamber, a considerable irregular aperture, which communicates with the cranial cavity.

The anterior and outer part of the under-surface of the squamosal is produced downwards into a great trihedral pillar, the obliquely truncated inferior face of which bears the articular surface for the mandible (*Gl*, Fig. 107). Behind this the squamosal presents a comparatively low wedge-shaped ridge (*a*, Fig. 108), between which and the "trihedral pillar" is a groove; while behind it, or between it and the ex-occipital, there is a deeper and wider transverse channel.

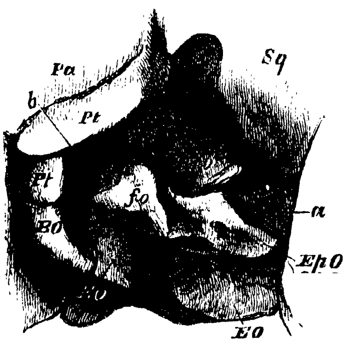


Fig. 108.—Enlarged view of the chamber which lodges the left tympano-periotic bone of the fœtal *Balæna australis*.—*a*, the "wedge-shaped ridge" of the squamosal; *C*, the aperture which leads into the interior of the skull; *f.o*, *fenestra rotunda*.

The periotic bone is irregularly triangular; the apex of the triangle, turned inwards and forwards, is thick and rounded, the anterior, posterior, and outer edges being thinner and more or less irregular. The upper smooth and concavo-convex surface of the periotic adjusts itself to the under-surface of the squamosal, where it forms the roof of the funnel-shaped cavity. The apex of the periotic, however, projects beyond this, and incompletely divides the irregular aperture above mentioned (*b*, Fig. 108) into an anterior division, which corresponds with the *foramen ovale* and *foramen lacerum medium*, and a posterior which answers to a *foramen lacerum posterius*.

The under-surface of the periotic, much more irregular, is divisible into three regions: an outer anterior; an outer posterior; an internal. The first and second are separated by a deep triangular notch in the outer margin of the bone, into which the inner end of the wedge-shaped ridge of the squamosal is received. The first, broad and short (*PrO*), presents a rough surface in front, with which the tympanic articulates, and eventually anchyloses; and behind, a concave surface, which, entering into the roof of the tympanic cavity, answers to the *tegmen tympani.* The second, narrower, elongated, and prismatic, fits into the transverse channel behind the wedge-shaped process (*a*). It corresponds with the *pars mastoidea*, and its rough outer extremity appears on the exterior of the skull, between the squamosal and ex-occipital.

The internal division, convex and rounded below, is formed by the pro-otic and opisthotic, and presents a large promontory with the *fenestra rotunda* (*f.o*) on its posterior surface, while the *fenestra ovalis* and Fallopian canal are visible upon its exterior. The tympanic bone (Fig. 109, *Ty*) is large, and scroll-like in form, very thick internally and below, and thin above and externally, where it presents the aperture of the external auditory meatus. It is by this thin upper and outer edge only, that it eventually anchyloses with the *tegmen tympani* and *pars mastoidea*, and hence, as its substance is very dense and brittle, readily breaks off.

In the adult Whale the *tegmen tympani* and *pars mastoidea*

Fig. 109.

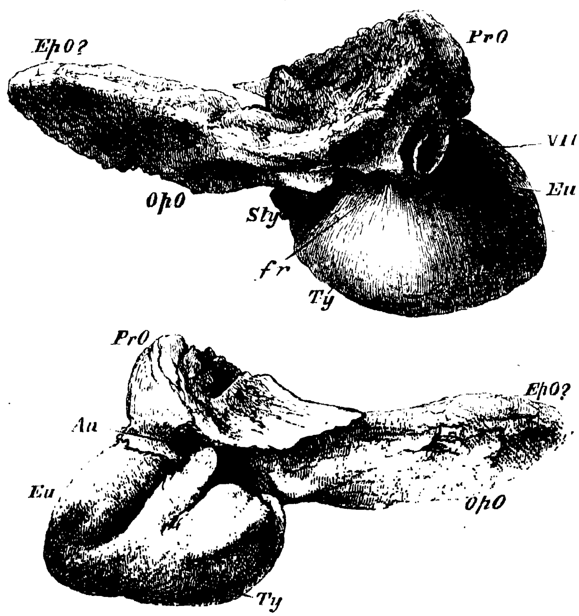


Fig. 109.—"Ear bones" of the adult *Balæna australis*. The upper figure gives the view from within; the lower, from without.

become greatly elongated and very rugged, the tympanic also acquiring a very large size (Fig. 109).

The vomer is a very long and large bone, deeply grooved above for the ethmoidal cartilage, which extends downwards and forwards between the premaxillæ and the maxillæ to near the anterior end of the snout. Its expanded upper and posterior end unites with the basi-sphenoid in the middle line, and with the pterygoid laterally. In front of the basi-sphenoid it embraces, not a distinct presphenoid (as in *Pterobalæna*, according to Eschricht), but the inferior surfaces of the orbito-sphenoids, which are very thick; and, being applied together by their flat median faces, apparently replace the proper presphenoid.

Both these bones and the alisphenoids are small, and almost confined to the base of the skull.

The supra-occipital and inter-parietal are united together, and completely overlap and hide the parietals in the roof of the skull. The separate frontals only enter into the anterior wall of the skull, and between them and the orbito-sphenoids an oval aperture is left, doubtless diminished in the recent state by the ethmoidal cartilage. Laterally, the frontals are prolonged outwards and backwards into two great supra-orbital processes, which nearly meet the zygomatic processes of the squamosal. The short jugal bones, absent in the specimen figured, extend in the *Balænoidea* from the zygomatic process to the anterior and external angles of the supra-orbital prolongations, and are distinct from the lachrymals.

The pterygoids are completely separated by the palatines (Fig. 107). In front of the latter the maxillæ almost wholly exclude the premaxillaries from the palate, while they send great processes obliquely outwards and backwards, in front of the supra-orbital prolongations of the frontal. The long premaxillæ, on the other hand, pass upwards and backwards on each side of the elongated and symmetrical nasals to meet the frontals, and exclude the maxillæ altogether from the anterior nares.

The rami of the lower jaw are very narrow, and so much arched outwards as to be able to enclose the baleen plates attached to the upper jaw when the mouth is shut.

Eschricht has described, with much care, the changes which the skulls of the *Balænoidea* undergo in passing from the fœtal to the adult condition, justly remarking that the skull of even a large fœtus is more different from that of the adult, than the skulls of distinct species of the same genus of Whales are from one another.

The growth of the walls of the cranial cavity relatively to that of the external prolongations of the cranial bones and to

Fig. 110.

