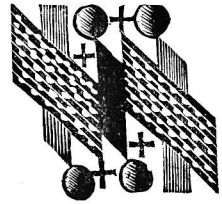
THOMAS HENRY HUXLEY, born at Ealing in 1825. Medical apprentice at thirteen; entered Charing Cross Hospital, 1842; assistant-surgeon on H.M.S. *Rattlesnake*, 1846–50; F.R.S., 1850; President of the Royal Society, 1883; retired from public work, 1885. Died in 1895.

LECTURES AND LAY SERMONS



THOMAS HUXLEY

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II. 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, 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 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. 11, 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. 11, 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. 11, 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. 11, 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 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. 11, 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. 11, C, *b*). But I have so frequently

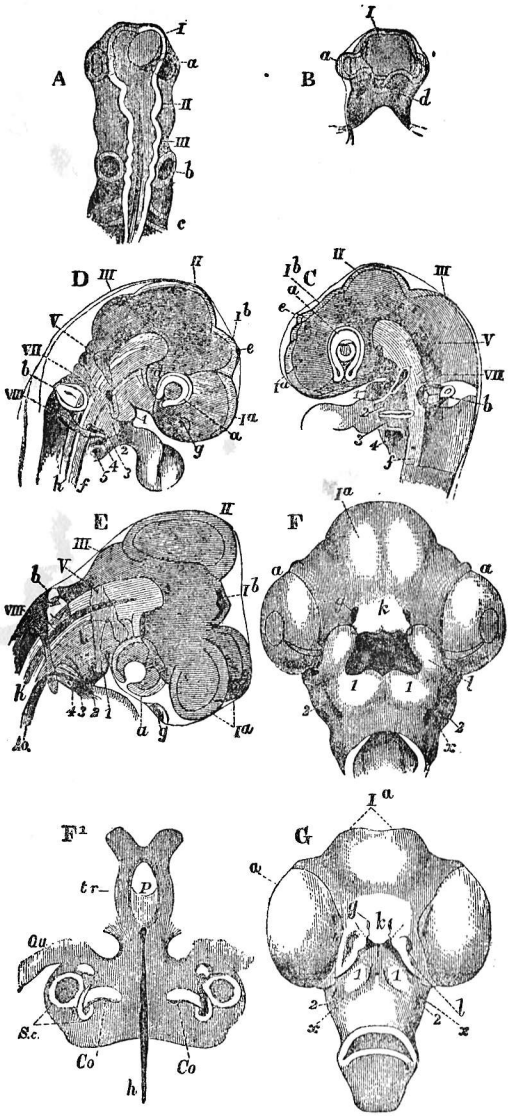

Fig. 11.—Successive stages of the development of the head of a chick.—*I*, *II*, *III*, first, second, and third cerebral vesicles; *Ia*, vesicle of the

verified Huschke's and Remak's statement that it does so arise, that I entertain no doubt whatever of the fact.[1] 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*) 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

cerebral hemispheres; *Ib*, 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*, proto-vertebræ; *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.

F¹, 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.

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

the former being determined by the edges of a depression of the integument which will eventually become the buccal cavity (Fig. 11, C). A third, fourth, and fifth visceral arch are developed in successive order behind the first and second (Fig. 11, D); 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 developmentis, *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. 11, 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. 11, 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. 11, 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. 11, 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

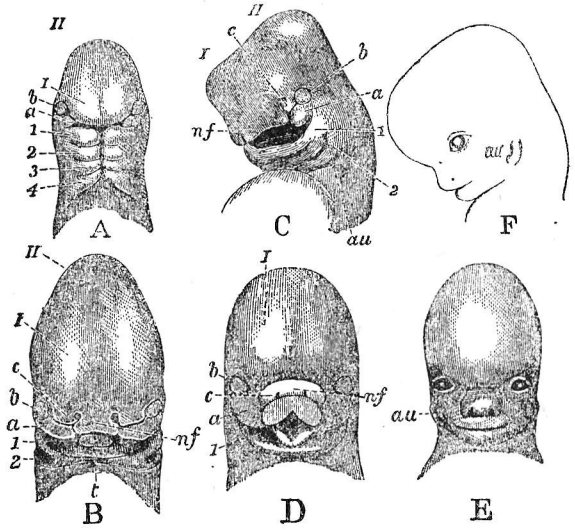

Fig. 12.—Successive embryonic conditions of the human head (after Ecker).—*I*, *II*, the first and second cerebral vesicles. 1, 2, 3, 4, the visceral arches; *a*, the maxillary process; *b*, the eye; *nf*, the middle naso-frontal process; *c*, the lateral naso-frontal process; *t*, the tongue; *au*, 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.

