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HOMOLOGIES OF THE ALISPHENOID AND PETROMASTOID BONES IN VERTEBRATES

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To those unfamiliar with modern views upon the morphology of the skull it may not be known that any difference of opinion still prevails among anatomists as to what bones in the skull of the lower vertebrates should be regarded as homologues or representatives of the great wing of the sphenoid and petromastoid in the skull of Man and other mammalia. Considering the numerous and important palæontological and embryological researches made in recent years, and in view of the fact that the remains of extinct animals and the development and structure of existing ones have been described so elaborately, it might naturally be supposed that the question of the special homologies of the bones of the skull would have long since been definitely settled.

So far, however, from this being the case, as a matter of fact anatomists, in certain instances at least, on the one hand designate the same bone by different names and on the other, different bones by the same name. The confusion of ideas thus engendered by obscure nomenclature makes it often very difficult to understand what particular bone is referred to, especially when the description relates to the cranial bones of some extinct animal. Apart from this consideration it is obvious that unless the special homologies of the bones of the skull of different vertebrates are determined, and identical bones be designated by the same name, it will be impossible to assign to an animal its proper position in the order of Nature or determine its phylogeny in the light of evolution, especially if the animal be an extinct one and its natural affinities obscure. The hope of dissipating some of the confusion prevailing as to the nomenclature of certain of the bones in the skull of Man and other vertebrates prompts the author to submit a resumé of some well-known osteological facts with, however, an interpretation of the same not hitherto presented, at least as far as known to him. Even if the latter be not accepted, the determination of the synonyms of the bones in question may, at least, not prove superfluous hereafter to co-workers in this field of research.

The prevailing view among anatomists at the present day appears to be that the petromastoid portion of the temporal bone is developed in Man from three distinct centres of ossification, named respectively prootic, opisthotic and epiotic; that the prootic and opisthotic coalesce to form the pars petrosa, the epiotic giving rise to the specially mastoid part of the pars mastoidea, and later joining the other two.

According to this view the homologues of these three centres of ossification of the petromastoid of Man exist in the skull of the lower vertebrata either as distinct bones or more or less coalesced with each other or with adjacent bones. The bone formerly considered as the homologue of the great wing of the sphenoid or the alisphenoid, Figs. 1, 2, *a* is regarded as the prootic or the homologue of the upper part of the human pars petrosa. The alisphenoid proper, *t*, is often but little developed or even absent in the skull of the lower vertebrates; the bone formerly named occipital externe or paroccipital is regarded as the homologue of the opisthotic or epiotic, while the latter is often represented by a small ossification coalesced with the supra occipital.

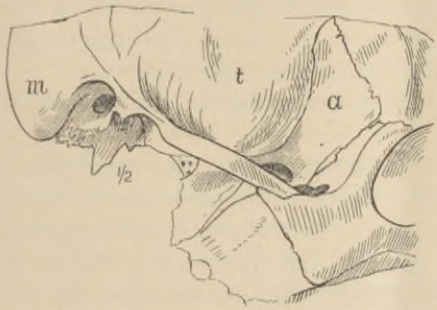

FIG. 1. Side view of human skull.

So far as known to the author Kerckringius is usually regarded as having been the first anatomist to describe the petromastoid portion of the temporal bone as developed from three centres of ossification. Unless the author has misunderstood the meaning of the text, however, that which Kerckringius refers to as being developed from three centres of ossification is not the whole petromastoid but only that part of the pars petrosa which constitutes the mammillary process or pars mastoidea, the pars petrosa proper having been more or less developed before and independent of the three centres.

FIG. 2. Interior view of human skull.

In the fifth chapter of his Osteogenia Foetorum,[1] published in 1690, Kerckringius observes: "Ossis petrosi pars illa, quae processum mammilluarem constituit, terna de novo acquisivit ossicula; unum pyriforma, acutiore, sui parte squamoso annectitur; alterum scutum ovale referens, magnitudine, priori vix cedens, media cartilagine ab eo separatur; uti &c., tertium ab utroque, quam vis hoc magnitudine neutri sit aequiparandum, vix aciculae majoris caput adaequans sunt autem eo situ ordine collocata, quem tabula foetus v, mensium, usurpata oculis facilius ad mentem quam verba transmittet. . . . Constat ergo os temporum hoc quinto mense sex distinctis ossiculis; osse videlicet, squamoso, anulo, osse internam civitatem efformante &c., tribus notabilibus quae hoc mense ex orta esse diximus. Sexto mense pyriforme, &c. ovale scutiforme coaluerunt in unum; tertium non nihil auctum est magnitudine. . . . Septimo mense jam tertium illud ossiculum duobus mense superiore inter se coalitis accessit."

That these three centres of ossification, viz., the "pyriforma," "scutum ovale" and "tertium" do not correspond exactly to the prootic, epiotic and opisthotic centres in the sense in which these terms are used by modern anatomists, appears from the text of the latter part of the passage quoted, beginning "constat ergo," the temporal bone being said to consist at the fifth month of six distinct ossicles, which would be impossible if two of the "tribus notabilibus" coalesced to form the "osse internam cavitatem efformante," which, however, as we shall see hereafter, they do a little later. That by the "osse internam civitatem efformante" is meant that part of the pars petrosa developed before and independent of the appearance of the three distinct ossicles becomes evident from the description of the state of the development of the temporal bone at the previous or fourth month, Kerckringius stating that the bone at the end of that month consists of three ossicles: "annulo," "osse squamoso" and "illo jam commemorato," the latter being the "osse internam" or that part of the pars petrosa developed at that period. "Quarto mense mirum visu, quam cito & quanto perfectione os squamosum magnam partem factum sit osseum. Os petrosum jam rubicunda cartilagine signavit cavitatis suae formam organorum auditus capacem, nihil tamen adhuc praesefert osseum, praeterquam unam in longitudi-

[1] Theodori Kerckringii, Osteogenia Foetuum. Bibliotheca Anatomica, T. II, Genevae, 1685.

nem protensam crassiusculam & inaequalem lineam, annulo seu circulo, antea nominato, subjectam &c. paulo longius protensam. Os itaque temporum hoc mense tribus constat ossiculis, annulo scilicet,[2] osse squamoso et illo jam commemorato.