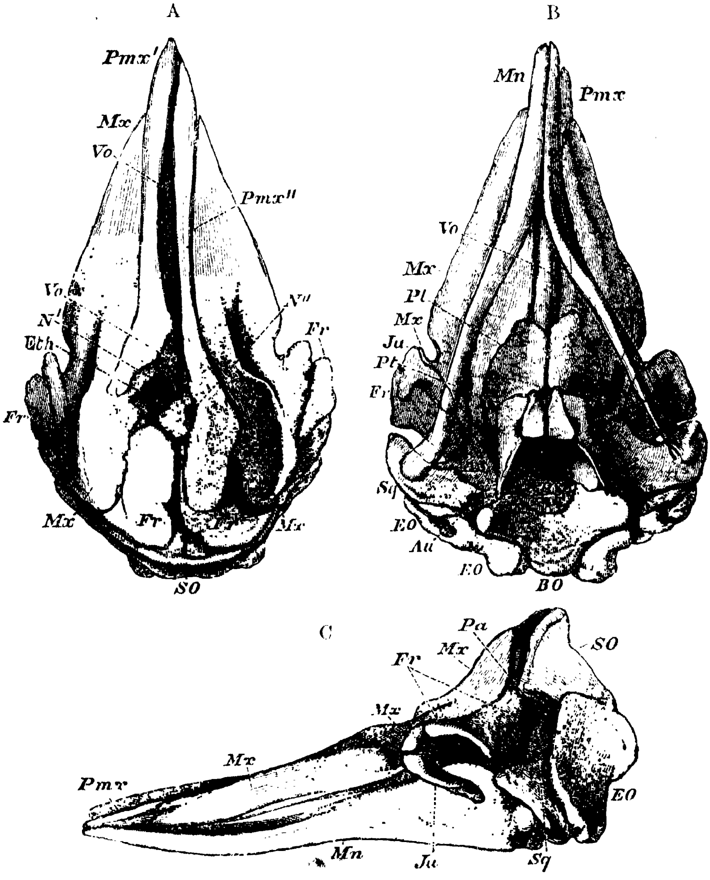


Fig. 110.—A, upper, B, under, and C, side views of the skull of a fœtal Cachalot in the Museum of the Royal College of Surgeons. The nasal bones are not represented in Fig. A.—*N'* left, *N''* right, nostril. The hinder extremity of the jugal, *Ju*, has fallen down from its natural connection with the zygomatic process of the squamosal.

that of the jaws, is soon arrested, and in addition the position and relations of some of the cranial bones become altered. In the smallest fœtuses of the lesser Fin-back (*Pterobalæna minor*), for example, the parietal region is occupied by the inter-parietal bone and the great fontanelle which lies in front of it. In larger fœtuses the fontanelle becomes closed by the progressive backward growth of the frontals, but the extension of the bones does not cease with their contact. The parietals grow over the inter-parietal and spread over it until they meet in the middle line. Hence the inter-parietal is eventually visible only in the interior of the skull. Anteriorly, the parietals grow over the frontals almost to the same level as the nasals, and thus conceal the share which the frontals take in the formation of the roof of the skull. But, at the same time, the supra-occipital extends from behind over the parietals; so that, at length, in that region which, in the youngest fœtus, was covered only by the inter-parietal, three bones—the inter-parietal, parietal, and supra-occipital—are superimposed.

The skulls of the other great division of the *Cetacea*, the *Delphinoidea*—or Dolphins, Porpoises, and Cachalots—are almost all distinguished by their very marked asymmetry.

In the Cachalot, or spermaceti Whale (*Physeter*), for example, the right premaxilla is much longer than the left, extending far back upon the right frontal, while the left does not reach the left frontal; the left nostril, on the other hand, is much more spacious than the right (Fig. 110, A). On the base of the skull (Fig. 110, B) the pterygoid bones unite in the middle line and prolong the palate, as in *Myrmecophaga* and *Ornithorhynchus*. When they and the palatine bones are removed, the axis of the lower part of the ethmoid is seen to continue that of the basi-cranial bones, which are, as usual, quite symmetrical. Superiorly, however, the ethmoidal plate is twisted over to the left side, and deeply grooved on the right side to form the inner wall of the small right nostril.

The vomer, which embraces the ethmoid and the presphenoid below, is also asymmetrical posteriorly, presenting a long and shallow lateral excavation, on the left side, and a short and deep one on the right. The maxillæ are correspondingly unsymmetrical in the region of the nasal aperture, but elsewhere they are pretty nearly symmetrical. But it is the nasal bones which exhibit the greatest distortion, the left and right being very unequal in size and dissimilar in form.

The jugal and the lachrymal commonly become anchylosed.

The basi-occipital, as in the *Balænoidea*, gives off a lateral downward process, which unites, behind (Fig. 111), with an out-

Fig. 111.

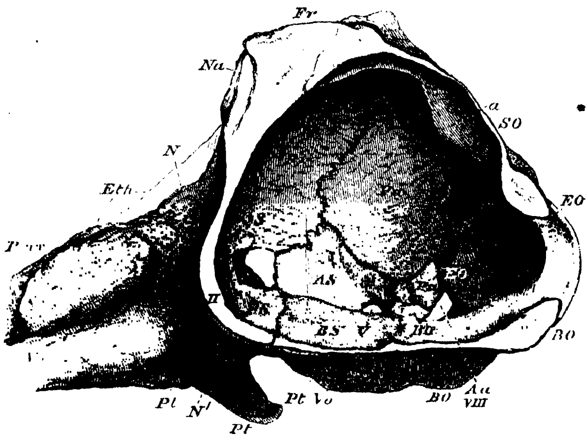


Fig. 111.—Longitudinal and vertical section of the skull of the White Whale or Beluga (*Delphinapterus*). * marks a distinct bony element interposed between the alisphenoid, the parietal, and basi-cranial axis; *a*, the ossified falx.

ward prolongation of the ex-occipital, and, in front, with the pterygoid, to constitute the inner wall of a deep chamber for the tympano-periotic. But the roof of this chamber is chiefly formed by the very large alisphenoid, which extends outwards to unite with the frontals, parietals, and squamosals, and backwards to the ex-occipitals. The aperture which is left between the hinder edge of the alisphenoid, the ex-occipital, basi-occipital, and basi-sphenoid, is exceedingly small, so that the tympano-periotic is still more shut out from the cranial cavity than in *Balæna*. In *Hyperoodon* and *Orca* the aperture is still further reduced; but this peculiarity cannot be said to be a distinctive character of the Delphinoid skull, as in *Platanista* the aperture is large, and the periotic appears in the interior of the cranial cavity in the ordinary way.

LECTURE XIV.

ON THE STRUCTURE OF THE VERTEBRATE SKULL.

THE THEORY OF THE VERTEBRATE SKULL.

In the preceding Lectures I have, as far as possible, confined myself to a statement of matters of fact, and to the conclusions which immediately flow from the application of a very simple method of interpretation to the facts. That method of interpretation is based upon the principle that, in any two skulls, those parts which are identical in their principal relations in the adult state, and in the mode in which they reach this state (or in their development) are corresponding, or homologous, parts, and need to be denominated by the same terms.

By the application of this method it has been possible to demonstrate the existence of a fundamental unity of organization in all vertebrate skulls; and, furthermore, to prove that all bony skulls, however much they may differ in appearance, are organized upon a common plan, no important bone existing in the highest vertebrate skull which is not recognisable in the lowest completely ossified cranium.

The enunciation of these results alone is a "Theory of the Skull," but it is by no means what is commonly understood as *the* theory of the skull.

For it will be observed that the statement just put forth confines itself to a simple generalization of the observed facts of cranial structure, and would be perfectly complete were the skull a self-subsistent structure, devoid of any connection with a trunk. On the other hand, that doctrine to which the title of "The Theory of the Skull" is ordinarily applied, embraces not only such a generalized statement of the facts of cranial structure as this, but adds a hypothesis respecting the relations of the skull to the spinal column. It assumes that the bony cranium (the cartilaginous and membranous states of the cranium it usually ignores) is composed of elements homologous with those which enter into the structure of the spinal column; that, in fact, it consists of modified vertebræ. And it is commonly conceived that it is the doctrine of the unity of structure of the skull and of the vertebral column, rather than the demonstration of the unity of organization of skulls, which is one of the chief glories of morphology.

