fortune to examine. On this account I have found it desirable to describe it in considerable detail.

In comparison with other members of the Insectivora, the skull (figs. 1 and 2) is remarkably broad and flat when viewed from above, approaching in this respect many of the Rodentia, and exceeding that of *Galeopterus* or *Myrmecobius*. When seen from the side its vertical depth in front of the orbits is much reduced, and the whole area of the top of the skull is wedge-shaped, with a more or less pointed extremity in front. The nasals are relatively short, being less than one-third the length of the skull, and at their anterior free extremities are thickened, and flared upwards; a little behind the center they are widened somewhat, and still behind this they terminate in sharp

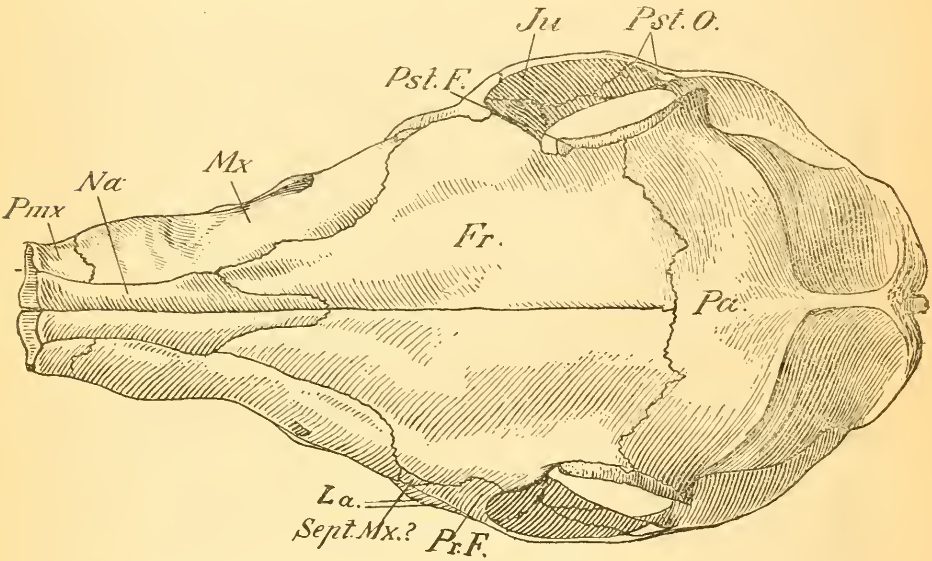

FIG. 1.—RYNCHOCYON PETERSI. NO. 182561, U.S.N.M. *Fr.*, FRONTAL; *Ju.*, JUGAL; *La.*, LACHRYMAL; *Mx.*, MAXILLARY; *Na.*, NASAL; *Pa.*, PARIETAL; *Pmx.*, PREMAXILLARY; *Pr. F.*, PREFRONTAL; *Pst. F.*, POSTFRONTAL; *Pst. O.*, POSTORBITAL; *Sept. Mx.*? SEPTOMAXILLARY. × 2.

points where they articulate with the frontals. The premaxillaries are short and do not send processes backward alongside the nasals but a short distance. Like the nasals, where they form the boundary of the anterior narial opening, they are everted or flared outward and at the point of junction with the nasals are somewhat thickened. This thickened border undoubtedly serves for the attachment of the unusually long cartilaginous snout, which is so common a feature of the Insectivora. The maxillaries form nearly the whole of the side of the face, which is separated from the top of the skull by a rather sharp angulated border. The infraorbital opening is large and issues just above the anterior border of the first molar. Behind this the face is deeply concave from above downwards, the concavity extending backwards underneath the prominent and flaring edge of the orbital cavity. At the posterior end of the maxillary, commencing above the anterior border of the second molar, is the unusually prominent masseteric ridge, which extends backwards on the underside of the jugal arch as far as the back of the orbit. The frontals entering into the formation of the top of the skull are unusually broad; they reach their greatest breadth where they join the lachrymals near the anterior border of the orbit, and terminate in front in pointed extremities which are received between the nasals and premaxillaries. Behind they articulate with the parietals by a gently curved suture, whose

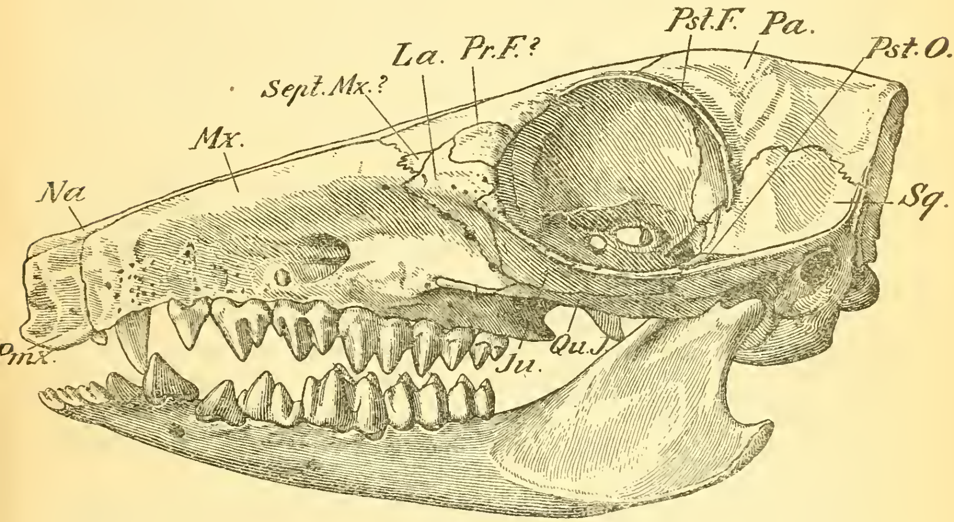

FIG. 2.—RYNCHOCYON PETERSI. *Qu. J.*, QUADRATOJUGAL; *Sq.*, SQUAMOSAL. × 2. (OTHER LETTERS AS IN FIG. 1.)

concavity is directed forwards, and upon the upper border of the eye cavity they are deeply notched.

The parietals, like the frontals, have an unusual breadth and are rather short from before backwards; they articulate in front with the frontals and behind with the occipital, quite in the usual way in the mammalian skull. There is a short inconspicuous sagittal crest, from the anterior end of which diverge two faint ridges passing almost directly outwards to the tips of the postorbital processes. These ridges, together with the occipital crest behind, are of importance as marking the area of attachment of the temporal muscle, and serve to delimit rather sharply the *temporal area,* of which more will be said later. The outstanding feature of the parietals is that they are produced upon either side into strong depending processes, which furnish the upper posterior boundary of the orbital cavity. The presence of a postorbital process is not unusual in the skull of the mammal, but in all other forms in which it is present, as far as I am aware, it is furnished by the frontal and not the parietal. It may arise at the junction of these two bones on the edge of the orbit, and the parietal may contribute a share in its formation, but *Rhynchocyon* is the only form that I know in which the postorbital is furnished exclusively by the parietal. In conjunction with this unique formation of the postorbital process there is another still more remarkable structure to be noted just at this point. On the rim of the orbit, reaching from the supraorbital notch of the frontal, and extending well down toward the tip of the postorbital process, is a long slender bone separated by distinct sutures on either side of the skull from both the parietal and frontal. This extra bone therefore forms the free projecting edge of the orbital rim and overlaps the junction between the frontal and parietal where they meet above the eye. In the specimen before us these bones are symmetrically developed upon the two sides of the skull.

The occipital surface is well separated from the sides and top of the skull by a well-defined though not unusually prominent occipital crest. The foramen magnum is relatively large and the condyles well separated. There is no trace of a paroccipital process. From the center of the occipital crest a sharp spinous ridge descends toward the foramen magnum, corresponding to the nuchal spine and serving for the attachment of the nuchal ligament. There is a considerable exposure of the mastoid portion of the periotic on the postero-lateral aspect of the occipital region, which extends as high up nearly as the top of the squamo-parietal suture.

Of the orbital cavity and the formation of the zygomatic or quadrato-jugal arch, there are some points of unusual interest and importance to note. The squamosal is of fairly good size, and extends well up on the side of the brain case, overlapping the edges of the parietal in the usual manner. The posterior root of the zygoma forms a wide concave projection behind the eye cavity, and passes backwards to become continuous with the descending branch of the occipital crest. In front it is produced into a relatively stout process, which articulates directly in advance of it with the bone which runs forward to the maxillary. It does not override this latter bone in its articulation, but abuts against it, being received into a more or less V-shaped pocket.

One of the most remarkable features in the composition of the jugal arch is the presence of a separate and distinct bone, lying near the anterior end of the zygomatic process of the squamosal, at its junction with the element in advance of it already mentioned. It is of an elongated splintlike form, extending forwards toward the maxillary and resting upon the two elements below it, presently to be described. It terminates behind in a more or less trihedral swelling or process, which rests upon the anterior end of the zygomatic process of the squamosal and forms the postorbital process of the jugal arch, for the attachment of the postorbital ligament, which connects the tip of the postorbital process of the parietal with the zygoma, thus completing the posterior boundary of the eye cavity.

Immediately in advance of the bone just mentioned is a broad, thin concave bone which forms the principal part of the floor of the orbit upon the outer side. It is thin and extended outwards in such a manner as to give a characteristic flare to the lower and anterior portion of the floor of the eye cavity. In front it touches the maxillary and is continued forwards to articulate with the lachrymal, thus forming the anterior lower free rim of the orbit.

No less astounding in the formation of the jugal arch of this remarkable skull is still another element, which occupies a position upon its under surface. It articulates in front with the maxillary, sending a long pointed process forwards upon the outer side of this latter bone at the masseteric ridge, and extending backwards on the underside of the zygoma, beneath the zygomatic process of the squamosal. In its backward extension it reaches the glenoid cavity, and takes almost as great a share in its formation as in the Marsupials. Upon its under surface it is produced into a well-defined sharp ridge, which is a direct continuation of the prominent masseteric ridge or process of the maxillary. Above it is in contact with the so-called malar or jugal, and the small bone which forms the postorbital process of the jugal arch already described.

The anterior boundary of the orbit is formed principally by the large lachrymal, which spreads out upon the face, and articulates below with the malar, upon the orbital rim. Above, it articulates with the frontal, and in front with the maxillary. Within the orbital cavity it has the usual relations found in the Macroscelididae, and is perforated by a large lachrymal foramen situated entirely within the orbit. Lying at the angle of junction between the maxillary, frontal, and lachrymal, upon the side of the face, at some distance from the edge of the orbit, is another small bone which is not common in the mammalian skull. It is of a triangular form, with a relatively long pointed extremity, extending backwards between the frontal and lachrymal, and is equally and symmetrically developed upon the two sides of the skull.

Near the middle of the lachrymal, on the anterior edge of the orbit, is seen the remains of a suture, which runs forwards more than half the length of the bone and then ceases in such a way as not to divide the lachrymal completely, nor to complete the boundary of another element. No distinct traces of this suture can be made out, however, on the inside of the eye cavity, and if the lachrymal was really divided into an additional segment it will require a younger stage of the skull to establish the fact beyond question.

As it is not the object of the present study to go into the question of the relationship of *Rhynchocyon* and its allies, I shall omit a description of the base of the skull, teeth, etc. The lower jaw, however, displays several features which come within the scope of the present study, and I here call attention to them. The back part of the jaw has a very characteristic and peculiar appearance, which is not at all usual in the Mammalia. This is seen in the eversion or outward twist of its angular portion, the long backward slope of the ascending portion of the ramus, the very small coronoid, and the unusually high position of the condyle. The condyle has its greatest development in a transverse direction and is convex from before backwards. That which is of the greatest interest, however, is what appears to be an indistinct suture, separating the articular surface or head of the condyle from the rest of the bone, as if it were an epiphysis. This suture, if it is really the remains of one, follows the limits of the articular surface closely in front, but is not so evident behind. In a like manner, upon the inner surface of the jaw situated just below the opening of the inferior dental canal is a small sunken tubercle or bony knob, well marked off by a distinct fissure, resembling the remains of a suture and connected behind by a distinct groove, which extends backwards to the edge of the jaw just below the angle. This groove when examined carefully has the appearance of being the remains of a suture, but this may be deceptive. It may be said of both of these peculiarities of the jaw that they are symmetrical or exactly alike in the opposite halves.

Cercoctenus and other Macroscelididae.—The first of these genera is represented by some 32 skulls of all ages, of the species *Cercoctenus sultana*. In this species the lachrymal has a small though distinct preorbital extension with the opening of the lachrymal canal within the orbital cavity. On the rim of the orbit it is produced into an unusually prominent *crista orbitalis*, which is greatly augmented by the addition of two flattened plate-like ossicles, articulating by their applied edges, with its superior and outer border. The upper of these ossicles, which is the smaller of the two, lies at the junction of the lachrymal with the frontal, and the lower or larger, articulates with the lachrymal and malar near the point where these two bones join.

The lachrymal has the usual form and relations in this group of Insectivores, articulating above with the frontal, in front with the maxillary, on the rim of the orbit with the malar, and within the eye cavity with the palatine, maxillary, and frontal. The presence of these ossicles here described, together with the prominent *crista* to which they are attached loosely by suture, give a characteristic winglike appearance to the anterior part or edge of the orbital cavity not seen elsewhere among mammals.

Of the 30 or more skulls of this species in the collection, all of them without exception show the presence of these bones, where they have not been scraped away or detached in the course of preparation. Even in those skulls in which they have been lost, the thickened and roughened edge of the *crista*, however, gives ample evidence of their having been present in the fresh state, and I conclude, therefore, that their occurrence is a constant and well-marked feature of this species. Of the 20 specimens out of 32 in which these ossicles are preserved there appears to be little variation, either in the size or position which they occupy on the edge of the orbit.

At least one of these ossicles is found in the same position on the border of the lachrymal, as just described in *Cercoctenus sultana,* in one of the three skulls of *Petrodromus tetradactylus* in the collections; but there can be little doubt from appearances that it was originally present in all three cases, but has been subsequently lost in preparation. I am unable to say just what degree of constancy it has in the skull of this species, but it is not altogether unlikely that it is very generally present. In a like manner in a single skull of *Macroscelides,* there is one of these ossicles present upon one side with evidence that it has been lost from the other. In the remaining genera, *Nasilio* and *Elephantulus,* these ossicles are occasionally present, but it is always as a very thin and weak spicule of bone. Just to what extent its absence may be due to faulty preparation I am unable to say, but I am of the opinion that careful investigation will show its frequent presence.

None of the preceding genera exhibits any of the remarkable characters of the jugal arch of *Rhynchocyon,* above described. The skull is high and narrow in front of the orbits, the nasals are long and narrow, and the premaxillae send long-pointed processes backwards between the nasals and maxillaries. There is no postorbital process of either frontal or parietal above, and but a very faint indication of a postorbital process of the jugal arch, which is weak and slender. In the lower jaw the ascending portion of the ramus rises more abruptly, but the condyle is placed high above the tooth row, and the coronoid is small as in *Rhynchocyon.*

Skull of Tupaia.—In the species of this genus the skull has a very considerable interorbital width, as in *Rhynchocyon;* the snout is long and pointed, but the brain case is much more capacious, and as a consequence the upper part of the cranium is more rounded. The postorbital process above (fig. 3), while not as primitive as that of *Rhynchocyon,* is, however, in a stage of development not far removed from it; it apparently arises from the frontal, as a long slender strip of bone, is directed backwards and outwards, being closely applied to the parietal for a considerable distance, and passes down behind the eye cavity to join the ascending process of the postorbital process of the jugal arch, with which it becomes continuous, and in old individuals firmly united by suture. The orbital cavity is thus completely encircled by bone, by the completion of its posterior boundary.