Further, according to Kerckringius the "pyriforma" (prootic) coalesces at the sixth month with the "scutum ovale" (epiotic) to form one bone, the latter being joined at the seventh month by the "tertium illud ossiculum" (opisthotic), whereas, as we shall show, it is the opisthotic and not the epiotic that combines with the prootic to form the pars petrosa. As to what Kerckringius meant by his "tria petrosi ossis distincta ossicula," we will try to make clear in our description of the manner in which the petromastoid develops in Man.

The work "De Aure Humana" by Cassebohm appeared in 1734–1735. The description of the development of the ear given by this author, while agreeing in the main with that of Kerckringius, differs from it in some respects. Cassebohm recognized, however, with Kerckringius, the fact of the pars petrosa being more or less ossified before the appearance of the "tria ossicula," as shown by numerous passages in his text as well as by his excellent figures.[3]

In the judgment of the author, Meckel, rather than Kerckringius or Cassebohm, was the first anatomist to describe the petromastoid of the temporal bone as arising from three distinct centres of ossification. According to this author[4] the first part of the labyrinth to ossify is that immediately surrounding the fenestra rotunda, whence

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[2] Kerckringius, loc. cit.

[3] Tractatus Quatuor Anatomici de Aure Humana. Halae Magdeburgicae, 1734 p. 19:—"Kerckringii relatio de osse temporum in foetu trium mensium, cum mea observatione de foetu totidem convenit excepto. . . . Idem ille porro in foetu quinque mensium, partem petrosam, circa processum mastoideum tria ossicula habere refert, quorum due mense sexto coaulere: verum in his mensibus, in loco indicato nulla ossa peculiaria sed cartilaginem vidi Tab. 3, Fig. 22, lit. K."

Tractatus Quatuor &c., p. 45:—Antequam tympani membranam removebam, cochleae tuber membranae hujus partem superiorem & mediam tangebat & quam vis cartilaginem esset, foraminis tamen rotundi (quod ad cochleam & ducit & pertinet) margo erat osseus partem que annuli posteriorem attingebat." . . . . Cochleae que tuber ex fusco quem habebat, colorem nigrum acquisivisset, tunc foraminis rotundi margo albus osseus que apparebat."

Tractatus Quintus Anatomicus. Halae Magdeburgicae, 1735, p. 15:—"In foetu trium mensium cochleam, circa foramen rotundum osseam, reliquam vero cochleae partem cartilagineam. In foetu quatuor mensium cochleam vidi osseam, excepta lamina spirali, quae cartilaginea erat; hanc in foetu quinque mensium osseam demum conspexi."

[4] Handbuch der Menschlichen Anatomie, Band 4. Halle & Berlin, 1820, p. 49.

the spreading ossification produces the floor of the labyrinth. The second centre of ossification arising at the extreme end of the superior vertical canal, gives rise to the internal auditory meatus and the floor of the cochlea. The third centre of ossification begins as a scale upon the middle of the internal vertical semi-circular canal.

It is to be inferred that Meckel supposed the mastoid is developed from the latter centre, for though he does not say so in the passage just referred to, as he had some years previously[5] expressed the view that the mastoid is developed from a special centre distinct from that forming the pars petrosa, and as the latter is formed according to Meckel from the first two centres, the only centre remaining to form the mastoid is the third centre, that beginning as a scale upon the internal vertical semi-circular canal.

In his well known work on the temporal bone Hallmann also expresses the view that the mastoid portion is developed from a special centre of ossification, offering as a proof thereof the fact of his being able to scrape off, in certain specimens of the dried skull, the third oval centre of ossification without injuring the semi-circular canal.[6]

In 1848 Rathke, in describing the development of the turtle, regarded the two bones, the rocher[7] and occipital externe[8] of Cuvier, which, according to this author, form the labyrinth, as corresponding when taken together to the pars petrosa of the temporal bone of higher vertebrates:—"Die Knorpel Kapsel, welche sich auch bein den Schildkrœten um den häutigen Theil des Ohr labyrinthes bildet und anfangs eine sehr einfache Form und nur sehr dünne Wandung hat, bleibt in ihrer gegen das Gehirn gekehrten Hälfte bei mehreren Schildkrœten (namentlich in den Gattungen Emys und Chelonia), wenn nicht gar bei allen, zeitlebens knorplig. Ihre äussere und groessere Hälfte hingegen verknochert allmaehlig, so jedoch, dass in ihr zwei Knochenstücke einstehen, von denen ein jedes einen Theil des häutigen Ohrlabyrinthes, namentlich Theile der halbzirkel formigen Kanäle einschliesst und von denen nur das eine mit dem Namen des Felsenbeins belegt, das andere von Cuvier nicht recht

[5] Archiv, Band 1, 1815, p. 636.

[6] Die vergleichende Osteologie des Schläfenbeins, Hannover, 1837, p. 3:—"Dieser Knochen kern zeigt sich am trocknen skelet als ein ovales Knöpfchen, das ich leicht abkratzen konnte, ohne die kanäle zu verletzen, zum zeichen dass dieser Theil als ein besonderes stück entsteht."

[7] Alisphenoid, Prootic.