The assumption that every skull repeats the organization of the trunk and consists of a certain number of modified vertebræ, evidently implies a belief in the unity of organization of skulls; but it is to be carefully noted that the converse proposition does not hold good; for it is quite possible to hold that all skulls are modifications of one fundamental plan, while wholly disbelieving that plan to be similar to the plan of a vertebral column.

Looking broadly at the history of the theory of the skull (using the phrase in its widest sense), I note three great lines of inquiry which have brought that theory into its present condition,—the first originated by Oken and Goethe; the second, not originated, perhaps, but chiefly fostered and developed by Geoffroy St. Hilaire and Cuvier; the third, originated, and almost exclusively worked out, by Reichert, Rathke, and their followers among the embryologists of Germany and England.

I. I have united the names of Goethe and of Oken as the originators of the hypothesis of the vertebral structure of the skull, as a matter of equity, and to aid in redeeming a great name from undeserved obloquy; though, in strict technical justice, the claim of the one to priority lapsed through lack of publication.

Goethe combined with a fervid creative genius, which has placed him on a level with the greatest poets of all ages, so much of observational acuteness and of intellectual precision as might have sufficed for the equipment of a well-reputed man of science. From his youth up, passionately devoted to the natural sciences, more especially to botany and to osteology; and induced by the habit of his mind to search for the general truths which give life to the dry bones of detail, Goethe had been led to drink deeply of the spirit of morphology, during his study of the metamorphosis of plants and his successful search after the premaxillary bones of man, imagined, before his time, to be wanting. With a mind thus prepared, it was no wonder that, as Goethe writes, the notion of the vertebral composition of the skull had early dawned upon him:—

"The three hindermost parts I knew before, but it was only in 1791, on picking up an old and broken sheep's skull amidst the sandy dunes of the Jewish cemetery in Venice, that I perceived the facial bones also to be made up of great vertebræ; and observing, as I clearly did, the gradual passage from the first pterygoid bone to the ethmoid bone and to the spongy bones, the whole became plain."

Not improbably deterred, however, by the many difficulties which must have presented themselves to him, in attempting to carry out these views with due scientific sobriety, Goethe kept them to himself, or shared them only with his immediate friends, for thirty years; the passage cited, in which they are first mentioned, bearing the date of 1820.

But, in 1807, Lorenz Oken independently originated and, what is more to the point, published, those views of the vertebral composition of the skull which have since attained such world-wide celebrity; so that the great poet's silent partnership in the affair would be hardly worth mentioning were it not that his reticence has been made the ground of severe attacks upon his honour and veracity. It has been suggested that Goethe, full of years and of honours, thought it worth while to attempt to steal from the young Professor of Jena the fame that had accrued to him. And upon the infamy of such petty larceny the poet's latest accuser has heaped the insinuation that the author of "Faust" and of "Meister" was so stupid a plagiarist, as to copy, not only Oken's views, but his account of the manner in which he came by them.

"Vaguely and strangely, however, as Oken had blended the idea with his *à priori* conception of the nature of the head, the chance of appropriating it seems to have overcome the moral sense—the least developed element in the spiritual nature—of Goethe, unless the poet deceived himself." *

"The circumstances under which the poet, in 1820, narrates having become inspired with the original idea are suspiciously analogous to those described by Oken in 1807, as producing the same effect on his mind."†

It would be difficult to couch an offensive accusation in stronger phraseology than this; but, by a singular chance, the scientific morality of its object has recently been fully vindicated. Goethe, when in Italy, kept up a correspondence with the family of his friend Herder. His letters have been published, and in one addressed to Madame Herder, and dated May 4, 1790, this passage occurs:—

"By the oddest, happy chance, my servant picked up a bit of an animal's skull in the Jews' Cemetery at Venice, and, by way of a joke, held it out to me as if he were offering me a Jew's skull. I have made a great step in the explanation of the formation of animals."

Can it be doubted that this "great step" is exactly that vertebral theory of which Goethe says, writing in 1820, he had as clear a view "thirty years ago?" It is to be hoped that this evidence, which Professor Virchow has so strikingly put forward, will henceforward silence even the most virulent of Goethe's detractors, although a careful perusal of the arguments used by Mr. Lewes, in his "Life of Goethe," might have already sufficed those who were open to conviction.

The idea, which dropped still-born from Goethe's mind, was, as I have said, conceived afresh by Oken, and came vigorously into the world in that remarkable discourse (occupying in print about fourteen quarto pages) with which he inaugurated his professorial labours at Jena.

It is hard to form a just judgment of this singular man; and, I must confess, I never read his works without thinking of the

* "Encyclopædia Britannica," eighth edition, vol. xvi., p. 501; article, "Oken."

† *Ibid.*, p. 501.

epithet of "inspired idiot," applied to our own Goldsmith: so strange is the mixture of insight and knowledge with what, to my apprehension, is mere "sound and fury, signifying nothing." But the "Programm" contains far more of the former and less of the latter ingredient than is usually noticeable in Oken's lucubrations, and it appears to me to be, at the present moment, by far the best specimen extant of the style of speculation about the skull, characteristic of the school which Oken originated. Indeed, if for the term "cranial vertebræ," "cranial segments" be substituted, I do not know that the plan of composition of the osseous brain-case can be better described than in the language which I shall now quote.*

The "Programm" opens thus:—

"A vesicle ossifies, and it is a vertebra. A vesicle elongates into a tube, becomes jointed, ossifies, and it is a vertebral column. The tube gives off (according to laws) blind lateral canals; they ossify, and it is a trunk skeleton. This skeleton repeats itself at the two poles, each pole repeats itself in the other, and they are head and pelvis. The skeleton is only a developed (*aufgewachsenes*), ramified, repeated, vertebra; and a vertebra is the preformed germ of the skeleton. The entire man is only a vertebra.

"I.

"Take a lamb's skull, separate from it those bones which are considered to be facial, and those bones of the cerebral capsule which take no share in the base, such as the frontal bones, the parietal bones, the ethmoid and the temporal bone, and there remains a bony column, which every anatomist will at once recognise to be three bodies of some sort of vertebræ, with their lateral processes and foramina. Replace the bones of the cerebral capsule, with the exception of the temporal bones (for the cavity is closed without these), and you have a vertebral column, which is distinguished from the true one only by its expanded spinal canal. As the brain is the spinal marrow more voluminously developed [in relation] to more powerful organs, so the brain-case is a more voluminous spinal column.

* "Ueber die Bedeutung der Schädelknochen. Ein Programm beim Antritt der Professur an der Gesammt-Universität bei Jena." Von Dr. Oken. Jena. 1807.

"If there are three vertebral bodies in the brain-case, there must be as many vertebral arches. These are to be sought out and demonstrated.

"You see the sphenoid separated into two vertebræ: through the first one pass the optic nerves, through the hinder the nerves of the jaws (*par trigeminum*). I term the former the *Eye vertebra*, the latter the *Jaw vertebra*. Against this last abuts the basilar process of the occipital bone with the petrous bone. The two form one whole. As the optic nerve traverses the Eye vertebra, and the jaw nerve the Jaw vertebra, so the hindermost vertebra is related to the auditory nerve. I therefore term it the *Ear vertebra*. Again, this is the first cephalic vertebra; the precedent, the second; and the eye vertebra, the third.