In studying a number of young skulls of the various species of *Tupaia* and allied genera the postorbital process of the frontal is found to be always separated from the frontal for a considerable distance forwards, almost as far, in fact, as the supraorbital notch, which in this group is converted into a foramen; and while I have never seen it completely separated from the frontal, there is every reason to believe, and I am fully convinced that younger specimens will show, that it exists as a separate bone, ossifying from a separate and distinct center. If this is true, then it follows that it is strictly homologous with, and corresponds to, the element in this position

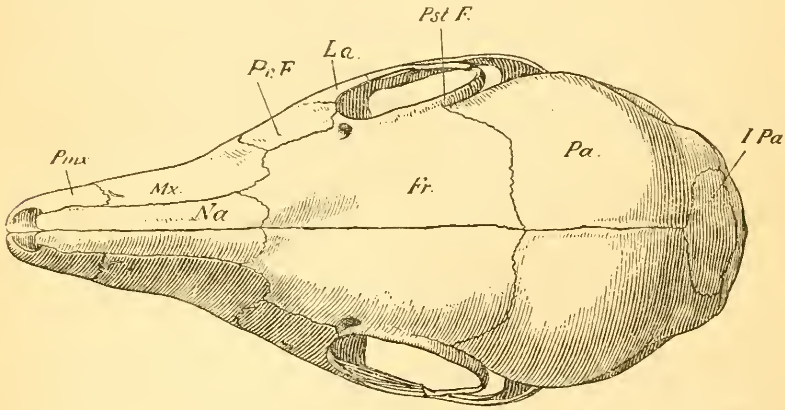

FIG. 3.—TUPAIA. *Fr.*, FRONTAL; *I. Pa.*, INTERPARIETAL; *La.*, LACHRYMAL; *Mx.*, MAXILLARY; *Na.*, NASAL; *Pa.*, PARIETAL; *Pmx.*, PREMAXILLARY; *Pr. F.*, PREFRONTAL; *Pst. F.*, POSTFRONTAL. × 2.

in the skull of *Rhynchocyon,* just described. The temporal area is somewhat larger than in *Rhynchocyon* and is sharply delimited by the diverging branches of the sagittal crest, which is very little developed even in aged individuals. The share which the squamosal takes in the formation of the outer wall of the brain case is small, and the considerable exposure of the mastoid portion of the periotic upon the postero-lateral aspect of the skull, rises well above the squamo-parietal suture. There is no paroccipital process.

The jugal arch of *Tupaia* offers some points of unusual interest. The most striking feature, at first glance, is the presence of a large foramen, fenestra, or vacuity, piercing the arch below and slightly in advance of the postorbital process of the zygoma, as it rises up to meet the corresponding process from above. Among the Insectivora this vacuity is peculiar to *Tupaia* and the closely related genera, in which it is usually very large and roomy, but is reduced to a small foramenlike aperture or may be entirely wanting in *Ptilocercus*. It is usually well developed in all the Primates, where it varies in size from a large fenestra to a small foramen, or complete absence.

That which is of the greatest interest in connection with this vacuity in *Tupaia* is the occasional presence of a well-defined suture, in young skulls, dividing the narrow rodlike upper boundary near its middle and a suture separating its posterior boundary, just in advance of the suture between the squamosal and jugal. This, it will be seen (fig. 4), cuts off a separate more or less T-shaped bone, with the short stem forming the upper back part of the boundary of the fenestra and two prongs curved slightly upwards, one rising up to meet the postorbital process from above and the other passing forwards on the upper border of the fenestra towards the lachrymal. Again in many young

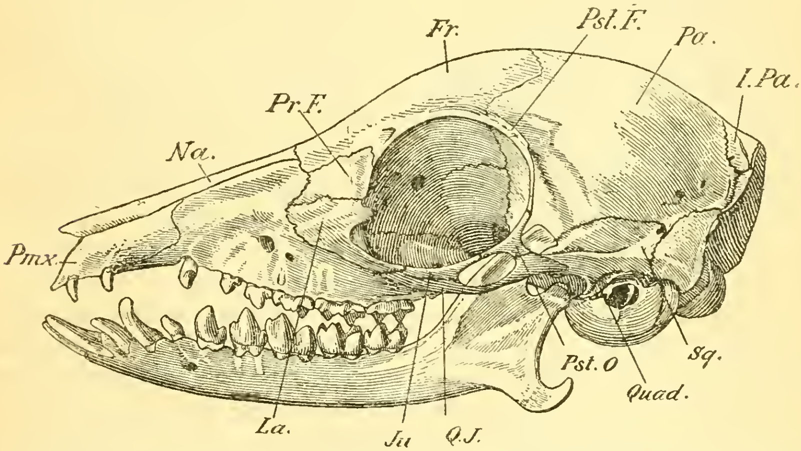

Fig. 4.—Tupaia. *Fr.*, frontal; *I. Pa.*, interparietal; *Ju.*, jugal; *La.*, lachrymal; *Na.*, nasal; *Pa.* parietal; *Pmx.*, premaxillary; *Pr. F.*, prefrontal; *Pst. F.*, postfrontal; *Pst. O.*, postorbital; *Q. J.*, quadratojugal; *Quad.*, quadrate; *Sq.*, squamosal. × 2.

skulls there is what appears to be the remains of a suture running forwards from the anterior border of the fenestra to the maxillary, just below the lachrymo-malar articulation. In no case that I have seen is this suture distinct and clearly defined, but the frequent appearance of a line as if indicating the union of separate ossific centers, points to the existence of separate pieces in the younger stages of development. It may be said of all these sutures above described that their presence is only occasionally indicated in skulls young enough to show the main sutures, but, taken in connection with what we shall presently learn of the development of the human malar, they assume an unusual importance and significance.

What I take to be easily one of the most important of all these newly discovered elements in the skull of the Insectivora is the presence in *Tupaia* and other forms of a small though perfectly distinct, pointed, more or less rod-like bone, lying upon the inner side of the postglenoid process of the squamosal and the back and inner side of the glenoid articulation. In *Tupaia* it occupies a deep groove at the outer base of the tympanic bulla between the bulla and the base of the squamosal, just in front of the external auditory meatus, and passes forwards and outwards projecting with a free extremity towards the tip of the pterygoid plate of the sphenoid, with which in the recent state it is connected by a separate and distinct ligament. Behind, it passes under or to the inside of the delicate tympanic ring, to overlap the *processus gracilis* or *processus foliatus* of the malleus. In old specimens it is doubtful if it exists as a distinct bone, but has every appearance of fusing with the tympanic ring with little or no trace of the suture left. Just what its relation to the malleus is in old or fully adult specimens I have not been able to determine with certainty, but it appears to remain free. Even in the younger stages it is closely connected to the *processus gracilis* by ligamentous attachment and requires careful investigation to separate it.

There is one other feature of the skull of *Tupaia* which is more reptilian-like than in any other mammal I have seen, and that is the relatively wide separation of the exit of the seventh and eighth pairs of cranial nerves as they enter the periotic. Of the two apertures, that for the seventh or facial nerve is placed above and a little in advance of the lower aperture, the two being separated by a ridge—the *falciform crest* of human anatomy. The foramen for the exit of the seventh nerve has a more or less oval form placed somewhat obliquely, of which the anterior lower part accommodates the facial and is thus the beginning of the fallopian canal, and an upper back part, the office of which I can not now state. On the falciform crest there is a distinct foramen which probably transmits the internal auditory artery. The opening for the eighth or auditory nerve is relatively large and at the bottom cribriform for the passage of the nerve filaments.

Other Insectivora.—Among the Erinaceidae I have been able to find but a single example, and that of a species of *Gymnura*, in which the jugal arch shows any extra elements in the adult stage. In all of them the zygoma is fairly well developed, but the jugal or malar portion is relatively short, occupying the middle part of the arch. There is but a faint indication of a postorbital process of the zygoma, and no postorbital process of the frontal or parietal. In the specimen referred to above (No. 114551) the jugal is divided by a longitudinal suture near the middle into an upper and lower moiety, and having about the same relations to the surrounding bones as in *Rhynchocyon*.

In *Gymnura* (fig. 5) the bone which has been described in *Tupaia* as occupying a position at the junction of the tympanic with the squamosal, just in advance of the external auditory meatus, is relatively larger than in the latter genus, is flattened and more or less lozenge-shaped; it is pointed at either extremity and broadly grooved upon its superior surface to receive the flattened spatula-shaped *processus gracilis* of the malleus, which lies in intimate contact with it and runs forward upon it to its anterior extremity. Its anterior pointed extremity projects freely from the bulla in the direction of the tip of the pterygoid, and as in *Tupaia* is connected by ligament with that process. Behind it terminates in a sharp point, which lies upon the outer side of the *processus gracilis* of the malleus. This bone in the adult, and I may say in the early adolescent stage, is firmly coossified with the slender tympanic ring, giving to its anterior extremity the appearance of a characteristic three-pronged enlargement. Careful investigation, however, shows that it was originally distinct from the tympanic since the longitudinal striae or grain of the latter bone can be seen crossing upon the outer side of the other at almost a right angle. It terminates in a pointed extremity behind, furnishing the posterior end of the tympanic above, where it is in intimate relation with the base of the *processus gracilis* but not attached to it. Upon its outer side it is produced into a more or less distinct blunt projection which lies just behind the postglenoid process of the squamosal.

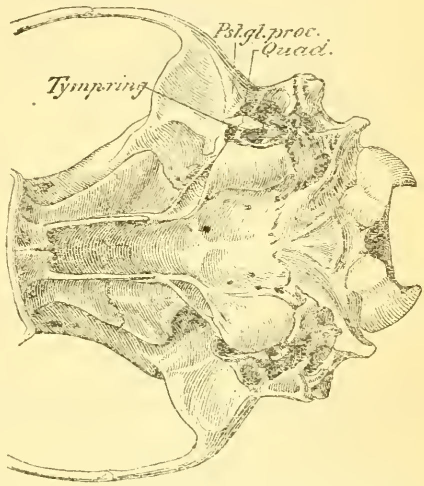

FIG. 5.—GYMNURA. *Pst. gl. proc.*, POSTGLENOID PROCESS; *Quad.*, QUADRATE; *Tymp. ring.*, TYMPANIC RING. × 2.

In the related genus *Hylomys* this bone has a very similar form and about the same relative proportions as in *Gymnura;* it is likewise firmly coossified with the slender tympanic ring, but perfectly free from the *processus gracilis* of the malleus.

In *Erinaceus* I have not been able to identify this element with certainty from any of the materials I have thus far studied. The *processus gracilis* is unusually large, broad, flat, and more or less spatula-shaped at its anterior extremity, where it laps over the expanded tympanic. Parker represents the anterior extremity as divided by a suture in his figure of the embryo,[1] and there seems to be little doubt that this divided extremity represents a separate ossifi-

[1] Philos. Trans. Royal Soc. London, 1886, vol. 176, pl. 12, fig. 11.

cation (fig. 6). In the adult or even the half-grown skull all traces of this division are obliterated, and the *processus gracilis* itself later becomes firmly attached to the tympanic ring by bony union.

In *Solenodon* this bone is represented apparently by a long, thin spicule which protrudes forwards from the *processus gracilis*, to which it becomes united in the adult. The *processus gracilis* likewise is firmly united to the tympanic ring.

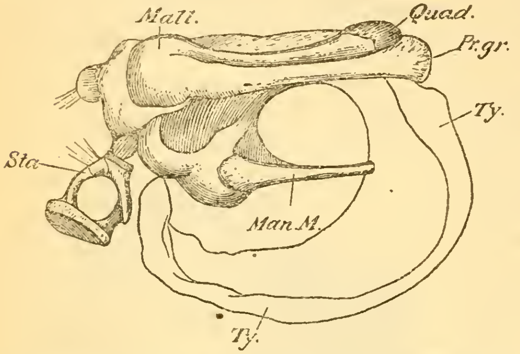

Fig. 6.—Erinaceus europaeus. After Parker. *Mall.*, malleus; *Man. M.*, manubrium of malleus; *Pr. gr.*, processus gracilis; *Quad.*, quadrate; *Sta.*, stapes; *Ty.*, tympanic ring.

In *Centetes ecaudatus* a considerable trace of this bone is left, much as in *Gymnura*, except that it is more reduced in size. It is very distinct from the malleus, but in the adult is coossified with the tympanic. In the embryo Parker represents a large element in this situation[1] which is developed independently in Meckel's cartilage in advance of the *processus gracilis*, and which is separated from the tympanic and the malleus (fig. 7). From the similarity of the appearances of these two elements in *Gymnura* and *Centetes*, coupled with the embryological evidence from Parker just cited, there seems to be no doubt that a separate and distinct element exists. In other members of the Centetidae I have been unable to discover any traces of this element in the adult at least. These include *Hemicentetes, Ericulus, Microgale.* In a like manner I have found no satisfactory evidence of its existence in any member of the Chrysochloridae, although it may be said that there are no young specimens upon which these observations were made.

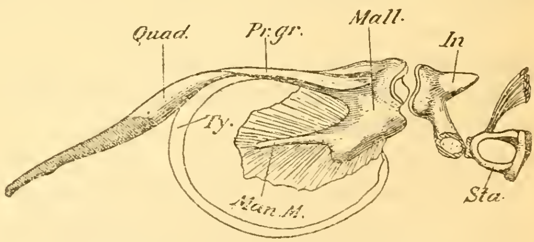

Fig. 7.—Centetes ecaudatus. After Parker. *In.*, incus; *Mall.*, malleus; *Man. M.*, manubrium of malleus; *Pr. gr.*, processus gracilis; *Quad.*, quadrate; *Sta.*, stapes; *Ty.*, tympanic ring.

It is rather surprising that *Galeopterus* should retain so few traces of these features in the adult skull, in view of the many marked resemblances of its skull to that of *Rhynchocyon*. For some unknown reason the skull bones of *Galeopterus* coossify very early, so as to

[1] Philos. Trans. Royal Soc London, 1886, vol. 176, pl. 33, fig. 6.

obliterate all traces of sutures at a comparatively early period. A dearth of material of the proper age prevents a very satisfactory study of the subject in this group, but fortunately some embryos give additional light. The dissection of a young embryo skull shows that the lachrymal ossifies from a single center; that there is a separate center for the postorbital process of the frontal; that there are separate and distinct centers for the jugal, quadrato-jugal, and postorbital of the zygomatic arch. Parker's figures do not show these elements in the embryo, but in my own dissection they can all be distinctly made out. Parker's figures do show, however, that the condylar portion of the lower jaw is made up of a separate piece [1] (fig. 8). My material is evidently of a considerably younger stage than that figured by him and is not sufficiently advanced to make this out very distinctly. As for the element in connection with the malleus and the tympanic I have not found any satisfactory evidence of its presence.

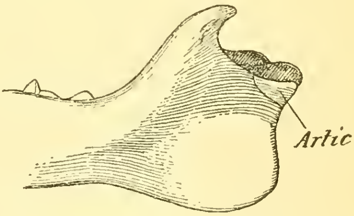

Fig. 8.—Galeopterus philippensis. After Parker. *Artic.*, articular.

Marsupials.—In this group of mammals a number of reptilian characters are met with, similar to those already described in the Insectivora. In the Virginia opossum the embryo skull shows that there is fairly distinctive evidence of the presence of a prefrontal lying near the anterior part of the orbit between the lachrymal and nasal; it shows, moreover, in a rather satisfactory way that the malar of the zygomatic arch is made up of two pieces which ossify from distinct centers, with the existence possibly of a third center at the junction of the squamosal and malar. This latter, however, is not certain. Of the element developed in connection with the tympanic ring and the *processus gracilus*, it may be said that in the fetal skull it develops from a distinct center in the premallear tract of Meckel's cartilage and is separated by suture from the *processus gracilis* up almost to the adult stage, when it usually becomes coosified with the malleus. Not infrequently, however, it remains distinct throughout the life of the animal. It never, apparently, coossifies with the tympanic with which it has the same general relations as already described in the Insectivora.