[8] Paroccipital, Opisthotic.

passend Os occipitale externum genannt worden ist. Beide Knochenstücke nun, die zusammengenommen eigentlich nichts anderes als das Felsenbein der höhern Thiere vorstellen.[9]

About the same time the late Professor Owen[10], in referring to the views of Kerckringius as to there being "tria petrosa ossis distincta ossicula," called attention to the primary independence of the base of the processus mastoideus as "a fact of much more significance than its brief and transitory manifestation would lead the author to divine." He further observed that "in the cold blooded vertebrates the mastoid retains with a few exceptions its primary embryonic distinctness as an independent element of the skull." It should be mentioned in this connection, however, that as Professor Owen regarded the bone now considered in the lower vertebrata as the squamosal to be the homologue of the special centre of ossification of the human pars mastoidea, he called it accordingly the mastoid.

In 1861 the view of Meckel as to the original distinctness in the embryo of the three parts of the petromastoid portion of the temporal bone was confirmed by Kölliker[11] in his description of the development of that bone in Man.

Finally, Professor Huxley in his lectures as Hunterian Professor at the Royal College of Surgeons of England, in 1863, and embodied substantially in his "Lectures on the Elements of Comparative Anatomy,"[12] developed at length and in detail the view that the petromastoid portion of the temporal bone in man is developed from three centres as described by Meckel and Kölliker, and further that these three centres are represented in the lower vertebrata as more or less distinct bones as held by Rathke and Owen.

The two bones described by Rathke as forming in the turtle the "felsenbein" were named by Prof. Huxley the prootic[13] and opisthotic[14]; that regarded by Owen as the mastoid was considered by Prof. Huxley to be the squamosal[15], and the "specially mastoid" part of the "pars mastoidea" the "scutum ovale referens" of Kerckringius was named by Prof. Huxley the epiotic[16].

[9] Ueber die Entwickelung der Schildkröten. Braunschweig, 1848, p. 52.
[10] On the Archetype and Homologies of the Vertebrate Skeleton. London, 1848, p. 29.
[11] Entwicklungsgeschichte des Menschen und der Höheren Thiere. Leipzig, p. 320.
[12] London, 1864.
[13] Op. cit. p. 222.
[14] Op. cit. p. 222.
[15] Op. cit. p. 230.
[16] Op. cit. p. 155.

The view of the morphology and terminology of the periotic capsule and adjacent bones as sustained by Prof. Huxley and most other anatomists of the present day is based upon two assumptions:

1st. That the petro-mastoid portion of the temporal bone in Man develops from three distinct centers of ossification named respectively prootic, opisthotic and epiotic and represented in the skull of the the lower vertebrata by three bones bearing respectively the same three names and more or less coalesced with each other or adjacent bones.

2d. That the bone lying in front of the exit of the inferior maxilliary division of the fifth nerve should be regarded in the lower vertebrata as the homologue of the great wing of the sphenoid in Man and named the alisphenoid, and the bone lying behind such exit as homologous with the upper part of the pars petrosa of Man and named the prootic.

The conclusion that follows if these two assumptions be admitted, will be that the alisphenoid or homologue of the great wing of the sphenoid is often but little developed or may be even absent in the skull of the lower vertebrata, its place being supplied by the prootic bone or the homologue of the upper part of the pars petrosa of man.

Notwithstanding the high authority of Meckel, Kölliker, Huxley and others, among whom may be mentioned the late W. Kitchen Parker, universally conceded while living to be the highest authority on all questions pertaining to the development and morphology of the skull, the three-fold development of the petro-mastoid portion of the temporal bone has been denied by anatomists and notably by the late Dr. Joseph Leidy.[17]

The author having had occasion recently to study the development of the temporal bone in Man has satisfied himself, at least, that the mastoid portion of the petrosal is not developed from a special centre of ossification but from the petrosal and squamosal portions of the temporal as described by Leidy,[18] and that there is no homologue, therefore, in the skull of Man, of the bone described as the epiotic in that of the lower vertebrata. Further, while there is no doubt that the petrosal part of the temporal in Man is developed, as we shall

[17] Science, Vol. 1. No. 18. June 8, 1883, p. 507.

[18] Op. cit. p. 507, Human Anatomy, 1889, p. 116.

see presently, from two distinct centres of ossification, these two centres, in the judgment of the author are not so exactly represented in the skull of the lower vertebrata that the names prootic and opisthotic can be given them.

At a period about the middle of the fifth month of intra-uterine life the temporal bone exhibits, according to the dissections of the author, three distinct ossifications: the squamosal, the tympanic and a ring surrounding the foramen rotundum of the otherwise cartilaginous labyrinth. A little later a second centre of ossification makes its appearance at the extreme end of the superior vertical canal. From these two centres of ossification, which we will name the upper and lower otic, as indicating their situation in Man, there arise, due to progressive ossification extending through the labyrinth, the pars petrosa and two-thirds of the pars mastoidea of the temporal, the remaining third of the latter being developed from the squamosal. From the lower otic ring-like ossific centre surrounding the foramen rotundum arise all that part of the pars petrosa seen beneath the cranium, viz.: the lower part of the cochlea, the promonotory, and lower part of the fenestra ovalis, the fenestra rotunda, the lower arm of the posterior semicircular canal, the lower part of the facial canal, jugular fossa, the carotid canal and the floor of the tympannum. From the upper otic ossific centre, (that appearing on the superior vertical canal) arise all that part of the pars petrosa seen within the cranium except that entering into the formation of the jugular fossa, viz.: the upper part of the cochlea including the cupola and the base, the internal auditory meatus, the upper part of the fenestra ovalis, the upper arm of the posterior and the superior and vertical semicircular canals, the upper part of the facial canal, the tegmen tympani.

The various structures just described as respectively produced from the two ossific centres having coalesced about the eighth month[19] or even earlier, to form the osseous labyrinth, there is developed as a continuous outgrowth of the latter the pyramidal and mastoid portions of the petrosal, the mastoid being formed more especially by outgrowths from the posterior and external semicircular canals. The outgrowth from the posterior semicircular canal appears as an "elliptical islet"[20]

[19] It should be mentioned in this connection that it is often impossible to determine exactly the age of a foetus, since foetuses of the same age vary as regards length, weight and development.