"It has given me unspeakable trouble to make out whether the petrous bone belongs to the first or to the second cephalic vertebra. Before I had taken into account the relations of the nerves, vessels, and muscles, my decision was based only upon the structure of the skulls of Birds, Lizards, and *Chelonia*; but now I have fortified it by a multitude of concurrent arguments, of which I will state only a few in this place.

"You will have observed, in fact, that each of the two anterior vertebræ has appropriated a sense. (As the jaws end in the lips, I reckon them also among the [organs of] sense, and I shall demonstrate that they are so, and how they are so.) Now, if the petrous bones belonged to the jaw vertebra, one vertebra would give off nerves to the sensory organs, while the first vertebra would be sent empty away. True, it transmits nerves to the tongue, but these are variable; and it will be shown in the sequel that neither tongue nor nose have, or can have, a proper vertebra. Lastly, in Lizards, the auditory apparatus lies distinctly in the occipital bone.

"The cephalic vertebræ are, therefore, *sensory vertebræ*, and only exist in correspondence with the [cephalic] senses. (The tongue and the nose are trunk senses, of which presently.) Vertebral divisions and cephalic sensory nerves go parallel with one another. Bones are the earthly, hardened nervous system; nerves are the spiritual, soft, osseous system—*continens* and *contentum*.

"Between the sphenoid and occipital bones, between the sphenoid and petrous bones, between the parietals (the temporal bones are away) and the occipital bone, draw a line, and you have marked off the first vertebra. Draw another line between the two sphenoids, or, in Man, in front of the pterygoid processes; laterally, through the *fissura orbitalis* in front of the *alæ magnæ*; lastly, between the frontals and the parietals, and you have the second vertebra separated from the last.

"1. Now, take the ear vertebra of a fœtus of any Mammal or of a Man; place beside it an incompletely-developed dorsal vertebra, or the third cervical vertebra of a Crocodile, and compare the parts of which the two are composed—their forms, their contents, and the exits of the nerves.

"According to Albinus and all anatomists, each vertebra of a fœtus consists of three separate pieces—the body and the two arches, which together form the spinous, transverse, and oblique processes. You have the same in the occipital bone, only more distinct and separate. The *pars basilaris* is a *corpus vertebræ* still more separated from the condyloid parts, which form the lateral regions; these are again separated from the *pars occipitalis*, which forms the spinous process. In fact, this part itself is often split again, like the spinous processes in *spina bifida*. The occipital bone, therefore, is decomposable, according to the mode of its origin, into five pieces, since the lateral, or articular, and the spinous parts appear as independent developments; as is found also in actual vertebræ, which consist of five pieces, and in the third cervical vertebra of the Crocodile. Finally, I need take no further pains to prove that the occipital foramen is the lower aperture of a vertebral canal; that the *foramen lacerum* is an inter-vertebral foramen, and the occipital protuberance is a spinous process; that, therefore, the occipital bone, in respect of form, as of function (since it encloses the cerebellum, as a continuation of the spinal marrow), is in every sense a true vertebra, since the mere naming of these parts is enough to cause their recognition as such.

"You will think I have forgotten the petrous bone. No! It seems not to belong to the vertebræ as such, but to be the sensory organ in which the vertebral—the auditory—nerve loses itself, and, therefore, to be an organ as completely separated from vertebral production as any other viscus, or as the ball of the eye; the deception lies only in this, that it is the essence of this organ to be ossified, as it is that of the eye to be crystalline.

"The mastoid process is, in animals, and also in the human fœtus, a proper bone, in which the styloid process lies. It is plainly inserted into the first vertebra, but it receives its signification from the tongue.

"2. Having entered so fully into the discussion of the first cephalic vertebra, I might, except for clearness' sake, spare you any delay over the second. But I will also demonstrate in this how completely the brain-case is formed according to the idea of a vertebra, and has even been partially produced as such.

"In every skull of a fœtus you may find the *alæ orbitales* of the sphenoid separate from it. They belong to the third vertebra. But, in the half-developed fœtus, the great wings and the pterygoid processes are also separate from the body of the sphenoid. The last-mentioned processes are foreign to the sphenoid, and only coalesced with it; they belong to quite another formation, and very probably have the same signification as the *os omoideum* of the Bird's head, as Cuvier has already indicated. I shall return to them.

"There remain, therefore, for the posterior sphenoid, or the jaw vertebra, three portions of bone—the body and the great wings, or the lateral and oblique processes of the vertebra. The spinous processes are formed by the two parietals, which, in many animals, coalesce so as to leave no suture, but are yet originally two. It is to be remarked that, in the Sheep, this vertebra is closed by the bones in question, without the intermediation of the temporal, which also does not belong to the vertebral group. The same occurs in the Chelonian, the Crocodile, &c.

"3. Whoso has recognised the second vertebra, as such, need only look at the third, especially in Ruminants, to discover quite the same structure. The anterior sphenoid with the *alæ orbitales* represents the body, together with the lateral processes; the two frontals form the spinous process, together with its lateral parts.

"The sphenoid is separated into two vertebræ, not merely in the human fœtus and in Ruminants, but also in the Apes, in *Bradypus tridactylus, Dasypus novemcinctus*, Dog, Wolf, Bear, Otter, Rodents, and probably in all Mammals, if examined in a sufficiently young state. The law is therefore universal.

"The inter-vertebral foramina are very well marked between these vertebræ. A deviation seems to exist, on account of the foramina which lie in front of the first cephalic vertebra, namely, the *foramen caroticum* and *lacerum*, concerning which I must leave it undecided, whether they are originally two, or only one which has become separated. On this point evidence enough is to be found among animals. The organ of hearing has here interposed itself. On the other hand, it is characteristic of the cephalic vertebræ that their sides are perforated by nerves,— by the optic nerve, the jaw nerves, and the hypoglossus, if we reckon the auditory and facial nerves as inter-vertebral nerves: a circumstance which demands further inquiry.

"So much of the cephalic vertebral column. I might have been able to treat more fully and thoroughly of it, and to have indicated the nerves, veins, and muscles, which in the head correspond to those of the trunk, and the like for the bones; but in a programme one must be content with merely putting forth one's view of a question.

"II.

"If the cerebral capsule is the repetition of the spinal column, only more expanded and organized (I speak as an anatomist), the head must repeat the outgrowths of the spinal column, the thorax, the pelvis, and the limbs; and, indeed, thereby must it attain completeness.

"By this union of the representatives of all the bones of the trunk arises the wonderful, but yet analysable, mixture and intercurrence of formations which appear as the facial bones. The spinal column becomes the brain-case; the walls of the trunk, with the extremities, become the face."

In developing this idea, Oken arrives at the conclusion that the nasal cavity is the thorax of the head, and the oral cavity the abdomen of the head. The squamosal is the conjoined scapula and ilium of the head; the pterygoid, the clavicle; the hyoidean apparatus, the other pelvic bones. The jugal arch represents the humerus, radius, and ulna; the maxilla, the hand; the premaxilla, the thumb; the teeth, the fingers. The lower jaw represents the legs of the head; the teeth the toes; and, of all imaginable hypotheses, the styloid processes are the sacrum of the head!