In other predaceous Marsupials, notably *Sarcophilus*, the *processus gracilis* appears to be made up as in the opossum of an unusually long slender curved rod of bone, which hooks over the tympanic and protrudes forward with a free extremety. Examination of a half-

[1] Philos. Trans. Royal Soc. London, 1886, vol. 176, pl. 38, fig. 4.

grown specimen, however, shows that this bony bar is made up of two separate pieces, as in the opossum, and evidently ossifies from a distinct center in Meckel's cartilage, in advance of the *processus gracilis.* This piece seems to be widely separated from any part of the malleus in the adult skull and is more or less joined to the tympanic.

In the jugal arch of *Sarcophilus* there is some evidence that it is ossified in the same way as in the opossum, namely, from three centers, but I have no embryos young enough to establish this with certainty. There is also evidence that there is a separate bone between the lachrymal and frontal in front of the orbit. Another point of unusual interest in the skull of *Sarcophilus* is the presence of a distinct bone just behind the external auditory meatus at the lower point of junction of the squamosal with the mastoid. This bone, as we shall presently see, is a very constant feature of the skull of the Carnivora, occupying the same position and having the same relations as in *Sarcophilus.* It probably also exists in the Dasyures, but I have not observed it in any other of the Marsupials. It is often met with in *Erinaceus,* however, and probably also in *Centetes, Ericulus, Solenodon,* and others. As this bone is such a constant feature of many of the Carnivora I propose for it the name of *paramastoid.*

The skull of a young kangaroo in the collection (No. 211) is of especial interest as showing the presence of a free premallear element, consisting of a relatively large triangular piece of bone, overlapping the tympanic, and intimately associated with the forward extension of the *processus gracilis.* This specimen furnishes confirmatory evidence, together with that already noticed in the opossum and *Sarcophilus,* of the statement of Parker, presently to be quoted, that in *Phascolarctos* there is a separate and distinct element developed in connection with Meckel's cartilage in front of the malleus.

The following species of Marsupials in the collection show the presence of an extra element at the junction of the malar with the zygomatic process of the squamosal not dissimilar to that described in *Rhynchocyon,* namely, *Macropus irma* (No. 155372), *Pseudochirus lemuroides* (No. 38714), *Phalanger,* sp. (No. 38470), *Dasyurus maculatus* (No. 38444), *Sarcophilus ursinus* (No. 155385), *Didephis virginanus* (No. 61842), and *Metachirus opossum* (No. 121414).

Cheiroptera.—Among the fruit-eating bats there are a number of species which show undoubted traces of these archaic characters. In *Pteropus* there are traces of a distinct bone, developed in connection with the postorbital process of the frontal above the eye; there is evidence of a separate element composing the postorbital process of the jugal, as well as less distinct evidence of a division of the malar into two parts. In young skulls there is always a distinct bone developed in connection with the anterior portion of the tympanic ring, which in adult specimens is coossified with it and with the malleus somewhat as in *Tupaia* and the other forms already described. In many species there is a distinct though small malar foramen.

Edentata.—There are some of the reptilian characters described in the foregoing pages to be met with among the Edentates, although by no means as commonly as among the Insectivora. As there is seldom a postorbital process of either frontal or parietal, no remains of a postfrontal is ever found. On the other hand, however, there is sometimes a rather large bone lying above the lachrymal between it and the frontal, near the anterior border of the eye cavity, in the young skull of the South American species of *Dasypus*. This bone is likewise found in the fetal skull of this species, so that its presence I suspect is not uncommon in the younger stages. In a like manner in *Euphractus villosus*, there is very commonly a distinct ossicle on the rim of the orbit, at the junction of the lachrymal and malar, overlapping the anterior orbital portion of the latter bone. I have met with this element in eight adult skulls of this species, or nearly 50 per cent of the specimens examined. It is of an elongated triangular form and occupies a position on the edge of the orbit. There is more rarely an ossicle developed in the jugal arch, at the junction of the malar and squamosal, corresponding to the postorbital process of the zygoma, but I have not found traces of this ossicle in the embryo of *Dasypus*.

The ossicle developed in connection with the tympanic ring and the *processus gracilis* of the malleus, occurs as a distinct element in the South American *Dasypus*, in *Tamandua*, and very probably in *Cyclopes*. Indications of its presence are likewise to be seen in the Aard Vark and other species of Edentates. Those species in which the tympanic ring is little expanded, like so many other forms, show it most distinctly, while in those in which the tympanic is inflated to form an osseous bulla, it disappears by coossification with this latter bone, and is not found in the adult skull.

Parker's statement, as well as his figures of this element in the embryo of the two-toed sloth, *Choloepus hoffmanni*,[1] are of unusual interest and importance as establishing beyond question the fact that there is not *one*, but at least *two*, extra elements developed in the premallear tract of Meckel's cartilage in this form. I here reproduce Parker's figure of that part of this interesting embryo (fig. 9). I have not been able to find any trace of these ossicles as separate elements in the adult skull, but there is very distinct evidence of their having coossified with the tympanic. Upon the interior wall of the tympanum is a relatively large, more or less triangular piece of bone lightly attached at its back part to the periotic by a very thin bony

[1] Philos. Trans. Royal Soc. London ,1886, vol. 176, p. 65, pl. 9, fig. 7.

spicule. This may be the remains of the enlarged portion of these elements figured by Parker.

Sirenia.—The American sea cow shows at least three elements in the jugal arch in the adult skull—namely, a quadrato-jugal piece, articulating with the zygomatic process of the squamosal, a jugal element underlying the orbit, and a post orbital piece which forms the postorbital process of the arch. There are, in addition to these, in some specimens, a small ossicle developed just above the vestigial lachrymal and a pair of ossicles lying below and upon the outer side of the reduced nasals. As there is no postorbital process of either frontal or parietal, no trace of a separate element in this situation is found. In all of the specimens which I have thus far examined I have been unable to detect the presence of an element associated with the tympanic, which corresponds to that already described in *Tupaia*, *Gymura*, and others, although from certain appearances of the dried skull, it is not altogether unlikely that carefully prepared younger specimens may show its presence.

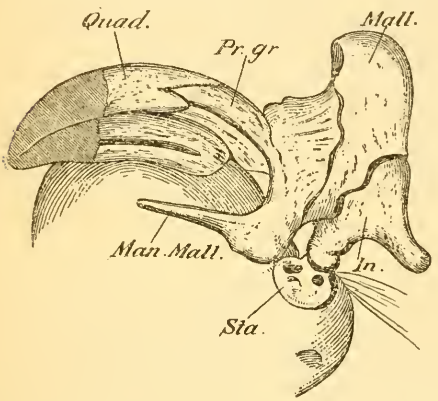

FIG. 9.—CHOLOEPUS HOFFMANNI. *In.*, INCUS; *Mall.*, MALLEUS; *Man. Mall.*, MANUBRIUM OF MALLEUS; *Pr. gr.*, PROCESSUS GRACILIS; *Quad.*, QUADRATE; *Sta.*, STAPES.

Ungulata.—Among the Ungulates the horses show the presence of at least two elements composing the malar in the younger stages, one of which represents the jugal and the other the quadratojugal. It is more than likely also that the bony bar bounding the posterior part of the orbit is composed of an upper and lower element in the young stages, although I have not seen the evidence to confirm this.

Rodentia.—The chief point of interest in this group as far as the presence of these reptilian elements is concerned relates for the most part to the composition of the zygomatic arch. There is considerable evidence in both the Hystricoidae and the Sciuroidae that there were originally at least two elements entering into the arch, namely, a jugal which has disappeared in many forms and the quadrato-jugal, which now constitutes the principal remaining piece. In the squirrels that part of the long malar which runs forward to the lachrymal along the under edge of the orbit is sometimes cut off by a suture into a distinct bone, as is likewise the case somewhat more frequently in the Hystricoidae.

Lagomorpha.—In the Lagomorpha the maxillary seemingly runs backwards behind the glenoid cavity and forms the whole of the zygomatic arch. Sufficiently young skulls show, however, that this apparent backward extension of the maxillary is in reality a distinct element that is separated by suture and represents the quadrato-jugal. The jugal, as well as any representative of the postorbital are apparently missing in the adult. This interpretation of the zygoma of the Lagomorpha gives a clue to the composition of the arch in *Ornithorhynchus,* which is without much doubt made up of the usual three elements. I can not accept the interpretation figured by Broom,[1] since there is pretty clear evidence from a fairly young skull in the collection that the lower piece of the arch is separated by suture from the maxillary and is therefore the quadrato-jugal. The bone figured by him as the jugal is much more likely to be the postorbital. In embryo skulls the jugal may be present.

Carnivora.—In the composition of the jugal arch the Carnivora not infrequently display evidences of the compound nature of the so-called malar. Thus a large percentage of the skulls of bears show the postorbital process of the zygoma to consist of a distinct element, the suture separating which is very frequently more or less evident. This is likewise often seen in the various species of the Felidae. In some 8 or 10 fetal skulls of blue foxes the anterior part of the zygomatic process of the squamosal is cut off as a distinct piece, which I take to represent this same element composing the postorbital process of the arch in the Canidae. The same division is sometimes found in the adult skull, and has been figured by me in the extinct Creodont *Dromocyon vorax.*

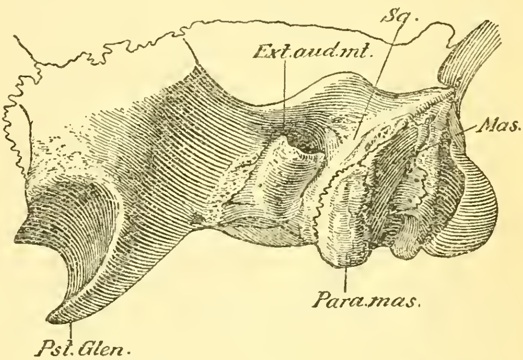

FIG. 10.—URSUS HORRIBILIS. *Ext. aud. mt.*, EXTERNAL AUDITORY MEATUS; *Mas.*, MASTOID; *Para. mas.*, PARAMASTOID; *Pst. Glen.*, POST-GLENOID; *Sq.*, SQUAMOSAL.

At the junction of the squamosal and the mastoid, near the lower end and just posterior to the external auditory meatus is a distinct bone, which is so constant in the bears as to be almost a distinguishing feature of this group. It sometimes exists as a cap or epiphysis, but in other instances it is united by strongly dentate suture. A similar element is found in the Mustelines, raccoons, and many other species of Carnivora with great frequency. As already noted the same element is seen in certain of the Insectivora and Marsupials. On account of its possible important relationship with the quadrate I propose a name for this bone, already suggested on a former page (14), namely, the *Paramastoid* (fig. 10).

[1] On the Structure and Affinities of the Multituberculata. Bull. Amer. Mus., 1914, p. 130.

Of the existence of a separate element in advance of the malleus it may be said that there is a pointed spicule protruding under the upper edge of the tympanic in the civets, apparently most distinct in *Paradoxurus*, and in the otters among the Mustelines, which, from what we have already seen in so many other species of mammals, probably indicates its presence. I have not been able to determine its exact relations with the *processus gracilis* in these forms.

Primates.—Comparatively few of the reptilian elements described in the foregoing pages are to be seen in the adult skull of the primates, notwithstanding the embryological evidence seems to be very conclusive that they are to be seen in the early stages of development. We thus find three centers of ossification for the malar; one for the postorbital process of the frontal, one between the lachrymal and frontal, and one alongside the nasal spine of the frontal. All these centers of ossification can be easily interpreted on the basis of reptilian anatomy. As we shall presently see, the malar foramen, which is unusually large in some of the primates, is likewise, in all probability, the vestige of an important opening in the reptilian skull.

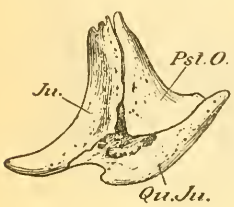

FIG. 11.—HOMO SAPIENS. AFTER TOLDT. *Ju.*, JUGAL; *Pst. O.*, POSTORBITAL; *Qu. Ju.*, QUADRATOJUGAL.

In studying the ossification centers of the human malar I have found it very difficult to distinguish the sutures separating them when seen from the outside, but when they are viewed from the inside they are much more evident on account of the lack of scale-like overlapping upon the inside of the arch. Evidence of the original separation of at least two of these pieces persists until as late as the seventh month of fetal life, while from the outside they always appear to be fused by the end of the third month. I here reproduce Toldt's figure (fig. 11) of the malar of a seventh month fetus,[1] which shows this well. In the young stages the malar foramen is not easily distinguished. There seem to be a number of openings through the malar, some of which disappear as age advances. Just which one of these finally becomes the malar foramen or foramina I have been unable to determine with satisfaction, but it would seem that the foramen which remains is developed near the edge of the orbit and is apparently not homologous with the large opening found in certain other primates, notably in the spider monkeys, howlers, and teetes of South America, and in some of the Madagascar lemurs. There seems to be a great deal of variability in this opening among the primates.

The divided malar in the human skull, which occurs not infrequently as an anomaly,[2] represents the lower or quadrato-jugal element of many mammals in which it remains distinct. In a young

[1] Die Zerteilung des Jochbeines und andern Varietaten desselben, Sitzungsber. kais. Akad. Wissensch Wien, 1903, pl. 1, fig. 5.
[2] See also Aleš Hrdlička, Amer. Naturalist, 1902–1904.

skull of *Nycticebus* (No. 142240) and of a *Perodicticus* (No. 184229) this lower piece is shown on both sides with the remains of the suture distinct. In the South American primates with the large malar vacuity, when the malar consists of more than a single piece, the parts are arranged in such a way as to radiate from the malar opening.

Not infrequently there is a suture in certain species of South American apes, cutting off that part of the malar which lies upon the orbital rim, below and to the outside of the eye cavity, and less frequently an element which lies behind the malar foramen near the junction of the malar with the squamosal. In a like manner there is often evidence of a distinct element extending from the supraorbital foramen to the junction of the malar, upon the upper and outer edge of the orbital rim. I can find no traces of a premallear element nor paramastoid in any specimens of primates which I have examined.

Monotremes.—The skull of the duckbill (*Ornithorhynchus paradoxus*) exhibits a number of features which are of great interest in connection with the present study. On account of the early coossification of nearly all the cranial bones and the obliteration of the sutures it is not easy to determine their limits and relations from the ordinary museum specimens. The only figures purporting to give this information are from Van Bemmelen [1] and Broom,[2] but these are so different from that of a fairly young specimen in the collection that I have deemed it advisable to give the interpretation of certain of the elements as afforded by this skull.[3] The zygomatic arch as here shown is composed of the three elements already described in *Rhynchocyon*, and while there may be some doubt in regard to the division of what appears to be the long zygomatic process of the squamosal running forwards to the postorbital process of the arch, yet the specimen shows what appears to be the remains of a suture in the situation where it should appear. The supposed backward extension of the maxillary process to the glenoid articulation in the lower part of the arch, as figured by Broom, is shown to be a distinct element separated from the maxillary by a well-marked suture.

That which is the most important and interesting feature of the skull before us, however, is an indication of the presence of a relatively large distinct bone lying just internal to the glenoid cavity, between it and the periotic; it projects downwards and backwards and the appearance of the surface of its lower free extremity so closely resembles that of a synovial joint that there is apparently no mistaking its significance. This piece is distinctly separated by well-marked suture from the squamosal, the exoccipital, and the alisphenoid, but in the present specimen not completely cut off from the periotic. If it is not distinct from this latter bone in the still

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[1] Ueber den Schädel der Monotremen, Zool. Anz., 1901.

[2] Structure and Affinities of the Multituberculata, Bull. Amer. Mus. Nat. Hist., 1914, p. 130.