[20] "Epiotic," Huxley, Op. cit. p. 155.

(Fig. 3, 4, *e*), in the cartilage situated between the squamosal, parietal and occipital bones and constituting, therefore, part of the wall of the cranium. The elliptical islet having been developed, a second "quadrate" islet (Fig. 3, 4, *q*) now appears in the cartilage and more particularly in the part of it lying between the elliptical islet and the squamosal. The two islets, the elliptical and quadrate, subsequently uniting together form the mastoid portion of the petrosal. If the latter be developed in the manner just described then the "pyriforma" and "scutum ovale" of Kerckringius would be the parts described by Leidy as the "elliptical" and "quadrate" islets, since the former, like the latter, "coalescent in unum" but not to the prootic and opisthotic centres, since the latter are developed and coalesce before the islets even appear, and for the reason already given that it is the pyriforma or prootic and the scutum ovale or epiotic that unite according to Kerckringius, not the prootic and opisthotic.

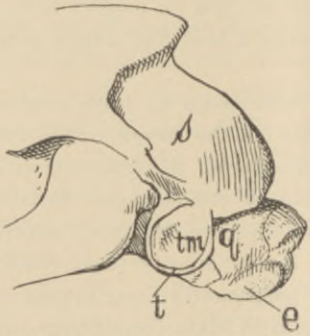

Fig. 3. Temporal bone of human foetus.

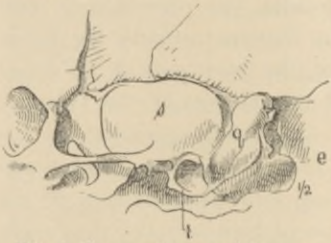

Fig. 4. Temporal bone of human foetus.

The third ossicle of Kerckringius, however, the "vix aciculæ majoris caput adaequans" corresponds to that part of the lower otic or opisthotic that, growing outward and backward, makes its appearance at the edge of the tympanic ring at an early period of intra-uterine life and which soon combines, as we have seen, with the upper otic or prootic to form the pars petrosa, the latter subsequently uniting with the squamosal to form the mastoid portion of the temporal.

Fig. 5. Upper anterior portion of skull of cod-fish.

If, however, there is no distinct mastoideus or epiotic centre of ossification in the temporal bone of Man what interpretation is there to be offered as to the homologies of the bones present in the fish and

turtle and described by Cuvier [21] as mastoideus and occipital externe, by Owen [22] as mastoid and paroccipital, and by Huxley [23] as squamosal and epiotic in the fish and squamosal and opisthotic in the turtle? In reply to such query, in the judgment of the author the bone, No. 8, (Figs. 5, 6, 7, 8) described by Cuvier as mastoidien and by Owen as mastoid in the skull of the lower vertebrates, should be regarded as it is by Huxley and most modern anatomists, as the homologue of the squamosal (Fig. 3, *s*) of the temporal of Man. The bone No. 4, (Figs. 5, 8, the occipital externe (perch) Cuvier, the paroccipital of Owen, the epiotic of Huxley in fish, opisthotic in turtle, is not, however, represented as a distinct bone in the skull of Man but as the "eminentia aspera"[24] of the occipital bone or the "scabrous ridge extended from the middle of the condyle towards the roots of the mastoid process."[25]

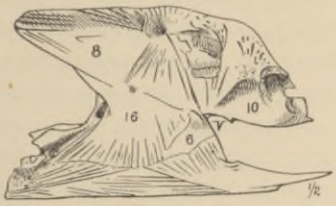

Fig. 6. Side view of skull of cod-fish.

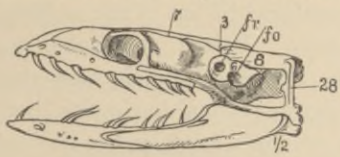

Fig. 7. Skull of python.

The name occipital externe, or its English equivalent external occipital, may as well then be retained for the bone No. 4 as simply expressing the fact that there exists in the skull of the lower vertebrates a bone lying external to the supra and ex-occipital irrespective of any preconceived hypotheses. The names paroccipital and epiotic should be discarded, as the former implies that the bone No. 4 is the parapophysis of the first cranial vertebra, the latter that it is the homologue of the special centre of ossification of the mastoid in Man.

It has been urged in favor of the bone No. 4 being called the epiotic in the fish that it enters into the formation of the ear-chamber, its inner surface being excavated for the reception of part of the posterior and external semicircular canal. Such argument, however, loses all force when it is remembered that the exoccipital is similarly

[21] Histoire Naturelle des Poissons, Tome 1, p. 236.
[22] Anatomy of Vertebrates, Vol. 1, p. 97.
[23] Op. cit. p. 174.
[24] S. T. H. Soemmering "De Corporis Humani Fabrica," T. I, 1794, p. 105.
[25] Alexander Monro. "The Anatomy of the Humane Bones," Edinburgh, 1732, p. 110.

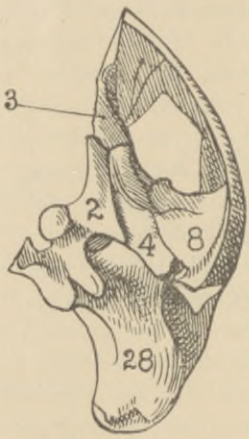

Fig. 8. Posterior view of skull of turtle.

excavated, and that the latter bone, together with the alisphenoid (prootic) petrosal (opisthotic) squamosal and post-frontal bones enter into the formation of the otocrane. It should be mentioned in this connection that the external occipital bone, No. 4, (Figs. 5 and 8), though presenting in the turtle the same characters and similar relations as in the fish, is usually described in that animal and in the alligator, etc., as the opisthotic bone, the epiotic being supposed then to be represented by an independent centre of ossification which, while distinct at an early period of life, later coalesces with the supra-occipital, No. 3+ (Fig. 9).