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

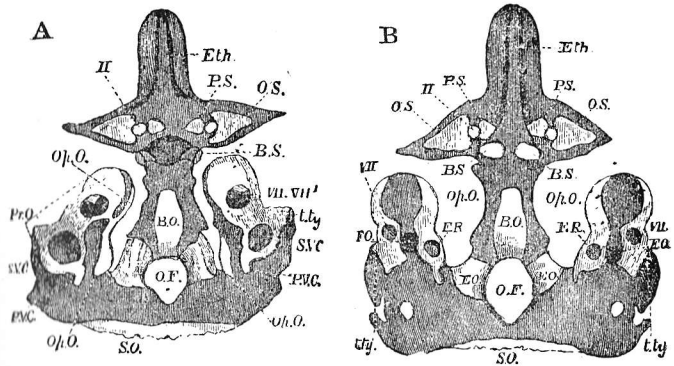

Fig. 13.—A, upper, and B, under view of the basis cranii and periotic cartilage of a human fœtus eight inches long. The alisphenoidal and immediately adjacent parts of the basi-sphenoid are omitted. The cartilage is darkly shaded, while the osseous deposits are left white, or but lightly shaded. The 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.

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 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 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. 13, *P.S.*) These centres coalesce with the orbito-sphenoids of their own side before they unite with one another.[1] The osseous orbito-

[1] 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

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

the third month, I also find two other centres 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 [7½ 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.

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

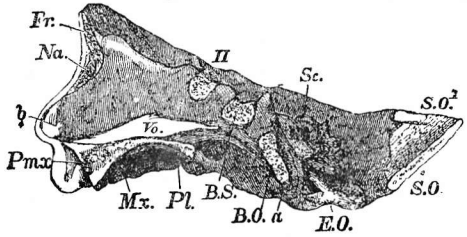

Fig. 14—Longitudinal and vertical section of the *basis cranii* of a fœtus somewhat older than the foregoing (Fig. 13). The basi-sphenoidal and presphenoidal centres have coalesced; but they and the basi-occipital are severally separated by wide interstices of cartilage, of which the whole ethmoidal region is still constituted.

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 sincipitis ferè, os autem cuneiforme omnino 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. 15, 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. 13, A, p. 149), 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. 15, 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. 15, B, *Op.O.*)

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. 15, B, *Ep.O.*)

Thus, in a fœtus between the fifth and sixth months, the "*pars mastoidea*" exhibits the appearance represented in Fig. 15, 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*,[1] 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. 13, 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

[1] 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.

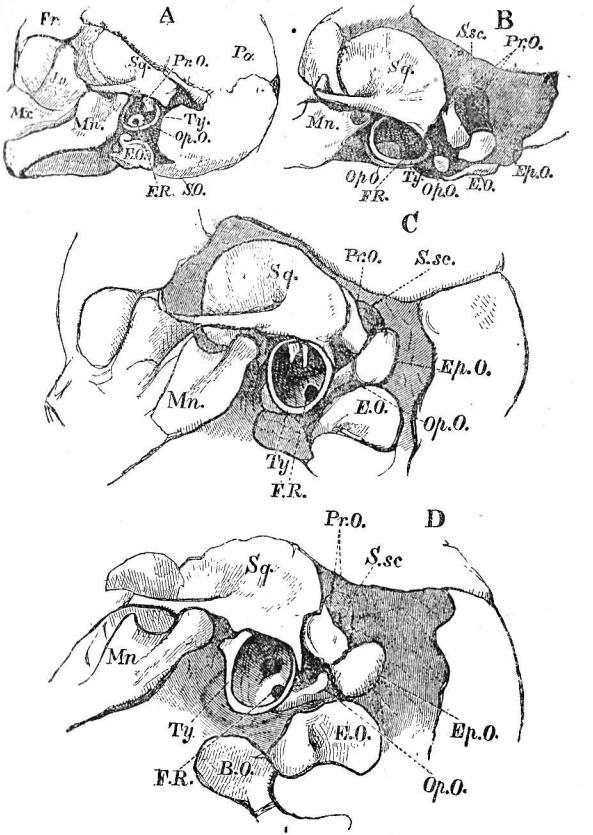

Fig. 15.—Development of the temporal bone.