[3] Watson's paper was received too late for use in this connection.

younger stages, then I can not understand why it should be in the present specimen partially, and I may say almost completely, separated from it by suture which shows alike on the two sides. By its upper posterior extremity it articulates with the squamosal and exoccipital, there being no mastoid portion of the periotic exposed in this region of the skull that I can find. In front it is produced into a more or less pointed free extremity directed forwards and inwards toward the pterygoid. It is attached above to the periotic.

Scarcely less interesting than the foregoing is the presence of a relatively large foramen or vacuity passing from behind forwards just above the glenoid articulation, being bounded above and on the outside by the squamosal, on the inner side by the exoccipital, and below by the exoccipital and squamosal. The parietal above does not enter into the formation of this vacuity, but reaches down almost to its upper boundary. In the curious rodent *Lophiomys* this vacuity is represented in part. Instead of running forwards entirely above the articulation, as it does in *Ornithorhynchus*, it enters just back of the joint and has the periotic for its internal boundary. A large venous foramen in the Marsupials in this situation may represent the remnant of the same structure in these forms.

Homologies of these supernumerary bones.—From a careful consideration of the foregoing facts, what conclusions or deductions can be drawn as to the homologies of these elements, and what light do they throw upon the broader problems of the descent of the Mammalia from the Batrachia or Reptilia? With the rather incomplete embryological evidence which we have I think we are justified in assuming that the occurrence of such characters in *Rhynchocyon* as above described, even though they may be largely obliterated in the adult skull, and are only occasionally to be met with in exceptional specimens, is none the less very strong presumptive proof that these vestigial structures represent separate and distinct elements in certain mammalian skulls, at least, which were once to be found in practically all stages and ages, just as in the Reptilia. As to the frequency of the occurrence of these remarkable features of the skull in *Rhynchocyon* I have little or no additional evidence to offer, further than that furnished by the figures of the skull by Peters [1] of *Rhynchocyon cirnei*, in which some of the sutures, at least, delimiting these elements are represented. There can be little doubt that if his specimens were carefully studied with the object in view of determining this point, they would offer conclusive confirmatory evidence of the facts above set forth. At all events, in the light of such embryological testimony as we have, respecting the presence of certain of these elements in the Mammalia, we may, in my judgment, safely conclude that when

[1] Naturwiss. Reise nach Mossambique, 1852, pl. 13.

this evidence is fully known in the case of *Rhynchocyon*, it will be in no wise different.

It is stated in Cunningham's Human Anatomy [1] in speaking of the ossification of the malar, "the malar ossifies in membrane most probably from three centers, disposed as follows: One in the posterior part of the bone, the other two in connection with the orbital process and orbital margin. Appearing as early as the eighth week, these centers are confluent by the beginning of the fifth month of fetal life." Again, it is stated in Gray's Anatomy, Spitzka, 1913, in speaking of the same subject: "The malar bone generally ossified from three centers, which appear about the eighth week—one for the zygomatic and two for the orbital portion—and which fuse about the fifth month of fetal life. The bone is sometimes, after birth, seen to be divided by a horizontal suture into an upper and larger and a lower and smaller division."

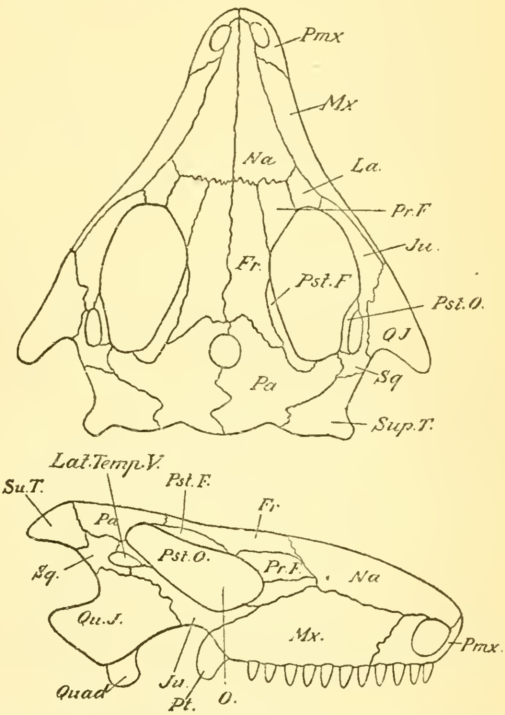


FIG. 12.—PROCOLOPHON TRIGONICEPS. AFTER SMITH WOODWARD. *Fr.*, FRONTAL; *Ju.*, JUGAL; *La.*, LACHRYMAL; *Lat. Temp. V.*, LATERAL TEMPORAL VACUITY; *Mx.*, MAXILLARY; *Na.*, NASAL; *O.*, ORBIT; *Pa.*, PARIETAL; *Pmx.*, PREMAXILLARY; *Pr. F.*, PREFRONTAL; *Pst. F.*, POSTFRONTAL; *Pst. O.*, POSTORBITAL; *Pt.*, PTERYGOID; *Quad.*, QUADRATE; *Qu. J.*, QUADRATOJUGAL; *Sq.*, SQUAMOSAL; *Sup. T.*, SUPRATEMPORAL.

Taking first the bone developed in connection with the postorbital process of the parietal, in *Rhynchocyon*, at the upper and back part of the rim of the orbit, it is to be observed that it not only occupies the same position, but is very much alike in form to the corresponding bone in certain reptilian skulls. This element is therefore to be homologized with the *postfrontal* of the reptile. This is its exact position in such a reptilian type as *Procolophon trigoniceps*, of the South African Karoo bed (fig. 12), as figured by Smith Woodward.[2] It is important to note, moreover, that it has the same general shape in the two, being a long slender bone, occupy-

[1] Article, Osteology, by Arthur Thompson, 1902, p. 133.
[2] Vertebrate Paleontology, 1898, p. 149.

ing the upper edge of the orbital rim, overlapping the junction of the parietal and frontal, and passing down upon the outside of the depending process of the parietal, which goes to make up the principal part of the postorbital process above. As already pointed out, *Rhynchocyon* is in this respect wholly unique among the Mammalia, being the only form which to my knowledge has retained in its entirety this primitive reptilian feature, as displayed so perfectly by the extinct reptilian genus above mentioned. I shall refer to this subject on a subsequent page. Of the exact homology of this element in the two forms, I do not think, therefore, that there can be the slightest question or the faintest doubt.

If the element above considered be the true representative of the *postfrontal* of the reptilian skull, then the element lying below it in the jugal arch, forming its postorbital process, can be no other than the *postorbital* bone, since its position is almost if not exactly the same as in *Procolophon*. Its form, moreover, when compared with the corresponding element in this extinct reptile, is seen to be strikingly similar. Its relations at its lower end are almost exactly alike in the two forms, lying upon the upper side of the arch, near the junction of the squamosal and jugal. In *Rhynchocyon* it terminates above in a free extremity, while in *Procolophon* it extends upward to join the depending process of the parietal (postorbital process) and the squamosal. It would require but a slight extension of the bone upward in *Rhynchocyon* to meet this downward projecting process of the parietal to produce almost the exact relations above as found in *Procolophon*. It is of course to be taken into consideration that the change from the reptilian to the mammalian condition has produced considerable alteration in relations of certain parts of the squamosal. In *Rhynchocyon* the upper part of the *postorbital* is reduced and it has lost all contact with the squamosal above, as shown in *Procolophon*. That it was formerly larger in *Rhynchocyon* or its ancestors and may have joined either the postfrontal or the parietal, or both, is not altogether unlikely, but whatever the former relations of its upper end may have been does not affect the main question of its homology with the *postorbital* element of the reptilian skull.

In a like manner the element composing the lower part of the arch, and extending from the maxillary in front to the glenoid cavity behind, I homologize with the *quadrato-jugal* element of reptilian anatomy, for the reason that its general and usual relations among the Reptilia are of this character. It thus has the squamosal above, the quadrate below, behind, and to the inner side, and the jugal in front and above. With the disappearance of the quadrate it has been shifted forward somewhat and has developed a connection with the maxillary, which it does not seem to have in the reptilian skull, but it still clings to its original position, as far as its relations to the squamosal, jugal, and, as we shall presently see, to the quadrate, are concerned. In *Procolophon* the quadrato-jugal is a relatively large deep bone, and the similarity of this element in the two forms is not very close. Its position corresponds in the two, however, almost exactly.

By exclusion, therefore, the remaining element entering into the composition of the jugal arch in *Rhynchocyon* must represent the *jugal* bone of the reptilian skull. Its position and relations are again in strict accord with the corresponding element in *Procolophon* and other Reptilia, namely, it lies above the quadrato-jugal at its posterior end, it passes under the edge of the squamosal behind, and in front it forms the lower edge of the orbit, overlying the posterior end of the maxillary and passing forward on the orbital rim to join the lachrymal. All these relations, it may be added, are typically reptilian.

In view of the uncertainty of a division of the lachrymal by the imperfect suture above described, in connection with that bone, it may not be wise, with the present material, to attempt to establish any homology with a distinct reptilian element. However, if the embryology or the development of the lachrymal in *Rhynchocyon* finally shows it to be derived from two centers, as this suture would seem to indicate, then in that event the upper element lying between the frontal and lachrymal would undoubtedly have to be homologized with the *prefrontal* or *adlachrymal* of the reptilian skull and the lower piece containing the lachrymal canal would represent the true lachrymal.

If this latter homology is established, what, then, is the significance of the small bone lying at the junction of the frontal, lacyrhmal, and maxillary on the side of the face? Its backward extension by a pointed extremity toward the rim of the orbit would seem to indicate a former position in connection with the eye cavity, and as it lies above the lachrymal I have been disposed to consider it homologous with the prefrontal of the reptilian skull. The relatively large size and a position much nearer the orbit of a bone which is occasionally seen in *Dasypus*, as already described, would seem to favor this view. On the other hand, as we have already seen in the Sirenia, there is a pair of ossicles lying above the lachrymals, between them and the frontals, which undoubtedly represent the *prefrontals* for reptiles, and an additional pair, lying upon the outside, and below the vestigial nasals, which I take to represent the *septo-maxillaries* of many reptiles, of the monotremes, and *Tritilodon*, as figured by Broom. It may be possible, therefore, that the bones in question in *Rhynchocyon* may represent the septo-maxillaries, but their wide separation from the nasals would be against this interpretation. Whatever elements they may represent in the reptilian skull, the same interpretation must be given to them in *Lemur*, in which they sometimes occur in the same position as in *Rhynchocyon*.

Parker in his notable work on the morphology of the skull in the Insectivora,[1] figures an embryo skull of *Rhynchocyon cirnei*, but the stage apparently is too advanced to show the centers of ossification of the lachrymal, which is represented as completely ossified without any trace of sutures. From what I know of the ossification of the lachrymal in the fetal skull of *Tupaia* I should say that it would require a considerably younger stage to show whether there are one or more centers in *Rhynchocyon*. It is not clear from his figures whether there is a distinct postfrontal or not, but it would appear so from the side view of the skull. In a like manner there seems to be a large distinct prefrontal represented between the lachrymal and frontal near the orbital margin, a fact which seems to strengthen the evidence in favor of the view that the corresponding bone in the adult skull, as described above, is a true homologue of the prefrontal. If upon further investigation it is found that the lachrymal ossifies from two centers, as it does in *Tupaia*, then one of these extra elements would have to be interpreted as a supraorbital. He does not represent the zygomatic arch as divided into the three elements as shown in the adult skull of *Rhynchocyon petersi* above described, nor does he say anything in the text about any of these bones. The lack of information upon these important points is upon the whole rather disappointing in a work of such magnitude.

The homologies of the ossicles found in connection with the lachrymal in the other genera of the Macroscelididae, notably those of *Cercoctenus sultana* and *Petrodromus tetradactylus*, are less certain of identification as reptilian elements. In view, however, of the apparent complete absence of any other trace of a true jugal element in some very young skulls of these species, it is not altogether unlikely that the ossicle occurring at the junction of the lachrymal with the remaining element of the zygoma may represent the vestigial or reduced true jugal, which was originally larger and occupied a more posterior position on the orbital rim, being now represented by its anterior portion alone. In that event the principal element in the jugal arch would be homologized as the quadratojugal. In a like manner the upper ossicle attached to the lachrymal may represent a prefrontal or supraorbital element which has been crowded out, and has finally come to occupy a position on the edge of the lachrymal. If this explanation be correct, it then follows that all lachrymal crests, tubercles, protuberances, etc., so frequently seen in the skulls of Marsupials, Insectivores, Rodents, and many other groups, are to be interpreted in the same way and probably

[1] Philos. Trans. Royal Soc. London, 1886, vol. 176, pl. 36.

represent the final stages in the coalescence of these elements, which remain free in the Macroscelididae.

As regards the Tupaiidae the evidence in favor of the undoubted presence of certain of these reptilian elements, while it is not quite so direct and positive as it is in *Rhynchocyon*, is nevertheless very suggestive. That the so-called postorbital process of the frontal represents a distinct element is not susceptible of absolute proof at present, yet there is considerable evidence in favor of such a view. The single embryo skull of *Tupaia* which I have dissected was unfortunately of too young a stage to show many of these points clearly, but there is some evidence of a separate center, lying behind the supraorbital foramen, which begins to ossify much later, apparently, than the other bones of the skull. This is likewise true of the bones of the jugal arch and squamosals, since in the embryo above referred to no ossification in these elements had yet started. The lachrymal, however, had begun to ossify and it is of great interest to note that it starts from *two centers,* one below surrounding the lachrymal canal and the other above adjoining the frontal. The evidence is conclusive, therefore, that this latter element represents the prefrontal of the reptile.

In regard to the bones surrounding the so-called malar foramen the only direct evidence as the case now stands is based upon the anomalies already described; but when we take into consideration the embryological evidence derived from the human malar quoted above, from the adult condition shown in *Rhynchocyon,* the evidence from the embryo of *Galeopterus,* the embryo of the opossum, the young skull of the sea cow, as well as those of so many other mammals, the assumption is warranted that there are three elements represented in the jugal arch of *Tupaia,* corresponding to the jugal, quadrato-jugal, and postorbital bones of the reptilian skull, and that they are, moreover, disposed around the malar foramen and form its boundaries quite in the same way as they do in certain of the primates. If this so-called malar foramen is thus surrounded by and forms the central meeting point of these three bones, then the interesting question arises as to its homology. That it is not a foramen in the ordinary sense is shown in *Tupaia* by its large size in proportion to the relatively small size of the structures which it transmits. This same condition is seen in many apes.

A careful comparison of this malar foramen, as thus bounded in *Tupaia,* with the lateral temporal vacuity of such a reptilian type as *Procolophon* reveals a surprising degree of similarity. Thus it will be seen that in both it is placed below and more or less posterior to the orbital cavity, it has an oval form and is near the beginning of the jugal arch. In *Procolophon* a small sliver of the squamosal excludes the upper part of the quadrato-jugal from taking any share in its boundary and the squamosal furnishes the principal part of the boundary behind, but with the great changes that have occurred in this latter bone in the transition from reptile to mammal it is not surprising that the vacuity should have been shifted forward slightly and the squamosal entirely withdrawn from its boundary. In *Tupaia* the anterior end of the zygomatic process of the squamosal lies just behind it, and the change from the relations exhibited in *Procolophon* to those seen in *Tupaia* would be very slight indeed.

Upon the whole, therefore, the presumption that the so-called malar foramen of *Tupaia,* of certain of the primates, and possibly of the fruit-eating bats, is the remains of the lateral temporal vacuity of the reptilian skull, finds a fair and reasonable measure of support.