Even if such be universally the case it would only prove that either the supra-occipital develops in reptilia from two centres in the embryo, or that there exists a bone (epiotic) in the skull of reptiles that has no homologue in that of fish or Man, not that the bone No. 4 is the opisthotic. Indeed, as we shall see presently, there is no reason to believe that an opisthotic bone that is the supposed homologue of the rocher or petrosal in the fish (cod) of the lower part of the pars petrosa of Man exists in the skull of the reptile (turtle) at all.

Admitting that the petromastoid portion of the temporal bone in Man develops from two centres of ossification, it remains now to determine whether there exists in the skull of a cod-fish, snake, turtle or alligator the homologue of these two centres, two bones to which the names prootic and opisthotic can be appropriately given and which, taken together, represent therefore the pars petrosa of the of the temporal bone in Man.

In considering this question let us begin by first pointing out in what respect the bone No. 6, (Fig. 6) in the cod resembles and differs from the prootic or upper portion of the human pars petrosa, (Fig. 2, *p*). It resembles it in its inner concavity usually supporting the anterior part of the vestibule and the anterior vertical semicircular canal. It differs from it in not presenting a fenestra ovalis, a cochlear roof, osseous semicircular canals, internal auditory meatus or tegmen tympani, no such parts

being present in the cod, and in not transmitting the portio dura of the seventh nerve, the latter also not existing in the cod-fish.[26] If the bone No. 6 in the cod-fish be compared, however, with the great wing of the sphenoid in Man (Figs. 1, 2, *a*) it will be observed that it agrees with the latter (alisphenoid) in articulating with that part of the basi-cranial axis corresponding to the basi-sphenoid, and with the parietals in entering into the formation of the lateral wall of the cranium, supporting the mesencephalon, and in being notched anteriorly (perforated in the carp) for the transmission of the superior and inferior maxillary branches of the fifth nerve. The bone No. 6 in the cod differs from the alisphenoid in Man, as already mentioned, in supporting part of the membranous labyrinth and in the notch transmitting the inferior maxillary branch of the fifth nerve being situated in the anterior part of the bone rather than in the posterior part as is the case in Man.

In the consideration of the relative posterior of the notch *v* in the bone No. 6 in the fish and that of the foramen ovale in the alisphenoid of Man, (Fig. 2, *fo*), the fact appears to have been entirely lost sight of that the notch or foramen in the fish corresponds to two distinct foramina in Man: the foramen rotundum, (Fig. 2, *r*) and the foramen ovale, (Fig. 2, *fo*) transmitting respectively the superior and inferior maxillary branches of the fifth nerve, and that the part of the notch in the fish, (Fig. 6, V) corresponding to the foramen rotundum in Man, is situated anteriorly just as is the case in Man. The situation of the exit of the superior maxillary nerve is therefore substantially the same in the bone No. 6 in the cod (and absolutely so in the carp) as in the alisphenoid of Man. The objection that might still be urged that that part of the notch corresponding to the foramen ovale is situated anteriorly in the fish but posteriorly in

[26] The author is familiar with the view entertained by some anatomists that hyomandibular branches of the fifth nerve represent in the fish the branches of the portio dura of the seventh nerve or facial in Man. Such an interpretation is, however, untenable, being based upon the assumption that the quadrate bone (jugal caisse hypotympanic) in the fish is the homologue of the incus in Man, the articulare corresponding then to the malleus. As the quadrate and malleus are, however, developed as ossifications of the proximal ends of Meckel's cartilage (mandibular arch) the quadrate must be the homologue of the malleus, not the incus, if it be homologous with either of the ear bones. The hyomandibular bone (temporal mastoidien epitympanic) in the fish is homologous with the incus, these bones being developed through the ossification of the proximal ends of the hyoid arch. It must be admitted, however, that this last view leaves still unexplained why the articulare in the mandibular arch of the fish and the same bone together with the others entering into the formation of the lower jaw of the alligator are not represented in Man.

Man has no significance, since in Man and mammals generally there is always a small portion of the alisphenoid behind the foramen ovale, amounting, indeed, in the sheep to about one-half the bone.

The statement often made that the bone lying behind the exit of the fifth nerve is the homologue of the upper part of the human pars petrosa is simply not correct so far as concerns Man and mammals.

In view of the facts just mentioned some anatomists have considered the bone No. 6 in the fish as the homologue of the alisphenoid in Man and have so named it. Other anatomists, on the other hand, impressed with the fact that the bone supports a part of the membranous labyrinth, have regarded it as the homologue of the upper part of the human pars petrosa and called it accordingly prootic. In the judgment of the author an insuperable objection to accepting the latter view is that it involves the inevitable but absurd conclusion that its homologue, or the prootic portion of the pars petrosa, must transmit the superior and inferior maxillary branches of the fifth nerve. On the other hand, it might be urged that the bone No. 6 can not be the homologue of the alisphenoid in Man since the latter never supports any part of the membranous labyrinth.

In reply to the latter objection, though at the risk of committing a petitio principii, the author must say that it is just in this respect that the skull of the cod-fish differs from that of Man: The bone No. 6, in the fish, the homologue of the alisphenoid in Man, protects the anterior part of the labyrinth as is done by the upper part of the human pars petrosa, the difference being conditioned by the part of the membranous labyrinth being relatively enormously developed in the fish, the osseous covering but little so, whereas in Man the labyrinth is but little developed while the pars petrosa is much so.

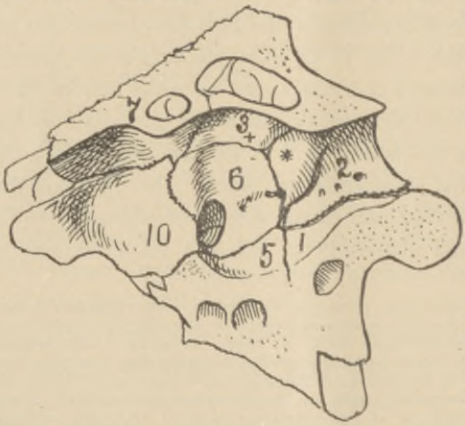

Fig. 9. Interior view of auditory region of alligator.