Reasons, worthy of the name, for these identifications are not to be found in the "Programm." Oken, having assumed once for all, that, as the brain-case repeats the spinal canal, the facial bones must repeat the other appendages of a vertebral column and the limbs, seems to have troubled himself no further about demonstration. What a bone should be, in order to fit plausibly into his scheme, that it was at once settled to be—an appeal to the "idea" dispersing all doubts.

A few years later Oken modified his original conception so far as to regard the nasal apparatus as a fourth vertebra.

Whatever may be thought about the more speculative passages of the extract above cited from Oken's work, and of his *à priori* conception of what a skull must be, it contains ample evidence that he did, *à posteriori* and inductively, demonstrate the segmented character of the bony brain-case; and had nothing more ever been written on the subject, this great truth would have remained as a splendid contribution to morphology. But Oken greatly amplified the observational basis of his own doctrine; Spix took it up, in a modified form, and worked it out, in his own way, through the series of the *Vertebrata* in his great illustrated "Cephalogenesis," published in 1815; Bojanus did the like in the pages of the "Isis," and in the "Parergon" of his splendid monograph, the "Anatome Testudinis;" and, finally, C. G. Carus developed the doctrine, as far as it could well go, both *à priori* and *à posteriori*, in his "Urtheilen des Knochen und Schälen-Gerustes," published in 1828; in which, under the names of "Grund-form" and "Schema," we have, among other things, "archetypal" diagrams of the *Vertebrata* generally, and of each vertebrate class.

Under these circumstances, the following passage, extracted from the article in the "Encyclopædia Britannica" already cited (*suprà*, p. 281), may not improbably excite in other minds as much astonishment as it has in mine:—

"As to the question of the superiority of the deductive over the inductive method of philosophy, as illustrated by the writings of Oken, his bold axiom that heat is but a mode of motion of light, and the idea broached in his essay on 'Generation' (1805), viz., that 'all the parts of higher animals are made up of an aggregate of *Infusoria*, or aggregated globular Monads,' are both of the same order as his proposition of the head being a repetition of the trunk, with its vertebræ and limbs. Science would have profited no more from the one idea without the subsequent experimental discoveries of Oersted and Faraday, or by the other, without the microscopical observations of Brown, Schleiden, and Schwann, than from the third notion, without the inductive demonstration of the segmental constitution of the skull by Owen. It is questionable, indeed, whether in either case the discoverers of the true theories were excited to their labours, or in any way influenced, by the *à priori* guesses of Oken; more probable is it that the requisite researches and genuine deductions therefrom were the results of the correlated fitness of the stage of the science, and the gifts of its true cultivators at such particular stage."—P. 502.

Thus does the moralist upon Goethe's supposed delinquencies think it just to depreciate the merits of Oken, and exalt his own, in the year 1858. But if he himself had not been "in any way influenced" by Oken, and if the "Programm" is a mere mass of "*à priori* guesses," how comes it that only three years before Mr. Owen could write thus?*

"Oken, ce génie profond et pénétrant, fut le premier qui entrevit la vérité, guidé par l'heureuse idée de l'arrangement des os crâniens en segments, comme ceux du rachis, appelés vertèbres.'

And, after sundry extracts from Oken's "Programm," could continue:—

"Ceci servira pour exemple d'un examen scrupuleux des

* "Principes d'Ostéologie comparée, ou Recherches sur l'Archétype et les Homologies du Squelette vertébré."—P. 155. 1855.

faits, d'une appréciation philosophique de leurs rélations et analogies, en un mot de l'esprit dans lequel Oken détermine les rélations vertébrales des os du crâne."—P. 158.

And again:—

"Quand on commença à apprécier la vérité de la généralisation d'Oken, on se rappela, comme c'est l'habitude, que quelqu'un avait eu un idée à peu près semblable. . . . . Mais toutes ces anticipations ne sauraient enlever à Oken le mérite de la première proposition definie d'une théorie."—P. 161.

The space at present occupied by the proclamation of the weakness of the "moral sense" of Goethe may not unfitly be taken up, in the next edition of the "Encyclopædia Britannica," by the extrication of the author of the article "Oken," from the singular dilemma in which these citations place him.

The fact is, that, so far from not having been "in any way influenced" by Oken, Professor Owen's own contributions to this question are the merest Okenism, *remanié*. In the work I have cited, not a single fact, nor a single argument, can be found by which the doctrine of the segmentation of the skull is placed on a firmer foundation than that built by Oken. Two novel speculations are indeed brought forward, the one of which confuses the petrosal (in the Cuvierian sense) of the lower *Vertebrata* with the homologue of the alisphenoid of Man, and, consequently, would, if adopted, throw the whole subject into hopeless chaos; while the other—the supposition that the fore limb is an appendage of the head—can only be explained by that entire want of any acquaintance with, or appreciation of the value of, embryology which all the writings of the same author display.

II. The great works of Spix and Bojanus contain, apart from the theory which they attempted to establish, abundant evidence of the unity of composition of the bony skull, but it was Geoffroy St. Hilaire and, more especially, Cuvier, who demonstrated that unity of organization, apart from all hypotheses, most thoroughly and completely. The fresher one's study of the writings of the wilder Okenians—the more one has become weary of wading through empty speculations upon "connation" and "coalescence," "irrelative repetition" and "transposition," the *Dei ex machinâ* who are called in to solve every difficulty—the more heartily does one sympathise with the sarcastic vigour with which Cuvier annihilates the products of their exuberant fancy in the notes to the "Ossemens Fossiles," and the "Histoire Naturelle des Poissons." Nor is it possible to peruse without admiration the sagacious reasonings by which he was led to determinations which, in the majority of cases, have been accepted by those who have followed him.

Meckel, Köstlin, in his elaborate and valuable special work on the Vertebrate Skull, and Hallmann, in his excellent essay on the Temporal Bone, have built on Cuvier's foundations, applying further and, in some cases, bettering, his determinations of the homologues of particular bones. No one can study these works carefully and retain a doubt that osseous skulls are constructed upon a uniform plan, though he may, with Cuvier, give but a hesitating and grudging assent to the notion that it is, in some sense, a modified vertebral column.

III. That criterion of the truth or falsehood of the vertebral theory of the skull, for which the Okenians do not think it necessary to look, and which Cuvier seems to have sought in vain, has been furnished by the investigations of the embryologists from the year 1837 to the present time.

The first step was the discovery of the visceral arches by Reichert; the second, the demonstration of the mode of development of the skull, in all classes of the *Vertebrata*, by the remarkable researches of Rathke, contained in the "Vierter Bericht über das Naturwissenschaftliche Seminär bei der Universität zu Königsberg," which was published in 1839. I will quote Rathke's statement of his conclusions at length, so that we may have the means of fairly comparing his mode of going to work with that of Oken:—

"The following results, among others, are deducible from the observations which have been detailed:—

"(1.) At the earliest period of fœtal life the notochord extends backwards, as far as the end of the body; forwards, only to the interspace between the auditory capsules.

"(2.) The gelatinous investing mass, which, at first, seems only to constitute a band to the right and to the left of the notochord, forms around it, in the further course of development, a sheath, which ends in a point posteriorly. Anteriorly, it sends out two processes which underlie the lateral parts of the skull, but very soon coalesce for a longer or shorter distance. Posteriorly, the sheath* projects but little beyond the notochord; but, anteriorly, for a considerable distance, as far as the infundibulum. It sends upwards two plates, which embrace the future central parts of the nervous system laterally, probably throughout their entire length.