The homology of the vacuity lying just above the temporo-mandibular articulation described in the Monotremes is not difficult to discover when we compare it with such a type as *Sphenodon.* In this latter form the large opening from the temporal area on each side of the braincase, which is directed backwards (the supraoccipital vacuity) has for its boundaries above the squamosals and parietals, and below chiefly the exoccipitals. As will have been noticed in the description of this aperture in the duckbill's skull this is almost the exact boundary there seen. The only difference is that in *Sphenodon,* because of the small brain case the parietal enters into the bounding arch above, while in the Monotremes, owing to the enlargement of the cranial cavity, the parietal has been excluded, and the outer part only of the vacuity in the reptile skull is represented in the mammal. This homology is so clear and unmistakable that there is no room for doubt as to its correctness. If this conclusion is correct then the similar opening seen in certain Rodents, notably in *Lophiomys* and in the Marsupials is the inconsiderable remnant of the same supraoccipital vacuity of the reptilian skull.

Fate of the Reptilian quadrate in the Mammalia.—The determination of the homology of the premallear element or elements described in the foregoing pages involves a discussion of some of the most important problems connected with the morphology of the mammalian skull. The great question, "What has become of the quadrate?" in the evolution from the reptilian to the mammalian condition has fretted the minds of philosophers and baffled the best brains of morphologists for the last 50 years without any generally accepted and satisfactory answer. Without attempting to go into the extensive literature on the subject and follow out in detail the various theories that have been advanced, it must suffice here to say that the subject has finally settled down to two rival theories—namely: (1) The reptilian quadrate has been detached from its original position as a suspensorium of the lower jaw, has been much reduced in size, and has become the middle element of the ossicular chain of the tympanic cavity, namely the incus. The articular of the reptilian mandible has lost all connection with the lower jaw and has become the malleus of the mammalian ossicular chain. (2) The auditory chain of bones of the mammalian tympanum have been derived from and are strictly homologous with a similar chain of bones in the reptilian or batrachian skull frequently found as an undifferentiated rod of bone, the *collumella auris.* The quadrate has disappeared, having become either the tympanic (Gadow), the inter-articular fibro-cartilage of the glenoid cavity (Broom), or incorporated with the squamosal (Cope and Baur).

When one studies the quadrate in a large series of reptiles and birds he can not well avoid being struck with the superficial resemblances of this bone to the mammalian incus. This is heightened by the peculiar manner in which the quadrate articulates in birds and is attached to the side wall of the brain case by a ball-and-socket joint, not dissimilar to the way in which the short process of the incus is received into the *fossa incudis* of many mammals. Then, again, there is the peculiar and wholly characteristic double saddle-shaped articulation of the incus and malleus of the mammalian tympanum, which at once recalls the articulation between the quadrate and articular of the reptilian jaw, and lastly the relatively large size of the incus and malleus in certain of the lower forms of the mammalia, notably the monotremes. Another supposed fact which has been looked upon as having an important bearing upon the question and used in support of this hypothesis is the assumed complete absence of any representative of an articular element in the mandible of the mammal. This is stated by Gregory[1] as follows:

"In order to substantiate the conclusion that the mandibulo-squamosal joint in mammals is a wholly new structure, into which the quadrate and articular did not enter, we recall the facts (1) that embryological research gives no warrant for the belief that the mammalian jaw is composed of more than one element (except for the occasional vestiges of a splenial); (2) that all the oldest known mammalian jaws, from the Triassic, Jurassic, and Basal Eocene, never show any trace of sutures; (3) that in the Cynodonts the broad ascending ramus or corono-condylar region appears from Broom's researches to be a part of the dentary."

For the sake of brevity this theory may be called the transposition theory of the quadrate and articular.

The other theory of the fate of the reptilian quadrate in the mammalian skull assumes that it has gradually disappeared without having entered the tympanic chain; that the *ossicula auditus* of the mammalian tympanic cavity have been derived directly from a

[1] The Orders of Mammals, Bull. Amer. Mus. Nat. Hist., Feb., 1910, p. 138.

similar chain of bones in the promammalian reptiles or batrachians; that the articular has likewise in many instances been gradually crowded out and lost, its function having been usurped by the condyloid process of the dentary; that this same fate has in varying degree befallen the other jaw elements of the reptilian skull, save the dentary and splenial. In contradistinction to the transposition theory of the quadrate and articular this latter view may be called the absorption theory of these elements.

A consideration of the fate of the reptilian quadrate in the mammalian skull necessarily involves a discussion of the fate of the other elements of the reptilian jaw as well, since there can be little difference of opinion apparently that the mammalia have been derived by descent from the reptilia or batrachia, and that through some changes which are attempted to be explained by these various hypotheses the present state of affairs has been brought about in the mammals. If the quadrate has been transposed from its original position as a suspensorium of the lower jaw and transferred to the mammalian auditory chain, having its function completely altered, and the articular has been transformed into the mammalian malleus, as claimed by the advocates of this view, then a concomitant postulate which may be said to be absolutely vital to this hypothesis, is the complete and total absence of any element or homologous part in the mammalian jaw representing the reptilian articular. For if it can be shown that any element corresponding to this bone in the Reptilia is ever found in any mammal, then the whole theory falls and can not be considered to be explanatory of the fate of the quadrate, since it is utterly inconceivable how this latter bone could have ever been independently intercalated in the middle of a chain of bones connecting the eardrum with the fenestra ovalis, and which by common consent, all are agreed, have always been concerned in performing the highly important function of audition.

Another very vital matter involved in a discussion of this subject relates to the origin and manner of ossification of the various bones herein considered, for without a clear and definite understanding of just what is meant by the terms employed, as well as a precise and intimate knowledge of the histological processes by which these bones are developed, we shall never be able to make any satisfactory progress toward a final solution of the problem before us. It is very easy to speak of cartilage bones, membrane bones, splint bones, etc., as if they were perfectly and obviously distinct entities and to base important and far-reaching hypotheses upon a lax understanding of the subject, but can we always be sure that such conclusions are sound? That there are broad and well-marked distinctions between the various categories of ossifications, in their typical development, is undoubtedly true, but at the same time the fact must not be overlooked that there are many cases in which it is difficult if not impossible to decide to which particular category a given bone is to be assigned because of the intergradation of the various processes involved in its production or development.

Parker in his consideration of the osseous skull of the vertebrates makes the following classification:[1] "Calcareous deposit occurs in vertebrates in the following tracts: (1) Epidermis or epithelium (enamel of the teeth, and outer layer of Ganoid scales); (2) dermis (dentine of teeth, Ganoid and Teleostean scales); (3) subcutaneous fibrous mesh, immediately outside the perichondrium, and eating into cartilage (ectostosis); and (4) deep in its substance (true endostosis, central or subcentral). In most of these tracts the calcification may be such as not to gain the title of bone; but in all except the first, true bone may result from the process."

While this classification is in the main correct and in general accord with the more modern views of the subject, it is at the same time hardly explicit enough to serve our present purposes. According to the researches of histologists the formation of bony tissue, outside of Parker's first group, is divided into two categories, namely, an *intramembranous* and an *intracartilaginous* ossification. The chief and most important distinction between these two catagories is that in the former there is no cartilaginous mold or matrix which precedes the appearance of the bone tissue; while in the latter a cartilaginous mold or matrix is always present. In the intramembranous division, the membrane which occupies the place of the future bone consists of white fibrous connective tissue and ultimately forms the periosteum from which the osteoblasts are derived. At first a series of fine bony spicules are seen radiating from the point or center of ossification, known as the *osteogenetic* fibers, which are deposited under the influence of the osteoblasts. As these osteogenetic fibers grow out to the periphery they continue to ossify and give rise to fresh bony spicules. Subsequently successive layers of bony tissue are deposited beneath the periosteum and around the larger vascular channels, so that the bone increases much in thickness. It is further stated that the process of bone formation spreads laterally to the future suture, and here between the various bones a layer of fibrous tissue, the *cambium layer*, is maintained until the full size of the bone is reached. The cambium layer then ossifies and the bone ceases to grow at its edges. The persistence of this cambium layer and its failure to undergo final ossification is the cause of the maintenance of the sutures between bones which so frequently results in the anomalies which have been discussed in the preceding pages.

In the intracartilaginous method of ossification, on the other hand, as already stated, the future bone is preceded by a cartilaginous mold

[1] Morphology of the Skull, 1877, p. 343.

or matrix. The first step in bone formation in this manner consists in the multiplication and enlargement of the cartilage cells and their arrangement in rows at the center of ossification. The matrix in which they are imbedded increases in quantity so that the cells become farther separated from each other. A deposit of calcareous material then takes place in this matrix, between the rows of cells, so that they become separated from each other by columns of calcified matrix. These columns are connected by transverse bars of calcareous substance. While this process is going on within the substance of the solid cartilage of which the developing bone consists, certain changes are taking place on its surface. This is covered by a very vascular membrane, the *perichondrium*, entirely similar to the connective tissue layer, which forms the basis and constitutes the periosteum of membrane bone. On the inner surface of the perichondrium the cells become osteoblasts or bone-forming cells, through the agency of which a thin layer of bony tissue is being formed between the outer membrane and the cartilage, in a manner not dissimilar to that in which the formation of true membrane bone takes place. The two processes above described go on simultaneously in the development of cartilage bone. The second stage consists in the prolongation into the cartilage of processes of the deeper or osteogenetic layer of the perichondrium, these processes consisting mostly of blood vessels and osteoblasts. In this way the bone is gradually built up and finally reaches its adult condition. It will thus be seen that practically the only difference between a cartilage and a membrane bone consists in the presence of a cartilaginous mold or matrix, which precedes the former in the order of its development; but it frequently happens that a cartilaginous mold may be present, yet the resulting bone may be formed almost exclusively from the perichondrium without involving the cartilage to but a very small extent. There can be little doubt that if this subject were to be followed up carefully all kinds of intermediate conditions would be found connecting these processes of bone formation quite closely, save and except the presence or absence of a perachondrial mold or matrix. It frequently happens, moreover, that in some bones both processes are concerned in its formation, and that one portion of the bone may be formed by one method and another portion, in part, at least, by the other.[1]

[1] Huxley in his article on the Amphibia, quoted below, in speaking of the cranial bones of *Rana* says: "The ex-occipitals, prootics, and sphen-ethmoid are ossifications which involve the chondro-cranium, though they largely consist of secondary bone." And while he does not state directly that this is likewise true of the quadrate, we are left to infer as much from his further statement. Again, in speaking of the long bones, he says: "The long bones, both in the fore and hind limbs, consist of an axis of cartilage, sheathed in, and more or less replaced by a diaphysis of membrane bone." We may regard the para-sphenoid in the same light, and while loosely spoken of as a "splint bone" or a "membrane bone," yet it is morphologically an ossification primarily belonging to the chondro-cranium, developed in the perichondrium covering its base and afterwards incorporated into the ossifications of the cartilage.

Such an example is seen in the dentary bone of the lower jaw, found, as far as I know to the contrary, in all Mammalia; and as this is particularly germane to the subject herein considered, it will be well to mention it fully. For this purpose and in order to bring into stronger relief the elements which enter into a discussion of this subject I quote again at length from the statement of Arthur Thompson in Cunningham's Human Anatomy (p. 141) on the ossification of the human lower jaw, which is as follows:

The development of the lower jaw is intimately associated with Meckel's cartilage, the cartilaginous bar of the first visceral or mandibular arch. Meckel's cartilages, of which there are two, are connected proximally with the periotic capsule and cranial base. Their distal ends are united in the region of the symphysis. It is in the connective tissue overlying the outer surface of this cartilaginous arch that the bulk of the lower jaw is developed. The cartilage itself is not converted into bone, but undergoes resorption, except its anterior extremity, which is stated to undergo ossification to form the part of the lower jaw lying between the mental foramen and the symphysis. In a third or fourth month fetus the cartilage can be traced from the undersurface of the forepart of the tympanic ring downwards and forwards to reach the jaw, to which it is attached at the opening of the inferior dental canal; from this it may be traced forwards as a narrow strip applied to the inner surface of the mandible, which it sensibly grooves. The proximal end of this furrow remains permanently as the mylohyoid groove. The part of the cartilage between the tympanic ring and the jaw becomes converted into fibrous tissue, and persists in the adult as the internal lateral ligament of the temporo-maxillary articulation, its proximal end through the Glaserian fissure being continuous with the slender process of the malleus. The part which is applied to the inner surface of the lower jaw disappears. In the tissue overlying the cartilage, ossification begins by several centers as early as the sixth or seventh week of fetal life, in this respect resembling the clavicle, by which it is alone preceded. The dentary or basal center forms the outer wall and lower border. With this is united the splenial portion, which appears somewhat later, forming the inner table from near the symphysis backwards towards the opening of the inferior dental canal where it terminates in the lingula. By the union of these two parts a groove is formed, which ultimately becomes covered in, and in which the inferior dental nerve and vessels are lodged. As has already been stated, the part of the body between the symphysis and the mental foramen is regarded as directly developed from the fore part of the Meckelian cartilage. As will have been gathered from the above description, the upper part of the ramus and its processes have no connection with Meckel's cartilage. *The condyle and coronoid process are each developed from a separate center preceded by a cartilaginous matrix.* (Italics are mine.) These several centers are all united about the fourth month.

It may be here noted in regard to his unqualified statement to the effect that there is a separate and distinct center of ossification for each of the coronoid and condyloid processes, he is not in accord with all authorities who have written upon the subject. It is stated by others that while these cartilaginous molds or matrices are present, their actual ossification takes place by an extension of the adjacent membranous layer of the dentary, and that they then undergo absorption. The main facts in connection with the ossification of the lower jaw in man, and, in fact, in all other mammals in which the process is known, may be thus summarized: (1) for each entire ramus there is at first a cartilaginous matrix, mold, or bar (Meckel's cartilage), continuous with the base of the skull and around which the dentary and splenial bones are developed; (2) to this main cartilage there is attached, or at least in intimate relation with it, an accessory cartilaginous mold or matrix, which gives rise to the condylar portion; (3) the anterior part of Meckel's cartilage is entirely converted into that part of the dentary lying between the mental foramen and the symphysis, which is therefore true cartilage bone; (4) the posterior portion of the dentary arises from the backward extension of the perichondrium surrounding the cartilage, but the cartilage itself does not undergo ossification but absorption; (5) the splenial is developed from the same perichrondrial membrane as the posterior portion of the dentary; and (6) the cartilaginous molds preceding the coronoid and condyloid portions either ossify from separate centers (according to Thompson) or receive their ossific deposits by means of a posterior prolongation of the perichondrial membrane from the dentary.

Now, what can we learn from these facts and what bearing do they have upon the transposition theory as a whole, and the homology of the articular with the malleus in particular? If Thompson's statement in regard to a separate center of ossification for the condyloid portion of the human jaw is correct, then the whole matter is settled and requires no further discussion; for in that event this ossification would represent the articular of the reptilian jaw beyond all reasonable doubt. But if we allow that this statement is erroneous and is not borne out by the facts, we have remaining the all-important feature or circumstance, about which there can not be the least doubt or uncertainty, that a cartilaginous mold or matrix, in intimate association with the Meckelian cartilage, is always present and precedes in the order of development the purely secondary or subordinate process of deposit of calcareous matter in this part of the cartilaginous ramus. As between the presence of this cartilaginous mold and the secondary process of its calcification, in morphological importance, there can be no question or argument whatever.