If this view be correct then the bone No. 6 in the fish must be regarded as the homologue of the alisphenoid in Man

and the name given to it by Cuvier of grand aile or its English equivalent alisphenoid (Owen) retained.[27] If the bone No. 6 in the skull of the python (Fig. 7), turtle (Fig. 10), alligator (Figs. 9, 11), be compared with that so numbered in the cod-fish (Fig. 6), it will be found that while it resembles the latter in articulating with the basisphenoid and parietal bones, entering into the formation of the lateral wall of the cranium, presenting a notch or foramen for the transmission of the superior and inferior maxillary branches of the fifth nerve and protecting the anterior part of the organ of hearing, it differs from it in transmitting the filaments of the portio dura and mollis of the seventh nerve and in forming the anterior half of the fenestra ovalis of the vestibule.

In the latter respects, and in protecting the anterior part of the labyrinth, the bone No. 6 in the reptile certainly resembles

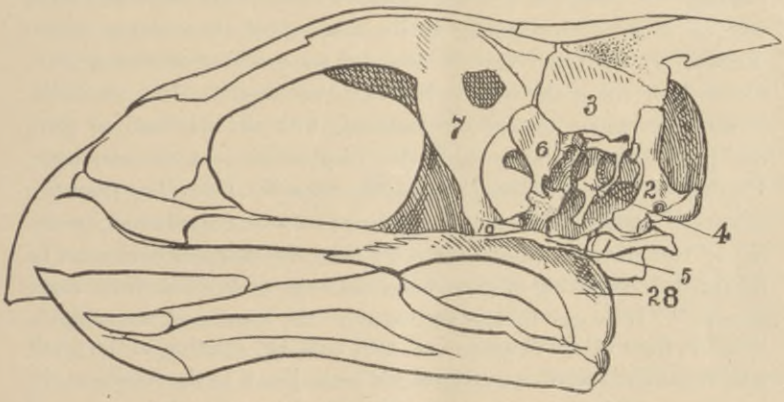

Fig. 10. Interior view of auditory region of turtle.

the upper or prootic part of the human pars petrosa and would be more appropriately named, therefore, the prootic than the bone No. 6 in the fish. The fact, however, of this bone in the reptile transmitting by notch or foramen[28] the maxillary branches of the

[27] It should be mentioned in this connection that there are present in the skulls of certain fishes (salmon and carp) three bones which have been regarded as the prootic, alisphenoid and orbito-sphenoid. As the latter bone, the most anterior of the three, is, however, inconstant and as we regard it when present as an interorbital bone, not the orbito-sphenoid, its presence or absence will not affect the argument as stated above, the so-called prootic in the carp, for example, being the alisphenoid, and the alisphenoid being the orbito-sphenoid.

[28] It will be observed in the case of the python (Fig. 7) that the two foramina in the bone No. 6 are as well marked as the foramen rotundum and foramen ovale are in the alisphenoid of Man.

fifth nerve is irreconcilable, as in the case of the fish, with the idea that it is the homologue of the upper prootic portion of the human pars petrosa. On the other hand, if the bone No. 6 in the reptile be regarded as the homologue of the alisphenoid in Man the difficulty presents itself that the former enters into the formation of the fenestra ovalis and transmits in the reptile the filaments of the facial and acoustic nerves, which the alisphenoid of Man never does, the fenestra rotunda and the nerves being confined to the pars petrosa. With the view of reconciling these difficulties the bone No. 6 in the reptile has been regarded by some anatomists as consisting really of two bones fused into one, the anterior and posterior parts being viewed respectively as alisphenoid and prootic bones.

The study of the development of the reptilian skull offers some confirmation of this view, since as a matter of fact, according to Parker,[29] the bone No. 6 in the snake develops from two centres, the anterior of which is regarded as the alisphenoid, the posterior as the prootic. If the latter view be accepted the result of development in the skull of the snake is very different from that in Man, since the prootic ossification, instead of combining with the opisthotic to form the pars petrosa, unites with the alisphenoid to form one bone. Further, it does not follow because the bone No. 6 develops from two centers of ossification that it must necessarily be regarded as consisting of two distinct bones, any more than the basi sphenoid must be regarded as consisting of three bones because it develops from three centres.[30] It seems to the author that the view most reconcilable with the facts of development as well as those relating to the adult condition of the skull is to regard the bone No. 6 in the reptile as the homologue of the bone so numbered in the fish and of the alisphenoid in Man.

In the absence of a pars petrosa in the skull of the reptile and bird some other bone or bones must fulfil the functions of that bone in supporting and protecting the labyrinth and in transmitting the facial and acoustic nerves. These functions are filled in the reptile more or less by the bones Nos. 6, 4, 2, 3, which we regard as the alisphenoid, external occipital, ex-occipital and supra-occipital, or,

[29] The Morphology of the Skull, London, 1877, p. 204.

[30] One for the median basisphenoid, two for the symmetrical basitemporals, the homologues of the lingulae sphenoidales of Man.

in regard to the latter more particularly, its inferior and internal part (epiotic),[31] No. 3 + (Fig. 9).