"(3.) The investing mass of the notochord is the material out of which the vertebral column and a great part of the skull, though not the whole skull, are developed.

"(4.) The most essential part of a vertebra is its body. With the exception of a few cartilaginous fishes, the cartilaginous foundation of that body (the notochord having disappeared earlier or later), has the form of either a ring, or a half ring; or, as is the case among the *Mammalia*, forms a solid mass, having the form of the segment of a cylinder. Subordinate parts of the vertebra are the vertebral arches and transverse processes, together with the ribs, which all, at the time they take on a cartilaginous character, appear as rays of the body, though sometimes they are not developed at all. Only in rare cases (*Petromyzon*) are vertebral arches developed without vertebral bodies; that part of the investing mass of the notochord which is, in other cases, applied to the formation of such bodies, acquiring only a membranous consistency.

"(5.) From that part of the investing mass of the cephalic part of the notochord, which consists of the anterior part of the sheath of the notochord and its anterior paired processes, are developed the basi-occipital, the basi-sphenoid, and the ethmoid, so that the ethmoid is the most anterior of the parts of the skeleton which take their origin from the investing mass of the notochord. The basi-occipital is formed in that part of this

* Perhaps with rare exceptions, as in *Fistularia tabacaria*.

mass which surrounds the cephalic part of the notochord like a sheath; the basi-sphenoid, in that part of it which lies between the paired processes (the *trabeculæ*) and the anterior end of the notochord; and the ethmoid (more particularly its body, or *pars perpendicularis*), in the anterior coalesced part of those two processes. The body of the presphenoid, on the other hand, is formed below the processes in question, rarely between them.

"(6.) The parts of the skull just mentioned, however, do not ossify in all *Vertebrata* with an osseous skeleton, but one, or several, of them sometimes remain cartilaginous, and then grow relatively far less than the others, so that they seem to be pushed aside and suppressed by the neighbouring bones. This holds good especially of the basi-occipital of the *Batrachia*, and of the basi-sphenoid of these animals and of osseous Fishes.

"(7.) The basi-occipital (or, at least, the substance out of which it will become developed) constitutes, originally, like the body of a vertebra, a sheath round a part of the notochord, and the ex-occipitals appear, whilst they chondrify, as outgrowths from the basi-occipital part; just as the arches of a vertebra, when this is normally developed, appear as outgrowths from its already chondrified body. For the rest, however, the normal development of the occipital bone is quite similar to that of a vertebra, and it therefore may with perfect justice be held to be a cephalic vertebra.* The *squama occipitis*, which occurs in many, but not in all *Vertebrata*, and which is not always placed between, but sometimes lies in front of the ex-occipitals, presents no difficulty in the way of this interpretation; it is an accessory structure, a so-called intercalary bone, the presence of which depends upon the excessive development of the brain.

"(8.) The two rings, on the other hand, which are formed by the two sphenoids, with the parietals and frontals as their intercalary bones, are no longer constructed upon quite the same type as the vertebra. That the alisphenoids and orbito-sphenoids, when they are already chondrified, do not appear to take the form of outgrowths of their centres, but are united with them by membrane, need not, perhaps, be taken very much into account,

* The *Foramina condyloidea*, which occur in the ex-occipitals of many *Vertebrata*, remind one of the holes of the vertebral arches of the Sharks.

since, in the Lampreys, the arches of the vertebræ arise independently within the lamellæ, which the investing mass of the notochord has sent out to embrace the central parts of the nervous system. Still less weight can be attached to the circumstance that not unusually, even when both sphenoidal centra are present, only one pair of the corresponding alæ appears; while, in other cases, two pair of alæ and only one central part are present, since the caudal vertebræ of *Mammalia* usually exhibit no traces of arches, and the Lampreys have such arches without centra. On the other hand, the circumstance is important that the basi-sphenoid, although it arises within the investing mass of the notochord, is not developed around this (as, so far as our present observations go, even the most posterior caudal vertebræ are), but in front of it, in a process of the investing mass; and that the body of the presphenoid is no longer developed, even in a part of this mass (except in a few *Mammalia*), but arises quite independently of it. Hence, the two sphenoids no longer agree perfectly with vertebræ in their development—the anterior diverging more widely from the vertebral type than the posterior.

"(9.) Yet the two sphenoids, like the proper vertebræ, still embrace segments of the nervous tube (such as is formed by the brain and spinal marrow, at any rate in the early stages of development), and they constitute, as the vertebræ at first normally do, open rings, or rather segments of rings, round that tube. The ethmoid, however, at no time surrounds a segment of the nervous tube in question; but, in a few animals only, imperfectly includes, by its hinder part, two anterior prolongations of that tube, whence the olfactory nerves arise. Its mode of development, and its ultimate form likewise, are of such a character that it no longer offers any special resemblance to a typically-formed vertebra. Nevertheless, considering that it arises from a part of the prolonged investing mass of the notochord—viz., from the anterior, early-coalescing parts of the two *trabeculæ*—and that its body (the *pars perpendicularis*) presents even a certain resemblance to the last caudal vertebræ of many Birds and osseous Fishes, it may well be considered to be a modified vertebra. We may look at it, in short, as the representative of only the body of a vertebra—such as normally each caudal vertebra of a Mammal is; and that from this, for the purpose of investing the olfactory apparatuses, which are developed at its sides, lamellar processes grow out, which are altogether peculiar to it. In any case, however, the ethmoid may be regarded as the anterior end of the vertebral column.

"(10.) From what has been stated, it appears that the four different groups of bones—the occipital, with its intercalary bone, the *squama;* the basi-sphenoid, with its intercalary bone, the parietals; the presphenoid, with its intercalary bones, the frontals; and the ethmoid, together with its outgrowths, the spongy bones and the cribriform plate—exhibit in their successive order from behind forwards, a greater and greater deviation from the plan according to which ordinary vertebræ are developed, so that the occipital bone is most like a vertebra, while the ethmoid is least like one.

"(11.) Among the bones of the face, the premaxillæ, the nasal bones, and the vomer are developed altogether independently of the investing mass of the notochord; and they never coalesce with parts of the skeleton, which are immediately derived from the latter. On this account, alone, they cannot be regarded as vertebræ, or parts of vertebræ. Furthermore, they at no time enclose, or help to enclose, a segment of the central nervous system. The nasal bones and the vomer are, properly speaking, 'splint-bones' (*Belegungsknochen*) for the ethmoid, such as occur in the vertebræ of no animal; and the premaxillæ are applied, although in a different plane, to the one end of the vertebral column, as, in Fishes, the median rays of the anal fin are applied to the other end of it.* Furthermore, the palatine bones are developed, together with the pterygoids, in lateral processes, or rays, which have grown out from the middle part of the base of the brain-capsule, and which, as regards their original form, disposition, and connections, resemble the ribs, and may be regarded as a pair of ribs united with the brain-case. In *Mammalia* the two mallei are developed in these two rays, and

* The study of the development of the skull necessitates the assumption that Sturgeons, Sharks, and Rays have no premaxillæ, and that their skulls end anteriorly with the ethmoid cartilage.

perhaps the quadrate bones of many other *Vertebrata* in a part of them. Around them, however, is developed, in animals provided with an osseous skeleton, a coating of bony plates, which becomes metamorphosed into the lower jaw.