If this strict homologue or corresponding part of the reptilian or batrachian jaw has been bodily plucked out and removed to another situation, with a completely altered function in the mammal, then it is utterly inconceivable to me and entirely passes my understanding to imagine how this could have been accomplished without taking along with it the morphologically fundamental part of which it primarily consists. That this portion should have been left behind in its original and primitive position is to my mind more than significant. The burden of proof lies with those who maintain the transposition view, and if this difficulty can not be completely removed or explained, they can not only have no standing in court but the verdict is very likely to be returned against them, and for this purpose no amount of specious or hair-splitting argument will suffice.[1]

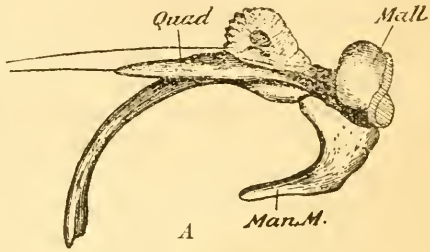
If it is found upon further investigation that there is never any independent and separate center of ossification developed in this cartilaginous mold in any mammal (and the whole list will have to be exhausted before this can be finally determined), then it is quite as reasonable, if not more so, to conclude that it has lost its power to develop calcareous matter within its substance and that this function has been entirely usurped by the perichondrial membrane of the dentary than it is to assume that it has been entirely removed from its original position. Numerous analogous cases can be cited from mammalian morphology in which an osseous element having a cartilaginous predecessor or antecedent has been lost and its function usurped by tissue of quite a different category. Thus in the second visceral arch, the epihyal element has completely disappeared in man and some other mammals and its function has been assumed by the connective tissue (stylo-hyoid ligament) which originally surrounded the cartilaginous rod of which it always consists in the embryo. The absorption, disappearance, and replacement of this rod can no more be taken to represent transposition of this element than the absorption and disappearance of the precondyloid cartilaginous mold of the lower jaw, it matters not what may subsequently happen to it in the way of substitution or ossification. If this precondyloid mold does not represent the reptilian articular element, then we have a right to ask what does it represent and why should it be so constantly present in the jaws of all mammals?

Along this line there is considerable evidence from the embryological side which, although not entirely conclusive, is at the same time strongly suggestive. I here call especial attention to Parker's figures of the developing jaw of *Galeopterus* (fig. 8), in which a separate and distinct piece is represented for a part of the condyle, or the jaw of the mole (fig. 13) in which not only the cartilaginous mold is clearly shown but the condyle itself is represented as distinctly separated from the remainder of the cartilaginous ramus. Such conditions as are seen in the mole are found in the developing jaws of many other Insectivora, and this accords well with the possible if not probable remains of a suture in this region of the jaw of *Rhynchocyon* already described. Among the Rodentia, moreover, especially some of the Hystricoidae as well as the Cricetine Myoids, the immature jaws so frequently show the remains of a suture separating

[1] In order to meet this difficulty, Gaupp *assumes* that this accessory cartilaginous mold is a purely secondary or new structure, which has been subsequently superadded to the mammalian jaw in the course of evolution. But such an assumption without the strongest kind of proof to support it does not add anything to the weight of his contention, for if it is not a part of, nor a derivative of, the original Meckelian cartilage, and according to his view is not connected with the formation nor development of any bone, what possible use can it subserve and why should it be present at all?

the condyle from the remainder of the ramus that it does not seem possible that it is altogether accidental. These same appearances are likewise seen in the young jaws of many other orders of mammals, and until such time as it can be shown by actual embryological investigation that these appearances are wholly deceptive and that no ossification ever takes place within the cartilaginous mold of the condyle we must continue to hold that it is not only possible but highly probable in some species of mammals at least.

From my experience in the examination and study of commencing ossification of the bones in mammals I have been especially impressed with the absolute necessity of selecting embryos of the proper stages of development in order to demonstrate any given point beyond possible doubt, and this among the rarer forms is by no means always convenient or an easy matter. In attempting to follow out this subject of the presence or absence of a separate and distinct center of ossification in the cartilaginous matrix of the mandibular condyle of the mammal, I am led to conclude that if ever it is present, which is more than likely, it is at best but feebly developed and is quickly overshadowed by the ingrowth of the osteogenic membrane of the dentary, and all vestiges of it obliterated.



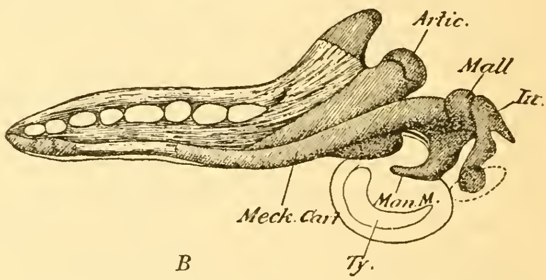


Fig. 13.—Talpa europaea. After Parker. A, advanced stage of development of Talpa europaea. B, young stage of development of same. *Artic.*, articular; *In.*, incus; *Mall.*, malleus; *Man. M.*, manubrium of malleus; *Meck. Cart.*, Meckel's cartilage; *Quad.*, quadrate; *Ty.*, tympanic.

In view of the facts and arguments above set forth, how premature appears the sweeping statement of Gregory to the effect that embryology gives no warrant for the belief that the mammalian jaw is composed of more than a single piece, already quoted. His second postulate in regard to the so-called Triassic and Jurassic mammals, if indeed they are mammals at all, does not appeal to me as having much weight. Out of all that are known, how many of them are sufficiently preserved to show the condyle at all, and of those that are thus sufficiently perfect how many are of a suitable age to show the sutures even if they had been present in the earlier stages of growth? One might argue with equal facility that the brain case of all bats, moles, or birds in a given osteological collection is composed of a single bone because it does not show sutures. By the same token, the basal Eocene representatives of any of the great orders of mammals lived but yesterday in comparison with the remote time when these changes were inaugurated. In a like manner, as no known Cynodont reptile can by any stretch of the imagination be considered directly ancestral to any group of mammals, no argument based upon their structure is very convincing.

Turning next to a discussion of the element or elements of the premallear tract of Meckel's cartilage mentioned in the preceding pages, I shall begin by quoting from Parker's description of the third stage of the embryo of *Choloepus hoffmanni*, in which he makes the following statement:[1]

> The main part of Meckel's cartilage has been used up—partly ossified and lost in the ramus and partly absorbed. The head of the Malleus, the osseous matter of which runs forward as the styliform "processus gracilis," has in front of it yet a large tract of the primary mandible. This thick semiosseous hook curves itself, after it becomes detached from the main bar, round the front of the tympanic cavity. The distal third is unossified; this bony tract is essentially a second "articulare internum" such as is seen in Holostean Ganoids. But this tract has a greater interest for the morphologist even than this, for such a remnant of the normal mandible is often present in adult marsupials, and for a time during the first autumn, the mole has a similar malleus, as I shall show in my next part. More than that, in a similar malleus of a young Koala (*Phascolarctos cinereus*) of the same size nearly as this young Unau, I find two small membrane bones in this premallear tract.

It seems strange to me that this highly important statement by Parker should have been so completely overlooked by subsequent investigators, since I have been unable to find any reference to it in any later work. In regard to that part of it, however, which speaks of "membrane bones" in the Koala, I have not had any suitable material of this species for study and I am unable to say, therefore, whether or not these elements of the premallear tract are "membrane bones," as he calls them. There can be no question, however, that they are preceded by a cartilaginous mold or matrix, just as much as are the incus and malleus, and whether they ossify wholly from the perichondrial membrane surrounding the cartilage, or whether a portion of the cartilage is involved in the process, they are certainly not entitled to the appellation of "membrane bones" in the same sense as this term is applied to the frontals, parietals, nasals, or other bones of this category. In the case of *Tupaia* and many other Insectivora, as well as in *Sarcophilus* and *Didelphis*, in which this element persists and undergoes ossification, the resulting bone is a solid rod or bar, and as far as I am able to judge, exactly like the stylo-hyal, epi-hyal, or cerato-hyal pieces of the hyo-mandibular arch.

[1] Morphology of the Skull, p. 65.

Now, no one would ever think of speaking of these hyo-mandibular elements as membrane bones, yet it would appear that their ossification takes place largely if not exclusively through the influence of the perichondrial membrane surrounding them. In the case of *Gymnura* and the kangaroo the ossification of the premallear element produces a solid, more or less thickened, three-cornered bony nodule, and this is to a certain extent true of this region of *Erinaceus*. In *Choloepus* again these elements are seen developing in and around the thick cartilaginous mold by which they are preceded, in a manner not at all dissimilar to that of the incus and malleus in the same stage of development, and what is here said of the Unau applies equally well to all other forms in which it is found. That the ossification of this element or these elements was originally the same and in no manner different from that of the incus and malleus, I do not think that there can be any reason to doubt, and if there are any differences at the present time they are due wholly to the fact that the latter are now functional elements still retaining their vitality and vigor, while the former are inconsiderable degenerate vestiges practically on the point of disappearance. If it can ever be shown that the cartilage itself is in the least involved in the process of ossification of these elements, in any of the species in which it exists, we can then conclude beyond any possible fear of error that it is a true cartilage bone and undoubtedly represents some missing element which originally pertained to the reptilian or batrachian suspensorium.

In all those cases wherein these elements appear in the premallear tract of the developing embryo, whether they be one or more than one, and continue into the half-grown or adult stages, it will be observed that the position is always the same, namely, to the inner side of the glenoid cavity and slightly posterior to it, passing around the inner edge of the tympanic ring, with which it often becomes intimately associated, and frequently having a free extremity projecting forwards toward the tip of the pterygoid, with which it is connected by ligament. This latter fact is highly suggestive, since it betokens a former bony connection between these elements, just as the stylo-hyoid ligament in the human subject connects the styloid process and the hyoid bone, and represents the missing bony element in the hyoid arch (the epi-hyal). Again, when we study this bone in such types as *Gymnura* and the kangaroo, we begin to realize that it has not only the exact position that would be assumed by a vestigial quadrate, but actually resembles certain parts of this bone in the reptilia. Thus we can imagine that the anterior pointed extremity represents the pterygoid process of the quadrate, the posterior extremity represents the divided posterior bar which joins the squamosal on the inner side and behind, and the blunt angular projection would be the remains of the articular head of the quadrate.

In a like manner the bone which I have described as the paramastoid may represent the vestige of that part of the quadrate which was formerly attached in this identical position.

In accordance with this conception that the vestigial element under discussion represents only a portion of the inner part of the original quadrate, we can readily understand its relations to the tympanic ring and why this latter bone should lie upon the outside of it. It will be recalled that the tympanic membrane or the eardrum is attached in the reptile largely to the outer edge of the quadrate, and when this bone began to disappear a new membrane bone was developed in the outer circumference or periphery of the membrane, namely, the tympanic ring—in order to afford the proper support for the drum. This is actually the case in some birds, notably the peafowl and others. Developing as it did in the periphery of the membrane, it would be manifestly impossible for it to be formed on the opposite side or inside of the quadrate, since its special office was the support of the eardrum, and hence as the quadrate was reduced to a vestige we find it lying upon the inner side of the tympanic. This fact supplies a powerful and convincing argument in favor of this interpretation of its homology with this part of the reptilian or batrachian quadrate. In fact I can not conceive of any other interpretation that can be placed upon it. It will thus be seen that the fate of the reptilian quadrate in the skull of the mammal was not, as supposed by Gadow, to become the tympanic, nor its transformation into the fibro-articular cartilage of the glenoid cavity as surmised by Broom, nor its absorption into the squamosal as held by Cope and Baur; but in a large number of mammals it still persists developed in the premallear tract of Meckel's cartilage, and either attached to the *processus gracilis* or incorporated with the tympanic or both.

In regard to the value of the evidence derived from the skull of *Ornithorhynchus*, already mentioned, I am not in a position at the present time, through lack of suitable material, to say whether or not the bone above described represents a distinct ossification and arises as a separate element from Meckel's cartilage in the embryo, but should such prove to be the case it will then offer powerful confirmatory evidence of the interpretation herein considered. It may be stated, however, that Watson [1] in a late paper on the Monotreme skull makes no mention of such an element, but whether his material was of a suitable stage to show it if present I have no means of knowing.

One of the insuperable objections that was urged by Gadow against this transposition theory, to the effect that it is inconceivable how the change could have taken place without seriously impairing,

[1] Trans. Philos. Soc., Ser. B, vol. 207, 1916, pp. 311–374, pls. 23–25. Not received in time for use in this connection.

if not completely destroying, the hearing, has never been met by the advocates of this view. Gregory attempts to reply to this objection in the following statement:[1]

Dr. Broom, in a letter to the writer dated July 20, 1911, wrote that he had decisive evidence showing that the doubted element is stapes and not tympanic. In Broom's figure ('11, p. 7, pl. 46, fig. 8) of the very primitive Cynodont *Bauria* this supposed stapes runs out toward the quadrate. Its distal end is imperfect, but Broom restores it in contact with the quadrate. The stapes is represented as reaching nearly or quite to the quadrate in *Cynognathus* (Broom, '04, pp. 490–498, pl. 25) and *Oudenodon* (Broom), *Dimetrodon* (Case), *Labidosaurus* (Williston), as well as in modern snakes, chameleons, tortoises, and some urodeles (Kingsbury and Reid) and caecilians (Kingsley). If, as now appears probable, the stapes touched the quadrate in Cynodonts, then it is clear that stapes, quadrate, and articular already formed a connected train of bones. Thus would be met Gadow's objection ('88) "that the incus can not be the homologue of the quadrate because of the impossibility of intercalating the quadrate as an incus into the ossicular chain as a link between the stapes (hyomandibula) and lenticulare (symplectic) and the malleus (articulare)." But the quadrate (incus) was not "intercalated" in the chain; it was there from the time that the hyomandibular (stapes) became attached to it (p. 28).

In just how far this statement constitutes an answer to Gadow's objection we shall presently see.

If we consider the subject from the broad standpoint of evolution alone, there are so many serious objections that can be raised against any such theory as to render it not only highly improbable but quite impossible. When we reflect upon the important rôle the function of hearing must always have played in the animal economy, and how necessary and vital it must have always been to those animals of a terrestrial habitat, we are then prepared to understand something of the nature of the evolution and development of this delicate and highly complex apparatus, which we have every reason to believe has taken untold generations to complete and perfect. As its highest development is now found in mammals, in which it is remarkably similar in all, we have a right to believe that the promammalian reptiles or batrachians from which they were derived had an auditory apparatus, which, while perhaps not as delicate and finely fashioned as that of the mammal, must have, according to the very nature of the case, approached it in delicacy, efficiency, and fineness of finish. There can be little doubt that it must have equaled at least in effectiveness that of birds or crocodiles living to-day, if it did not surpass them in this regard.

We may go even further than this and declare without fear of error that in all probability these promammalian reptiles, if, indeed, they were reptiles at all in the strict sense of the term, had a rudiment of an external ear; that they had a highly developed tympanic membrane stretched in front upon the quadrate, above

[1] Critique of Recent Work on the Morphology of the Vertebrate Skull, Especially in Relation to the Origin of Mammals, Journal of Morphology, vol. 24, No. 1. March, 1913.

upon the squamosal, and behind in the higher forms probably upon a delicate, commencing tympanic bone, similar to that seen in the peafowl among birds; that they had a capacious tympanic cavity, provided with eustachian tube opening into the pharynx, a fenestra ovalis and fenestra rotunda leading to the labyrinth; that across this tympanic cavity was stretched a chain consisting wholly of delicate bones or in part of cartilaginous elements, one end of which fitted into the fenestra ovalis and the other attached to the ear drum, in order to conduct the sound waves or impulses of the tympanic membrane to the lympth of the labyrinth; and, lastly, that the internal ear was provided with its proper semicircular canals, utricle, saccule, and cochlea, which may or may not have been spirally coiled.

Now, when we study the structure and function of this apparatus in its higher development, whether it be in the mammal or the higher Sauropsida, such as in the crocodile, in the birds, or even in the higher Batrachia, as in the frog, we are forced to conclude that one of the fundamental, essential, and all-important objects of its evolution has been delicacy and fineness of finish. This appears perfectly obvious, for the reason that without this delicacy of structure the finer sound waves could not be transmitted or recognized, and if its possessor were in any way dependent upon such recognition for any purpose whatever, then, in the event of its impairment, its further evolution would have been arrested and would have immediately ceased. If, on the other hand, we study the structure and function of this apparatus in its more primitive stages or less perfect manifestations, such as in the tailed Batrachia and many of the living Reptilia, we can begin to understand through what steps or stages it arose in the higher or more developed types. Thus, in all Batrachia except frogs there is no tympanic cavity and no tympanic membrane. There is no fenestra rotunda, and the internal ear is altogether primitive. In snakes and Amphisbaenoids there is no tympanic cavity nor tympanic membrane. In many Chelonia, in *Sphenodon*, and chameleons the tympanic membrane is covered with integument, etc. All of these facts, as well as many others that could be mentioned, simply go to show how the more perfected development has been brought about.