There remains now for consideration the question as to how much of the lower portion of the human pars petrosa is represented in the skull of the lower vertebrata. In other words, is there any distinct bone in the skull of the lower vertebrata to which the name opisthotic can be appropriately given? In the skull of the cod-fish, as in that of the Gadidae generally, there exists, though often but little developed or even absent in many fishes, a large and conspicuous bone, No. 16, (Fig. 6) which articulates with the basi-occipital, basi-sphenoid, ex-occipital, par-occipital, squamosal and alisphenoid bones and forms the posterior lateral wall of the cranium. This bone, No. 16, on account of supporting that part of the membranous labyrinth containing the otolithes has been usually regarded by anatomists (Cuvier, Owen, Huxley) as corresponding to the whole of the human pars petrosa or at least to some part of it, and has been accordingly named rocher, petrosal, opisthotic, etc. In the fish the labyrinth, however, is not exclusively and entirely enclosed by a special osseous covering as in Man. The cavity enclosing the organ of hearing is formed not only by the bone No. 16, but by the alisphenoid, ex-occipital, par-occipital, squamosal and post-frontal bones as well. It opens widely into the cranial cavity. It presents nothing comparable to the fenestra ovalis and fenestra rotunda of the pars petrosa. Such being the case it is impossible to determine whether the bone No. 16 in the fish represents the whole, or only a portion and more particularly the lower or opisthotic portion of the human pars petrosa. The author would therefore prefer to call the bone No. 16 in the fish simply the rocher or its equivalent, the petrosal, as indicating the probability of it corresponding to some part of the human pars petrosa.

The term opisthotic is objectionable as not only implying that the bone No. 16 in the fish corresponds to the lower or opisthotic part of the human pars petrosa, for which view there is no evidence, but further, for the reason already given that it is the bone No. 4 in the fish, not the bone No. 16, that is the homologue of the external occipital, the so-called opisthotic in the turtle. Indeed, the bone No. 16 of the fish does not appear to be represented as such either in

[31] Even Parker admits that "in some forms the periotic bones do not arise separately, but the supra-occipital and ex-occipitals extend into the epiotic and opisthotic regions respectively." Op. cit. p. 349.

the reptile or in the higher vertebrata. In some respects it is a peculiarly ichthyic bone though not invariably present even within the limits of the class, as already mentioned.

The ear-chamber in reptiles is more or less closed, internally at least, in the adult condition by three bones separated by a Y-shaped suture distinctly visible in the longitudinally divided skull (Fig. 9). The two lower, No. 2, 6, (Fig. 9,) of the three bones are situated on either side of the vertical stem of the Y-shaped suture, the third remaining bone No. 3 within the diverging branches of the latter. Externally the osseous vestibule presents a fenestra rotunda *fnr* (Fig. 11), situated entirely within the bone No. 2 and a fenestra ovalis, *fno*, the posterior half of which is formed by the margin of the bone just mentioned, the anterior half by that of the bone No. 6. The membranous labyrinth consists of a vestibule, semicircular canal and, in the turtle and alligator, of a rudimentary cochlea. The fenestræ are closed by membranes in the living animal and to that of the fenestra ovalis is attached a columellar-like bone which, on account of being connected with the membrana tympani, is regarded as the homologue of the stapes of the human ear. The membrana tympani is attached in turn to bone No. 28, (Figs. 7, 10) usually called the quadrate and regarded as representing either the tympanic bone or the malleus in Man.[32]

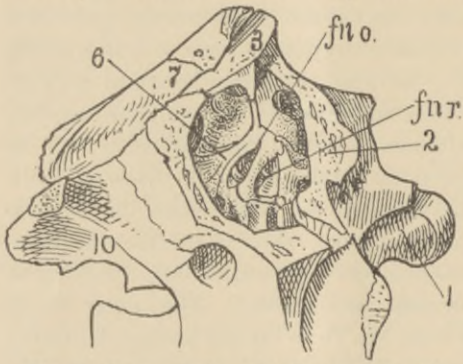

Fig. 11. External view of auditory region of alligator.

The tympanic membrane being so superficially situated, neither external auditory meatus nor external ear can be said to exist in reptiles. The nearest approach to an external ear is seen in the crocodilia which are provided with two cutaneous folds situated just

[32] Some of the reasons that may be regarded in favor of accepting the latter hypothesis as the correct one have already been stated.

outside the membrana tympani which, when approximated, close the entrance thereto. In the crocodilia each tympanum (Fig. 12, T) is not only provided with its own lateral Eustachian tube proper, LE, but the two tympana communicate directly with each other superiorly by means of a passage traversing the supra occipital bone, S, and inferiorly by anterior lateral passages, C, descending from the floor of the tympanum into the anterior branch, A, of median Eustachian tube, ME, situated just behind the posterior nares and indirectly by posterior lateral passages, B, given off on either side from the lateral Eustachian tubes proper, LE, and terminating in the posterior branch, P, of the median Eustachian tube, ME. Further passages extend from each tympanum, Q, through the quadrate, thence by a membranous tube into the articulare of the lower jaw.[33]

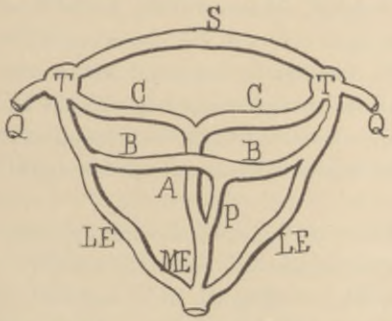

Fig. 12. Diagram of tympanic canals of alligator.

In the turtle the most posterior of the two lower bones entering into the formation of the ear-chamber is a distinct bone, No. 4, (Fig. 10), and, for reasons already given, is regarded by the author as homologous with the external occipital of the fish and is therefore similarly numbered and named. In the lizard, python and alligator the functions of the external occipital bone of the turtle, No. 4, (Fig. 10), are, however, filled by what appears, in the adult skull at least, to be a part of the ex-occipital bone, No. 2*, (Fig. 9). At an early period of development in the snake and possibly in all reptilia, this part of the ex-occipital exists as a distinct bone, notwithstanding that in later life it may have coalesced to such an extent with the ex-occipital that its original distinctness is entirely lost. If such be the case, which is not at all improbable, then that part of the ex-occipital in the alligator, No. 2*, (Fig. 9), entering into the formation of the internal ear-chamber, should be regarded as the homologue of the external occipital No. 4, (Fig. 10), in the turtle. The only essential

[33] Windischmann. De Penitiori auris in Amphibiis structura, 1831.
Owen, Phil. Trans., 1850.
Stannius, Handbuch der Zootomie, Zweite Aufl., Zweites Buch, 1856, pp. 58, 164.

difference in the two would then be that in the alligator the external occipital coalesces with the ex-occipital, whereas in the turtle it remains a distinct bone throughout life. It will be observed, however, whether the osseous part in question be regarded as an outgrowth of the ex-occipital or as a distinct bone coalescing with the latter, that in neither case would the name opisthotic be appropriate, since this bone or part, being homologous with the external occipital, should be so named.