"At the outer side of those parts, moreover, in which the pterygoid and palatine bones arise—or, in other words, alongside the processes of the 'rays'—a substance arises, whence the upper maxilla and the malar bone are developed.

"The upper maxilla and malar bone therefore might be regarded, like the lower maxilla, as splint bones or rib-like bones (which, however, do not occur in connection with true ribs), but not as parts of the vertebra itself.* The lachrymal bone, lastly, only fills up a gap between other bones of the face, and therefore, if analogies must be discovered, can only be regarded as an intercalary bone.

"(12.) The auditory capsules and the petrosal bones, which are developed out of them in many animals, may, in respect of their place and origin, be most fittingly compared with those intercalary bones which occur in Sharks and Sturgeons, between the arches of the vertebræ; but, in respect of their form, take a different course from these. And since those intercalary pieces can hardly be considered to be parts of vertebræ, the auditory capsules cannot be regarded as such."

Vogt and Agassiz, resting upon embryological observations which entirely confirmed those of Rathke, carry out the argument suggested by the latter more rigorously.

"It has therefore become my distinct persuasion (says Vogt) that the occipital vertebra is indeed a true vertebra, but that everything which lies before it is not fashioned upon the vertebrate type at all, and that all efforts to interpret it in such a way are vain; that therefore, if we except that vertebra (occipital) which ends the spinal column anteriorly, there are no cranial vertebræ at all." †

* In the *Chelonia* and a few *Mammalia* bony elements occur, which cover the ribs and, in the first-mentioned animals, even become united with the ribs; they are developed, however, in the integument, and belong to the integumentary skeleton, and not to the nervous skeleton, so that they need not be considered here.

† "Entwickelungs-Geschichte der Geburtshelfer Krote."—P. 100. 1842.

But the further investigations of embryologists have demonstrated that the occipital segment of the skull is, developmentally, as different from a vertebra as all the rest, seeing that, as Remak has more fully proved than any other observer, the segmentation into "urwirbel," or proto-vertebræ, which is characteristic of the vertebral column, stops at the occipital margin of the skull—the base of which, before ossification, presents no trace of that segmentation which occurs throughout the vertebral column. By this third great step the vertebral hypothesis of the skull seems to me to be altogether abolished; even though Professor Goodsir, whose thorough acquaintance with embryology gives his opinions on these subjects great weight, has endeavoured, in his learned and ingenious essays, to combine the facts of development with that hypothesis.

IV. A fourth line of investigation, not bearing so directly upon the vertebral hypothesis, but still of great moment, was opened up by the observations of Arendt on the persistent cartilaginous cranium of the Pike,* and by the subsequent investigations of Von Bär, of Dugés, of Reichert, of Agassiz, of Jacobson, Sharpey, Spöndli, and Kölliker, and all the discussions which have taken place on the "primordial cranium" question. The problems attempted to be solved by these inquiries are—Is there a clear line of demarcation between membrane bones and cartilage bones? Are certain bones always developed primarily from cartilage, while certain others as constantly originate in membrane? And further, if a membrane bone is found in the position ordinarily occupied by a cartilage bone, is it to be regarded merely as the analogue, and not as the homologue, of the latter? In other words, is histological development as complete a test of homology as morphological development?

At present the course of investigation appears to me to tend towards giving an affirmative answer to these questions; but much and careful observation is yet needed.

* "De Capitis Ossei Esocis Lucii Structura Singulari." 1822. Nesbitt, however, appears to have been the first to direct attention to the difference between membrane bones and cartilage bones.

Having concluded this rapid historical sketch of the gradual growth of the true theory of the skull, it may be well if I state, in a brief summary, what I conceive to be the present condition of our knowledge respecting its structure and development :—

1. All crania result from the modification of the anterior part of that "primitive groove" of the embryo, the posterior part of which gives rise to the vertebral column; and, at the very first, there is no discernible difference between that part of the groove which will give rise to the vertebral column, and that from which the skull will be produced.

2. The first changes which take place, in both the cranial and the spinal regions of the primitive groove, are also precisely similar, the dorsal laminæ growing up and uniting together in the middle line, so as to enclose a cavity which is, on the one hand, the primordial brain-case, and, on the other, the primordial spinal canal. So far, a unity of organization may be predicated of both brain-case and spinal canal; but the brain-case is not yet a skull, nor the spinal canal a vertebral column.

3. Beyond this point, the course of development of the cranial region differs absolutely from that of the spinal region. In the latter, that histological differentiation takes place which results in the formation of the proto-vertebræ, while in the skull no such process occurs. Again, the notochord extends throughout the whole length of the spinal column; while, as soon as the skull is distinguishable, as such, the notochord ceases to extend beyond the middle of its floor, stopping immediately behind that part which lodges the pituitary fossa.*

4. Furthermore, when chondrification takes place in the spinal column, separate masses of cartilage are developed in each proto-vertebra; but, when chondrification commences in the base of the skull, it gives rise to a continuous body of cartilage, which never exhibits any trace of transverse division, or segmentation; but is always divided under the pituitary body into two longitudinally-arranged crura, the "*trabeculæ cranii.*"

5. Hence it follows that, though the primordial brain-case and the primordial spinal canal are identical in general plan of construction, the two begin to diverge as soon as the one puts

* *Amphioxus* forms an exception, probably only apparent, to this generalization.

on the special characters of a skull, and the other those of a vertebral column; the latter taking one road, while the skull takes another. The skull is no more a modified vertebral column than the vertebral column is a modified skull; but the two are essentially separate and distinct modifications of one and the same structure, the primitive groove.

6. The skull, having assumed its special and distinctive characters, may pass through three successive states—the membranous, the cartilaginous, and the osseous—in the course of its development; and the order in which these states succeed one another is always the same, so that the osseous skull has a cartilaginous, and the cartilaginous, a membranous, predecessor. Nor does any one of these states ever completely obliterate its predecessor; more or less cartilage and membrane entering into the composition of the most completely ossified skull, and more or less membrane being discoverable in the most completely chondrified skull.

7. The adult skull may, however, have got no further than one of these states. In the *Amphioxus*, the skull (if skull it can be called) is membranous. In many Fishes, as we have seen, it is cartilaginous, with, at most, a superficial conversion into bone. In the rest of the *Vertebrata* definite bones are added, to the more or less complete exclusion of the cartilaginous cranium.

8. When definite cranial bones are developed, they arise in one of two ways, either in the substance of the cartilaginous cranium, as "cartilage bones," or in the perichondrium, or remains of the membranous cranium, as "membrane bones." It is highly probable that, throughout the vertebrate series, certain bones are always, in origin, cartilage bones, while certain others are always, in origin, membrane bones.

9. With the exception of *Amphioxus*, three sets of sensory organs—olfactory, optic, and auditory—are evolved in the walls of the skull of every vertebrate animal, and they are disposed, from before backwards, in the order in which they are named. All these sensory organs are originally developed in connection with involutions of the integument, which, in the case of the olfactory organ, remain open, but, in that of the eye

and ear, become shut. Each sensory apparatus is, throughout the Vertebrate series, related to the same nerves: the olfactory being supplied by the first pair; the optic, by the second; the auditory, by the *portio mollis* of the seventh; while the fifth pair leaves the skull in front of the auditory capsule, and the eighth pair behind it. These relations of the cranial nerves to the sensory organs, and consequently to the cranial walls, are established antecedently to chondrification, and *à fortiori* to ossification; so that the cranial nerves and the sensory organs serve as fixed points by which the nature of the various ossifications can be determined.