Another fact to be mentioned in this connection is that in all the lower types of structure of this hearing apparatus the quadrate is always present and strongly developed and acts as a suspensorium of the lower jaw, just as is the case with the articular, the element by means of which it is hinged or articulated with the mandible. But at the same time it must not be concluded that a delicate hearing apparatus is not consonant nor consistent with the presence and full development of these bones, for in birds a well-developed quadrate and articular are present and in their usual positions, and the hearing ability of birds, as is well known, is scarcely inferior to that of the most highly developed mammals. We are therefore not only at liberty to assume, but we are forced to conclude that the hearing apparatus of the promammalians, whatever they were, must have already reached a comparatively high state of development and was a delicate one before they passed into the mammalian stage, with both quadrate and articular still functioning as suspensoria and not as auditory bones, else they could not have been their forerunners.

Bearing in mind, then, the delicacy of this mechanism, with its chain of bones, one end of which was fixed in the fenestra ovalis and the other in the eardrum, and whose efficiency in performing the function for which it was especially evolved through untold preceding generations, was largely dependent upon its mobility and power to respond to the most delicate impressions made upon the eardrum, what may be asked would have been the result of any interference, however slight, with the free movement of any of these elements within their respective and prescribed arcs?

If one were to ask any physician who has had the least experience in treating diseases of the ear about such an interference, he would be compelled to reply that it would invariably result in permanent deafness or complete loss of hearing. Any thickening of the mucous membrane through inflammatory processes produces serious impairment of the hearing apparatus by reason of limiting or restricting the free movement of the ear bones. Even occlusion of the eustachian tube, by means of which the equalization of the density or rarity of the air in the tympanic chamber is maintained, results in deafness. Yet we are called upon to believe that a clumsy quadrate, in its supposedly new function could have impinged with impunity upon the delicately movable stapes, without producing an impairment of the hearing which could have had no other result than the extinction of the animal.

Gregory goes even so far as to picture a second eardrum, located in advance of the old one, and attached to the articular and quadrate, which in turn acted upon the stapes, both functioning at the same time.[1] If any such device ever existed in any mammal, it is indeed strange that embryology should not give us the faintest hint or clue, nor furnish the first scintilla of evidence of its former presence. As regards Gregory's reply to Gadow's objection, the question is not what may or may not have constituted a "train of bones," morphologically or otherwise, but *how could the quadrate have been intercalated functionally in an already delicately movable chain of bones without destroying or affecting the movement of the stapes?* As a reply to this question it is a failure. Since an impossibility can not be explained otherwise than as a thing that can not be done, we must

[1] Journal of Morphology, vol. 24, 1913, p. 34, fig. 23.

continue to hold that Gadow's objection constitutes a fatal and insuperable impediment to this impossible hypothesis.

If the facts and arguments above set forth are not sufficient to completely disprove the transposition theory, there is yet another, and I shall conclude the discussion of this subject by directing attention to a body of evidence which I regard as the most important and conclusive of all. Did this evidence stand alone without the support of the facts hereinbefore mentioned, it would be amply sufficient in itself to utterly annihilate and destroy any possibility of the truth of this hypothesis. It may be stated as follows: Huxley in his treatise on the anatomy of the Amphibia, in describing the skull of *Rana esculenta* says: [1]

> The slender permanently cartilaginous hyoidean cornu passes into the cartilage of the auditory capsule on the ventral side, between the fenestra ovalis and the articular surface for the crus of the suspensorium. The fenestra ovalis lies in a cartilaginous interspace between the exoccipital and the prootic and is filled by the oval cartilaginous stapes. The anterior face of this presents a concave facet for articulation with a corresponding surface occupying the posterior half of the inner end of the *columella auris*, the anterior half of which fits into a fossa of the prootic bone. The columella itself consists of three portions, a middle elongated osseous rod, an inner swollen cartilaginous part, which articulates with the prootic and partly with the stapes, and an outer portion, which is elongated at right angles to the rest, fixed into the tympanic membrane and attached by its dorsal end to the tegmen tympani.

What more completely homologous arrangement of the several parts of this auditory apparatus, as well as the homologies of the elements themselves, with that of the mammal could possibly be asked for? The essential points of similarity are seen in (1) that the proximal end of the hyoidean arch does not join the auditory capsule through the intermediation of the stapes or the columella, as in birds and reptiles, but is joined directly to it as in the mammals; (2) that the auditory chain consists of four main elements, namely: a cartilaginous stapes, a swollen cartilaginous inner end of the columella, a bony columella itself, and a cartilaginous portion fixed into the tympanic membrane; (3) that the stapes is short and nodular (mammalian) and not long and styliform (sauropsidan); (4) the element articulating with the stapes next upon the outside also articulates by a distinct facet with the prootic on the side wall of the capsule like that of a mammal and not like that of a reptile; (5) that of the transverse cartilaginous element, upon the outside, the ventral end is fixed into the tympanic membrane, and (6) that the element lying next upon the inside forms a bony connection between the last named piece and the base of the columella.

In attempting to determine the homologies of these several elements of the auditory chain in *Rana* and those of a mammal, it is not difficult to discover that the *stapes in the two is strictly homologous beyond any shadow of a doubt.* In a like manner there can not be

[1] Encyclopedia Britannica. Ninth Edition. 1875, pp. 661, 662.

the faintest doubt or uncertainty, it seems to me, *in homologizing the succeeding element of the frog with that of the incus of the mammal.* The outstanding and all-important foundation for such a homology, rests upon the fact that it articulates not only with the stapes by a distinct facet, but it likewise articulates with the prootic, in the side wall of the otic capsule, just as the short process of the incus is, without exception, received into the *fossa incudis* in all mammals and that, moreover, in the same identical position as in the frog. This is not the case in any known reptile or bird living or extinct.

If, therefore, we are thus enabled to establish the identity or homology of these two important elements in the auditory chain of *Rana* and the mammal, what of the remaining elements? They must clearly then correspond to, and be homologous with the malleus, the cartilaginous transverse portion, the ventral end of which is fixed between the layers of the ear drum, representing the *manubrium of the malleus*, the dorsal end having probably degenerated into the superior mallear ligament; and the osseous portion representing *the head and body of the bone in the mammalian auditory apparatus.* The correctness of this determination is further established by the researches of Kingsley, who has conclusively shown that the manubrium of the malleus arises as a separate element in the auditory chain of the mammal.[1]

That the mammalian auditory chain originally arose and was developed from a chain of elements *similar in all respects* to that now found in the Anourous Batrachia, there can be therefore apparently little or no question whatever. If on the other hand the auditory chain of the Reptilia has always been characterized by the essential features now displayed by the modern Sauropsida, then in that event they can not have had anything to do with the ancestry of the Mammalia, however much they may have approached them in other respects. These features are seen in the long styliform condition of the stapes, the absence of any element corresponding to the incus, which has attachment to both stapes and the side wall of the auditory capsule, and finally, the union of the proximal end of the hyoid arch with the auditory chain, instead of the auditory capsule itself, entirely independent of any part of the former. *These differences are fundamental and profound*, and they map out most clearly and distinctly the trend of the two lines of descent.[2]

[1] The Ossicula Auditus, Tufts College Studies, vol. 1, pp. 203-274, 1900.

[2] Huxley further states in the same article that in *Menobranchus* among the Urodela, in which there is no tympanic cavity nor tympanic membrane, the stapes is relatively large and conical in form, from the conical end of which a strong ligament passes to the posterior face of the suspensorium. The hyoidean apparatus is represented, upon each side by a cartilaginous rod, subdivided into a short hypo-hyal and a long cerato-hyal. A strong ligament extends from the face of the latter, below its free summit, to the suspensorium, reaching this at the same place as the stapedial ligament, into which it is continued. This in connection with the styliform stapes of *Amphiuma* which is articulated directly to the posterior part of the suspensorium ,together with the strong hyo-suspensorial ligament and the weak hyo-mandibular ligament, seems to foreshadow the sauropsidan condition of these parts in the Urodela, quite in the same manner that the auditory chain of the Anoura foreshadows that of the mammal.

Tested by these characters, where do the extinct Cynodonts stand? Comparatively little is known of the auditory apparatus in these forms, but such information as has been recovered seems to point in the direction of the Sauropsida and not the Mammalia. This is shown by the styliform condition of the stapes, alluded to above, which is known in some of them at least, and which resembles that of *Sphenodon*. As the styliform stapes goes with the hyoid attachment, as well as the absence of any element corresponding to the incus, with its peculiar and characteristic relations to the prootic the inference would naturally be that their real affinities are with Sauropsida rather than with the mammals. If these characters are true of all of them, then they would constitute an insurmountable barrier and completely shut them out from any further consideration as ancestors of the Mammalia, it matters little what other mammalian characters they may have possessed.

There are not wanting among investigators of the present day many who loudly proclaim the Cynodonts to be the long-sought ancestors of the Mammalia, but until such time as the important matters herein discussed can be thoroughly cleared up and disposed of, we must reserve our judgment and await future discoveries. At all events as shown above, the monstrously improbable, if not altogether wholly impossible hypothesis of the intercalation of the quadrate and articular into the mammalian auditory chain, can not serve any purpose other than to befog the issue and prevent any clear understanding of the subject. It may well be that we shall yet have to go back directly to the Batrachia to find the beginnings of the Mammalia, as Huxley long since pointed out with such masterful skill. This view has been subsequently defended by Kingsley.

In the study of the foregoing subject I have consulted the following papers, other than those specifically mentioned in the footnotes of the text, namely, the numerous papers by Gaupp, the highly important contributions by Gadow, as well as those by Broom, Fuchs, and others.

Some probable causes for the disappearance of the quadrate.—Taking the quadrate of an average reptile like that of *Sphenodon* (figs. 14,15,16) it is to be observed that it is solidly attached to the cranium by a series of bony arches, bars, and braces, which give firm support to the articulation of the lower jaw. Above and to the inside it is attached to the lower end of the temporo-occipital arch, furnished principally by the squamosal, where it is stoutly braced from within by an outward projection of the exoccipital. Upon the outside, on a level a little above the articulation, it is braced in front by the quadratojugal bar, and above by a depending process of the squamosal. Running forwards and inwards from the articular joint is a broad stout vertical lamella of bone which unites with the pterygoid constituting what may be regarded as the main brace of the quadrate. The braincase lies in the V-shaped interval between these two main braces of the quadrate almost adjoining it, and it is to be observed that the points of articulation of the lower jaw are widely spread apart and occupy a position nearly as far back as the tip of the occipital condyle.

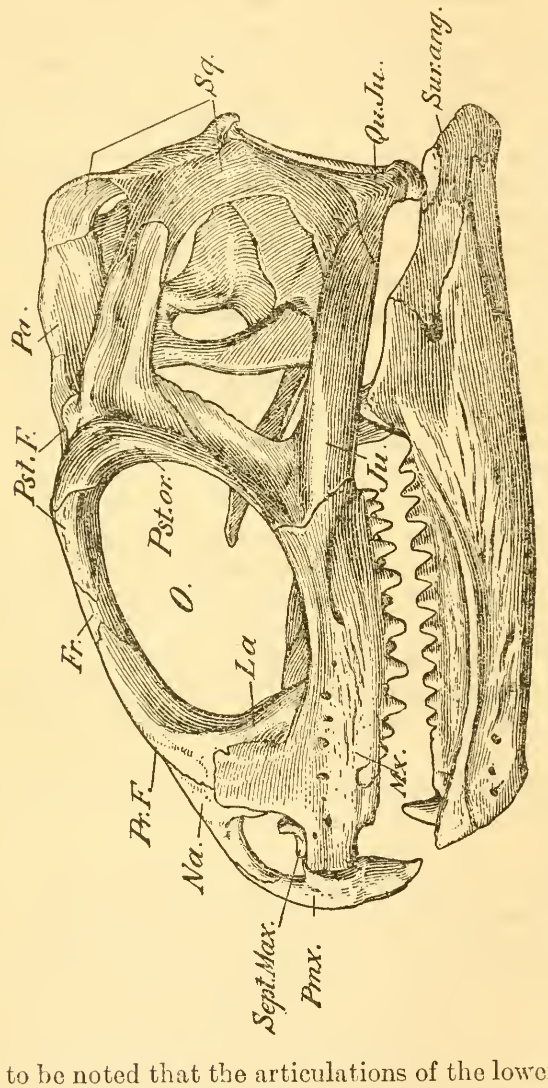


FIG. 14.—SPHENODON PUNCTATUS. *Fr.*, FRONTAL; *Ju.*, JUGAL; *La.*, LACHRYMAL; *Mx.*, MAXILLARY; *Na.*, NASAL; *O.*, ORBIT; *Pa.*, PARIETAL; *Pmx.*, PREMAXILLARY; *Pr. F.*, PREFRONTAL; *Pst. F.*, POSTFRONTAL; *Pst. or.*, POSTORBITAL; *Qu. Ju.*, QUADRATOJUGAL; *Sept. Max.*, SEPTOMAXILLARY; *Sq.*, SQUAMOSAL; *Sur. ang.*, SURANGULAR.

It is also to be noted that the articulations of the lower jaw lie upon a plain much below the base of the brain. Between the well-fixed quadrate and the side wall of the brain case there is a relatively large space which is occupied by the powerful pterygoid and temporal muscles, which close the jaws, and is in direct relation with the biting powers of the animal as well as its dental armature.

As we know so little about the immediate and direct reptilian or batrachian ancestors of the mammals, it is impossible to say just what the more precise relations of the quadrate really were originally, but in a general way they could not have been very different in arrangement and disposition to that seen in *Sphenodon*. That the quadrate was well fixed to the skull and afforded firm support to the lower jaw is a foregone conclusion, since without such an arrangement the powers of prehension and comminution on the part of the teeth could not have developed. If therefore we are to start with a more or less fixed quadrate, braced in a manner not dissimilar

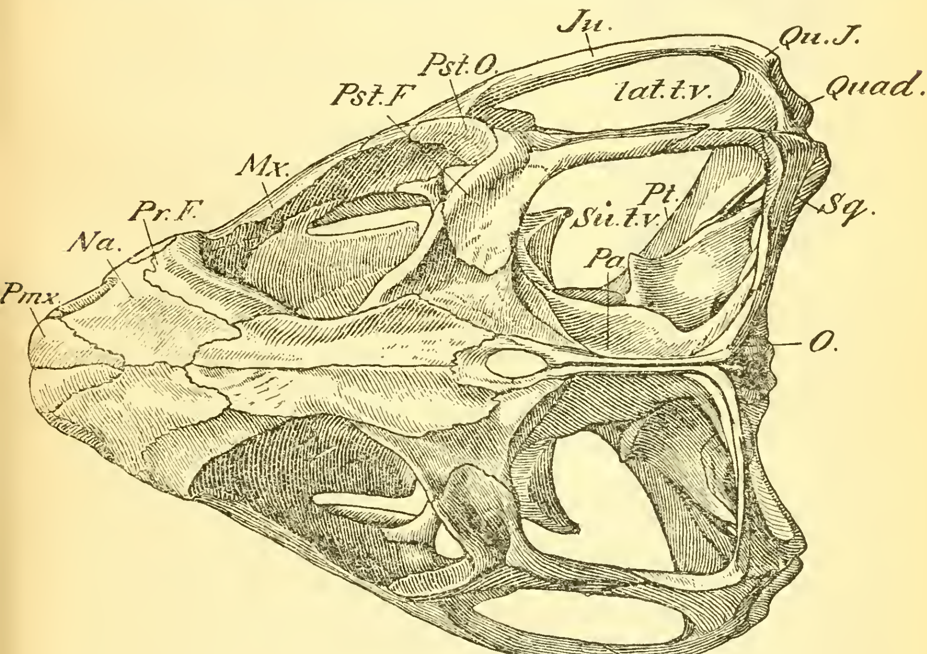


Fig. 15.—Sphenodon punctatus. *O.*, occipital. (Other letters as in figs. 14 and 16.)

to that already described in *Sphenodon*, what would happen to these braces of the quadrate did the brain case commence to enlarge? Obviously the main brace running forwards and inwards to the pterygoid would be one of the first to be encroached upon and interfered with, for the reason that it lies almost in contact with the brain case. If the brain enlarged in all directions, which we have every reason to believe that it did, and allowing that the pterygoid and temporal muscles remained the same, the space which they originally occupied would be diminished, and they would in turn exercise pressure upon their enclosing arches and cause profound changes in them. This process would powerfully affect the other supports of the quadrate. That some such factors were operative, and in a large measure responsible for the changes in the quadrate, is strongly suggested by the modifications of the *tegmen temporalis* or temporal bony roof of the more primitive Reptilia. Certain fenestrae or vacuities were formed in this bony covering, I apprehend as a result of muscular pressure, in order to allow more space for the expanding muscles when powerfully contracted. As the brain case continued to enlarge it finally reached a point where the squamosal came in contact with it and was applied to its outer wall, receiving its support and stability from this source and no longer existing as an expanded and widely separated arch.