It has already been mentioned that that part of the supra-occipital entering into the formation of the ear-chamber is said to be developed from a special centre of ossification, No. 3 + (Fig. 9), and in accordance with the idea of it being the homologue of the epiotic centre of the human mastoid, named the epiotic. As there is no reason, however, for supposing that such a third centre of ossification exists, even if the part in question be characteristic of reptiles, the name epiotic should be discarded because it is misleading. Finally, as the author regards the bone No. 6, (Figs. 6, 7, 9, 10), not as the prootic but as the homologue of the alisphenoid in Man, (Figs. 1, 2, *a*), there is no reason for retaining the names prootic, opisthotic and epiotic.[34]

Indeed, the periotic bones, or bone so named, should not be regarded as constituting any part of the proper cranial wall but as special ossifications of the ear-chamber depending upon the extent of the development of the organ of hearing.

In a general way it may be said that the transitory conditions through which the human ear passes in the course of its development are more or less permanently retained as such in the organ of hearing in the lower vertebrata. Such being the case we cannot expect to find the protective osseous covering of the ear in the higher vertebrata equally well developed in the lower ones. On the contrary, in proportion as the ear is undeveloped, we may expect to find any of the adjacent bones forming the wall of the cranium protecting and entering into the formation of the ear-chamber, just as the tympanum is formed in birds by the basisphenoid, squamosal and ex-occipital rather than by the pars petrosa as in Man. There is no more reason for supposing that there is an archetypal temporal bone,

[34] The author does not refer to the skulls of birds, since the latter being specialized reptiles the disposition of the parts in question, as might be expected, is essentially the same.

It should be mentioned, however, that the membrana tympani is not attached in birds to the quadrate bone as in reptiles but to the outer margin of the tympanum.

the different parts of which must exist in all vertebrata, than for believing that there is an archetypal vertebra and that the skull must consist of several of the same, at least in a Goethe-Oken sense.

It does not follow, however, because a difference ot opinion may prevail among morphologists as to the special homologies of certain of the bones of the head that there should be any question as to the truth of the general doctrine of the unity of organization of the skull, so firmly established by Cuvier and others.

On the supposition that the higher vertebrata have descended from the lower, it is to be expected that the general structure of the skull should be the same in both, the fundamental characters of the skull of the former having been acquired by inheritance from that of the latter. On the other hand, the skull should present greater or less modifications according to the special nature of the different vertebrata, such modifications being induced by the causes of variation incidental to different kinds of life.

The skull, like the organism in general, is not made according to a Platonic idea or pattern, but grows, its characters being acquired by inheritance as modified by variation.

Synonyms of Certain of the Bones of the Head According to French, German and English Anatomists.

Cuvier (1).	Meckel (2).	Owen (3).	Huxley (4).	
Occipital latéral.	Seitliches unteres Hinterhauptbein.	Ex-occipital.	Ex-occipital.	2
Occipital supérieur (perch reptiles and birds).	Hinterhauptschuppe.	Superoccipital	Supraoccipital.	3
Occipital externe (perch, reptiles), apophyse mastoid (mammals).	Seitliches oberes, Hinterhauptbein.	Paroccipital.	Epiotic in fish, Opisthotic in reptile.	4
Grand aile (fishes, birds, mammals), rocher (reptiles).	Felsenbein (fishes and reptiles), Grosserkeilbeinflügel (birds and mammals).	Alisphenoid.	Prootic.	6
Mastoidien (fishes and reptiles), temporal (birds and monotremes).	Zitzenbein.	Mastoid.	Squamosal.	8
Aile orbitaire.	Grosserkeilbeinflügel.	Orbitospenoid.	Alisphenoid.	10
Rocher (fishes, birds and mammals).	Felsenbein (fishes).	Petrosal.	Opisthotic.	16
Jugal.	Jochbein.	Malar.	Jugal.	26
Temporal (lizards, crocodiles and mammals), Jugal (birds, monotremes).	Schläfenbeinschuppe.	Squamosal.	Quadrato-jugal.	27
Caisse (ophidia, crocodiles, mammals), Os tympanique (lizards), Os carré (birds).	Pauke.	Tympanic.	Quadrate.	28
Temporal (fishes), Tympanique (batrachia).	Oberesgelenkbein.	Epitympanic (fishes).	Hyomandibular (fishes).	29
Symplectique (fishes).	Griffelförmiges, Stück des Schläfenbeins.	Mesotympanic (fishes).	Symplectic (fishes).	30
Tympanal (fishes).	Scheibenförmiges Stück des Schläfenbeins.	Pretympanic (fishes).	Metapterygoid (fishes).	31
Jugal (fishes and batrachia).	Unteresgelenkbein.	Hypotympanic (fishes).	Quadrate (fishes)	32
(1)	(2)	(3)	(4)	
Lecons d'Anatomie Comparée. Régne Animal. Histoire Naturelle des Poissons. Ossements Fossiles.	System der vergleichenden Anatomie.	Archetype of Vertebrate Skeleton. Anatomy of Vertebrates.	Elements of Comparative Anatomy Manual of the Anatomy of Vertebrated Animals.	