10. By the help of these landmarks, chiefly, it has been possible to identify the bones known as basi-occipital, ex-occipitals, supra-occipital; basi-sphenoid, alisphenoids, parietals; presphenoid, orbito-sphenoids, frontals; or, in other words, the constituents of the walls of the brain-case, throughout the whole series—from the Pike to Man. And it is found that these bones, when they all occur together, are so disposed as to form three, originally distinct, segments.

11. Recourse to long-established, but frequently-forgotten facts in the history of the development of the so-called "*pars petrosa*," and "*pars mastoidea*," or periotic bone, of the human skull, has shown that these parts ossify from three centres, which have hitherto received no names, and which I have termed the "pro-otic," "opisthotic," and "epiotic" bones. It has been one of the principal objects I have had in view to prove, by paying careful attention to the relations of these osseous elements, on the one hand to the nerves, and on the other to the parts of the auditory organ which they enclose, that they are very generally represented, sometimes in a distinct form, and sometimes coalesced with one another, or with other bones, throughout the series of skulls provided with cartilage bones; and that the pro-otic, especially, is one of the most constant and easily-identifiable bones throughout the series of vertebrate skulls.

12. The eye is not invested by any cartilaginous or osseous elements of the cranial wall; but the olfactory sacs become more or less enclosed in a capsule, formed partly by a median

cartilaginous plate, which results from the coalescence and outgrowth, beyond the boundaries of the brain-case, of the *trabeculæ cranii;* partly, by outgrowths from the superior and inferior edges of that plate; and partly, by a prolongation outwards of the front part of the outer wall of the brain-case, into an antorbital process, between the orbit and the nasal sac, on each side. Cartilage bone developed in the septum gives rise to the ethmoid; in the antorbital processes, to the prefrontals; in the superior, or inferior, lateral prolongations of the side walls, to the turbinal bones. Membrane bones developed upon the roof of these olfactory capsules give rise to nasals; beneath the septum, to vomers.

13. The ethmoid and its dependencies are developed within the median "fronto-nasal" process, which grows out from the front wall of the embryonic skull, between the rudimentary nasal sacs; and the inferior, broad, free edge of which bounds the mouth. It is in this free edge that the premaxillæ are developed, and they are, at first, perfectly distinct from the maxillæ. The latter, together with the palatine and pterygoid bones, are formed within the maxillary processes, which bound the sides of the primitive oral cavity, and run, parallel with one another, along the base of the fore-part of the embryonic cranium, uniting, behind, with the first visceral arch, but being, at first, completely separated, anteriorly, from the fronto-nasal process. Clearly therefore, if the premaxillæ and maxillæ, &c., are to be regarded as constituents of inferior arches of the skull, they are not parts of one arch, but of, at least, two distinct arches.

14. Of the first and second visceral arches, which lie immediately behind the mouth, the former, which gives rise to the mandible and quadrate bone, passes into the skull under the front part of the auditory capsule; while the root of the latter, in which a greater or smaller part of the hyoidean apparatus is developed, underlies the hinder part of that capsule. It is therefore impossible that the mandibular and hyoidean arches should be dependencies of any other parts of the skull than those which lie immediately in front of, or behind, the auditory capsules; and in the completely ossified skull we never, as a matter of fact, meet with these arches in any other position.

15. There is not a shadow of evidence that the mandibular and hyoidean arches suffer any shifting of position from before backwards, in the course of their development; but the extremities of those arches which are attached to the skull undergo very singular metamorphoses, the effect of which is, that the dentary part of the mandible is brought into closer connection with the skull the higher we ascend in the Vertebrate series. Thus, in the Fish it is separated from the skull by the hyomandibular, quadrate, and articular bones; in the Reptile by the quadrate and articular; while in the Mammal the quadrate and the articular are metamorphosed into the incus and the malleus, and the dentary comes close to the skull, articulating with the squamosal.

These are, I believe, the most important facts regarding the structure and development of the skull, which may now be regarded as well established. If we inquire how they bear upon theories of the skull, it will be obvious that they place the doctrine of the unity of organization of the vertebrate skull upon a perfectly sure and stable footing, while they appear to me, as clearly, to negative the hypothesis that the skull is, in any sense, a modification of vertebræ.

But though the skull has not a vertebral structure, and in its membranous and cartilaginous states is not even segmented, it assumes a very definite segmentation in its completely ossified state.

In every well-ossified cranium there is, assuredly, an *occipital segment* ("Ear Vertebra" of Oken), formed by the basi-occipital, ex-occipitals, and supra-occipital; a *parietal segment* ("Jaw Vertebra" of Oken), constituted by the basi-sphenoid, alisphenoid, and parietals; a *frontal segment* ("Eye Vertebra" of Oken), composed of the presphenoid, orbito-sphenoids, and frontals; and a *nasal segment* ("Nasal Vertebra" of Oken), formed by the ethmoid, prefrontals, turbinals, nasals, and vomer.

Leave out the hypothetical considerations that these segments are equivalent to one another, and that they are homologous with vertebræ, and Oken's expression of the broad facts of the structure of the completely ossified brain-case is, I believe, the best that has yet been given. Nay, we may go further with him, and look on the periotic bones as no part of the proper cranial wall, but as special developments within the otic capsule. But here we must stop, for neither anatomy nor development are reconcilable with the notions of the Okenian school respecting the limbs of the head. Carus suggested, from the Okenian point of view, that the premaxillæ and maxillæ must be cephalic ribs, and not cephalic limbs; but Rathke was the first to demonstrate that the inferior arches of the skull must be considered, if they are homologous with anything in the trunk, to partake of the nature of ribs rather than of that of limbs. But the confusion between analogy and affinity has led to such grave errors in the interpretation of the upper arches of the skull, that we must be upon our guard against running into similar mistakes with respect to the lower arches.

It is easy enough to enumerate four inferior arches to the skull, just as there are four superior arches—the premaxillæ forming the first of these arches; the palato-pterygoid and maxillary apparatus, the second; the mandible, with its suspensorium, the third; the hyoidean arch, the fourth: and it might be plausibly enough represented that the first of these is united with the nasal segment of the skull, the second with the frontal segment; while the third and fourth, being connected respectively with the anterior and the posterior parts of the periotic capsule, might be fairly considered to belong to the parietal and occipital segments.

But do they really belong to those segments? and if so, why do they not remain attached to them? What relation have the branchial arches to the skull, again? It is hard to see in what morphological character the first branchial arch of a fish differs from its hyoidean arch; and if so, is it an arch of the skull, or an arch of the vertebral column? What, furthermore, are the original connections of the palato-pterygoid arch? Does it grow out of the mandibular arch from behind forwards, as Rathke seems to think; or has it, primitively, that connection with the prefrontal region which is so constant a character of the palatine bone?

These questions must be answered before the theory of the lower arches of the skull can be placed upon as satisfactory a footing as that of the upper arches; and they can be answered only by the embryologist, who may be encouraged to the difficult task by reflecting on what he has done already; though keeping in view the adage of the Roman, and

"Nil actum reputans si quid superesset agendum."