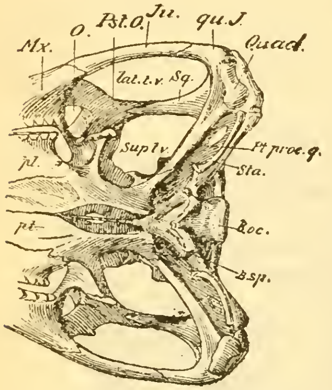


Fig. 16.—Sphenodon punctatus. *B. oc.*, basioccipital; *B. sp.*, basisphenoid; *lat. t. v.*, lateral temporal vacuity; *Pl.*, palatine; *Pt.*, pterygoid; *Pt. proc. q.*, pterygoid process of quadrate; *Quad.*, quadrate; *Sta.*, stapes; *Sup. t. v.*, supra temporal vacuity. (Other letters as in fig. 14.)

Since there must at all times have existed the most intimate relations between the movements of the jaw, the dental armature and the temporal and pterygoid muscles, as well as their area and points of attachment, and as these in turn reacted upon the bony supports of the quadrate, we may safely conclude, it seems to me, that the diminution and final loss of the quadrate may be traced directly to and was the logical result of these interacting mechanical forces and factors. As the quadrate lost its bony supports and braces and was no longer capable of furnishing a proper fulcrum for the leverage of the jaw, the articulation began to shift forward upon the more fixed squamosal where the joint was finally located, the quadrate dwindling away to the inconsiderable vestige which has already been discussed. If therefore, these modifications of the quadrate, the arches, the teeth, the jaws, and, more than likely, the palate as well, are traceable to these causes which were primarily inaugurated by the enlargement of the brain, or, in other words, those very changes which transformed the reptile or batrachian into the mammal in so far at least as the skull is concerned, then the interesting question arises were these modifications confined to a single group of reptile-like forms, or is it not possible that they could have been inaugurated in widely separated groups quite independently? If the progressive enlargement of the brain has been one of the prime determining factors in the process, then it would appear probable that it was not confined to any one group of promammalian reptiles or batrachians any more than this special character is confined to any particular group of mammals today. It is a well-known and universally recognized fact in evolution that similar habitat, environment, and conditions have produced similar structures to such an extent that it is often difficult to say in certain cases whether given resemblances represent real genetic affinities or are mere convergences. How much more likely that this should have happened where the result was dependent upon a single or a few primary factors, like the enlargement of the brain and the functional development of the teeth. Altogether I am disposed to look upon the polyphyletic origin of the Mammalia as not at all improbable.

The temporal area.—In the primitive reptilian skull the temporal area is completely covered over with a bony roof (*tegmen temporalis*), freely communicating in front with the orbital cavity and having a large opening behind on each side and above the foramen magnum, the supraoccipital vacuity. In the recent state this latter opening is largely occupied by the powerful neck muscles which are attached to the skull in this region, just as the space under the bony roof and between it and the brain case is occupied by the temporal and pterygoid muscles. Upon the outside and below the supraoccipital vacuity is a second opening piercing the quadrate from before backwards, whose boundaries may be furnished by the quadrate alone or in conjunction with quadrato-jugal. As the upper vacuity is called the supraoccipital so the lower should be termed the *lateral* occipital or quadrate vacuity.

In different orders of the Reptilia this bony roof loses its continuity and is interrupted by one or two openings called, respectively, the *supratemporal vacuity* and the *lateral temporal vacuity*, the various arrangements of which furnish some important characters for the classification of the major divisions. As a result, therefore, of the appearance of these vacuities, the *tegmen temporalis* is broken up into the various arches or arcades which furnish the boundaries of these openings. Thus we have in such a typically reptilian skull as that of *Sphenodon* (fig. 15) a temporo-occipital arch or arcade which occupies the position of the lambdoidal crest of the mammal, above and to the outside of the occipit, and separates the supraoccipital vacuity behind from the supratemporal opening in front. We likewise have a supratemporal arcade running backwards from the postorbital arch, cutting off the supratemporal vacuity from the lateral temporal opening and lastly the postorbital arch limiting the orbit behind and the quadrato-jugal arch completing the boundary of the eye cavity and the lateral temporal vacuity below.

It has been already noticed on a former page how in the transition from the reptilian or batrachian to the mammalian condition, because of the great enlargement of the brain case many of these arches and vacuities have either been obliterated or profoundly modified, most probably as a direct result of muscular pressure; and it now remains to discuss the possible or probable types of reptilian or batrachian skull from which some of the various types of mammalian skulls could have been derived. If we compare such reptilian skulls as those of *Cynognathus*, *Procolophon*, and *Sphendon* it will be seen that they differ from each other considerably not only in the disposition of the component bones and the arrangement of the vacuities, but in the general shape and form as well. Thus *Cynognathus* has an elongated, compressed, narrow type of skull with a small orbital cavity and a large supratemporal vacuity, while *Procolophon* exhibits a short, broad, flat type of skull without supratemporal vacuity and with a large orbital cavity. The large temporal area in *Cynognathus* with its strong sagittal crest and a well-developed coronoid process of the lower jaw is in direct correlation, moreover, with the size and strength of the temporal and pterygoid muscles, as well as with the enlarged canines and the more or less molariform character of the teeth. These features are in marked contrast with the small temporal area, the reduced coronoid, and the comparatively weak development of the teeth in *Procolophon*. Then, again, in this latter genus we observe how the parietal is extended laterally and sends down a strong process behind the orbit to assist in forming the postorbital bar. If this latter condition exists in any Cynodont I have been unable to find any mention of it or refer to any figure showing it.

If now we turn to the skulls of the mammals we see that these same different types are to be met with among them. Thus all the Carnivores and carnivorous Marsupials exhibit the compressed, narrow, elongate skull, with large temporal area and prominent crests for the attachment of the temporal muscles in direct correlation with the enlarged coronoid and the powerful laniary canines. The eye cavity is relatively small and the postorbital process of the frontal has been shoved far forwards in advance of the junction of the frontal and parietal where these two bones meet above the orbit. On the other hand, taking such types as *Rhynchocyon*, *Tupaia*, *Procavia*, *Galeopterus*, and to a less extent the skulls of the Rodentia, Primates, and *Myrmecobius*, it will be observed that the cranium is relatively short and broad, the temporal area is reduced, the coronoid of the mandible is small and the parietal sends a large process downwards and forwards to form either a large part of the postorbital bar or to contribute to its make-up. This is especially true in the case of the first four of these types in which the postorbital process springs either from the point of junction between the frontal and parietal or largely from the parietal alone, while in the others the origin of the postorbital bar above is slightly in advance of the parieto-frontal suture.

If this latter type of skull arose from a reptilian condition such as is seen in *Procolophon*—and this would seem to be reasonably demanded by the facts—then this region of the skull of *Rhynchocyon* must be the most primitive of all this group, since it most resembles the arrangement of the conditions seen in the reptile. From the structure and relations of the temporal area as exhibited in *Rhynchocyon*, to such a type as *Tupaia*, *Galeopterus*, or *Procavia*, the transition is easy and accomplished with very slight modifications. In the same way slight further modifications would produce the conditions found in the Primates, Cheiroptera, Rodents, and *Myrmecobius*, in which the point of origin above of the postorbital bar is located slightly in advance of the parieto-frontal union. If these conclusions are well founded, then it becomes a matter of considerable doubt whether the postorbital bar of the reptilian stage has ever been broken through and destroyed in such forms as *Tupaia* and the Primates, in which it is complete, but still lingers as a heritage from their reptilian ancestors. If, moreover, this type of mammalian skull is to be traced to a reptilian source of this nature, then it would appear that there must have been two or more types of reptilian skull from which the mammal was derived, since it is inconceivable that the form displayed by *Rhynchocyon* could have arisen from such a type as that shown by the carnivore or carnivorous Marsupial in which the relations of the temporal area and its surroundings are so fundamentally different.

If the Cynodonts have had anything to do with the ancestry of the Mammalia—and it is undeniable that they exhibit many decided approaches to the mammalian condition in their structure—then we must assume (1) either there existed an unknown group of them with a skull form not very different from that of *Procolophon* from which all mammals were derived, or (2) that the mammals arose from more than one type, or (3) that the mammalian resemblances of the Cynodonts are purely accidental and without any special significance as far as direct ancestry is concerned. These alternatives are suggested by the fact that the Cynodont skull as we at present know it could have given rise to the carnivorous type of skull alone, and it is unthinkable that the other type of mammalian skull as exemplified by *Rhynchocyon* could have been derived from this form. We can readily understand, on the other hand, how the compressed narrow type of skull could have arisen from the *Rhynchocyon* type, since we have the examples of *Cercoctenus* and *Petrodromus* before us, which are more or less transitional between the two and afford an explanation of how the other Insectivora may have reached their present condition. In these two genera there is no bony postorbital process above or below, but along the upper margin of the orbit and as far back as the parieto-frontal suture there is in the recent state a dense, thickened, more or less triangular fibrous pad, which is attached to a roughened area on the eye margin, which undoubtedly represents and is the remains of the postorbital process. This fibrous pad is intimately connected with the fascia covering the temporal muscle behind, the deep fascial lining of the eye socket, and sends down a strong band to the zygomatic arch to complete the posterior boundary of the orbit. The orbital edge of the parietal, moreover, is produced and angulated, furnishing a condition very similar to that seen in *Tupaia*, with the exception that the bony parts representing the post frontal and the postorbital have been reduced to the fibrous structure already mentioned. The general shape of the skull is more compressed and elongated than in *Rhynchocyon*, but the temporal area is small, the temporal muscle is weak and the mandibular coronoid is little developed. The extreme development of these modifications is to be seen in *Centetes* among the modern Insectivora in which the skull is long, narrow, and compressed, the temporal area greatly enlarged, with unusually high crests, and with complete absence of a postorbital process. Directly correlated with these latter characters is the loss of the zygomatic arch and the great enlargement of the mandibular coronoid. Thus the various steps may be conceived of just how the elongated and compressed type of skull could have arisen in the Insectivora at least.

Myrmecobius among the Marsupials occupies nearly the same position in this group with reference to these characters that *Rhynchocyon* does among the Insectivora, and if the Mammalia are of monophyletic origin then, in my judgment, we must look for the precursor of this type of skull in their reptilian ancestry rather than the carnivorous type. If, on the other hand, the various orders of mammals arose from more than one group of reptiles independently, which upon the whole appears to me not at all impossible or improbable, then it would be only reasonable to suppose that there were various forms of skulls developed while yet in the reptilian stage which passed into the mammal.

Mammalian interparietals.—Another matter of importance in connection with the temporal area in the mammalian skull is the presence of an extra bone often seen intercalated between the parietals and the occipital which is always referred to as the *interparietal*. Careful investigation of the development of this seemingly unpaired element reveals the fact that it is always developed from at least two centers, and there may be as many as four. I have not been able to find any ossification corresponding to an interparietal in any of the carnivorous Marsupials except the Bandicoots and *Myrmecobius*. In the former of these species there are two elongated ossicles surmounting the lambdoidal crest which without much doubt represent paired interparietals. In *Myrmecobius* these bones consist of a pair of sizable ossicles lying upon either side of the median line just in advance of the occipital crest at the junction of the occipital with the parietal. It is very commonly present in the adult skulls of the kangaroos and phalangers, and when sufficiently young stages are examined is seen to develop from at least two centers, if not more. The apparent absence of these elements in the majority of the carnivorous Marsupials may be due either to their gradual crowding out upon the occipital crest as seen in the Bandicoots or their union with the occipital at a very early period; but it may be said that in opossum embryos of very young stages they are not evident.

According to the researches of Parker no elements corresponding to interparietals are ever found in the Edentates except *Orycteropus*. I have not found any traces of them in very young embryos of *Dasypus*, and it is doubtful whether they exist in any of the American Edentates.

Among the Cheiroptera interparietals can always be distinguished in the young stages, and they arise from at least one and probably two pairs of ossific centers. This is also true of the Rodentia, although I have seen little or no evidence of a second pair of centers in this group. In the Insectivora one pair of centers for the interparietal can always be made out in the youngest embryos, and in *Ericulus*, as figured by Parker, there are two pairs of centers for these bones. In the human skull Thompson states that there are two pairs of centers which early unite to form the squamous part of the supraoccipital; and by inference this is true of the other Primates, although I have not seen sufficient embryological evidence to establish it beyond doubt. In *Cheirogaleus* and *Microcebus* among the Lemuroids there is a large and distinct interparietal in the adult skull, but in the adult stages, at least, it is absent in the skulls of other lemurs. Among the Carnivora an interparietal is present in the dogs, cats, seals, bears, raccoons, and probably in all others of this order in the younger stages of development. An interparietal is also found in *Procavia*, in the Ungulates, and the Cetacea, and lastly a pair of large interparietals are seen in the Monotremes.

The homology of one pair of these interparietal elements with the corresponding bones in the reptilian skull is apparently not difficult to discover, and if we can judge from the position and relations as seen in many reptilian types, they must represent what are called supratemporals by many authors. It does not appear certain from the numerous figures of the skulls of the extinct Reptilia whether or not there are any of them that have, in addition to the supratemporals, a pair of prosquamosals, but if such is the case then this second pair of interparietals would be homologous with them. There can be no doubt, however, that the extinct Batrachians always show three pairs of bones in this situation; and if the supposed reptilian ancestors of the mammals have only a single pair of these elements it is not easy to understand how they could have given origin to those mammals with two pairs of these bones.

In the preparation of the foregoing paper my best thanks are due to Mr. G. S. Miller, curator of the Division of Mammals in the United States National Museum, for the free use of the material under his charge, as well as for much kindly help and advice. I am also especially indebted to Messrs. J. W. Gidley and Charles W. Gilmore, of the Division of Vertebrate Paleontology of the Museum, for much valuable help and assistance. In the course of preparation of the manuscript I have discussed with these keen students of the subject each and every point of the conclusions herein reached, and I feel that they are entitled to something more than a mere formal acknowledgment. The illustrations have been faithfully executed by that veteran illustrator, Rudolph Weber, in his usual masterful manner.