A, from a fœtus 5¼ inches long, showing the commencing pro-otic and opisthotic ossification.

B, from a fœtus 8½ 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 10¼ inches long, the "tria ossicula" beginning to unite into the *pars mastoidea*.

D, from a fœtus 10½ inches long, the tria ossicula anchylosed.

F.R., *foramen rotundum*.

S.sc, superior semicircular canal.

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, 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. 15, 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. 16, 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. 17.)

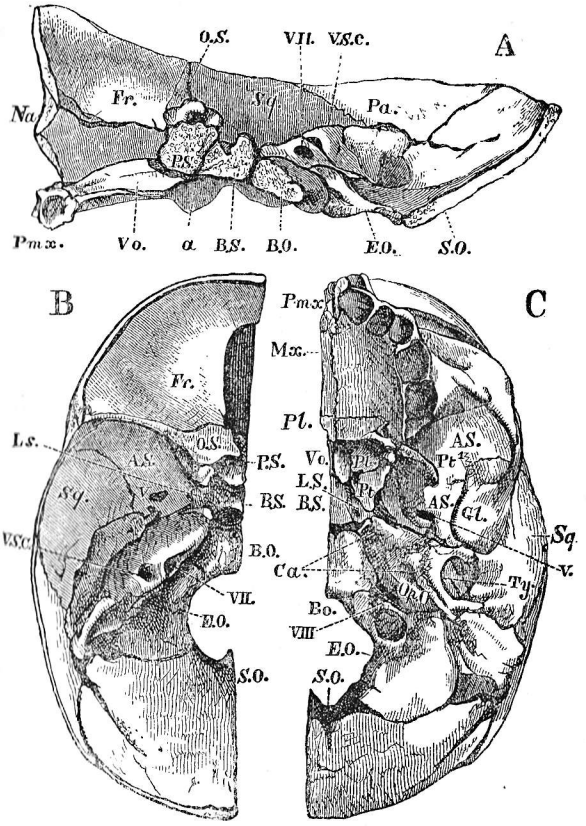

Fig. 16.—The human cranium at birth.—A, vertical and longitudinal section of the basal half of the cranium; B, upper, and C, under, view of the same preparation.

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. 16, C.)

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

Fig. 17.—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.

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.

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. 18).

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. 18), 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 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

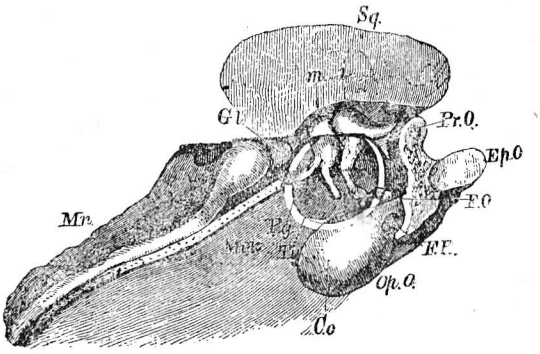

Fig. 18.—Part of the skull of a human fœtus at about the sixth month, dissected to show the auditory ossicles and Meckel's cartilage, *Mck*. *Gl*, the glenoid cavity. The *margo tympanicus* and adjacent parts of the squamosal are represented as if they were transparent, in order to show the position of the malleus (*m*) and incus (*i*). The tympanic bone (*Ty*) is merely indicated. *Co.*, the cochlea.

Reichert. Thus Gunther,[1] 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 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

[1] Beobachtungen über die Entwickelung des Gehörorgans bei Menschen und höheren Säugethieren. 1842.

is received by a pit, the future *fenestra ovalis*." The nodule grows 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.[1]

III. 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. 19) presents the most 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

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