THE SKULL OF *ORNITHORHYNCHUS*, ITS LATER DEVELOPMENT AND ADULT FEATURES

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The following description of the *Platypus* skull was inspired by, and is very largely based upon, a very fine series of young skulls placed at our disposal by Prof. Launcelot Harrison, and we have to thank him very sincerely for having given us this opportunity. We have also to thank Dr C. Anderson, the Director of the Australian Museum, for the loan of two adult skulls.

Actually we have had for study nine heads and skulls, of which the first five are those given us by Prof. Harrison.

A brief description of the collection follows.

Specimen A. This was the head taken from a foetus measuring 175 mm. from tip of snout to tip of tail. It should be noted in passing that this specimen was intermediate in age between Prof. Wilson's two foetuses studied by Watson. The skull of this specimen was dissected out and divided along the mid-sagittal plane, one half was dried and the other rendered transparent.

The prepared skull measured 25 mm. from tip of snout to the plane of the occipital condyles.

Specimen B. A dried skull measuring 48 mm. in length. This tiny little skull was completely disarticulated except for the group of bones depicted in fig. 1, p. 449.

Specimen C. A skull 50 mm. in length. In this only sufficient bones have been removed to expose the cranial cavity and the nasal cavity on one side. As would be anticipated there is practically no difference between the bones of these last two specimens, so that we have been able to use the disarticulated specimen to check off form and relations in this skull. There are retained in position in this specimen certain sheets of cartilage and connective tissue which will be described in connection with those bones which our material indicates are developed from them.

Specimen D. 65 mm. in length. In this young skull ossification is so far advanced that all the bones present nearly adult features. All the sutures are open except that between the hinder end of the pterygoid bone and the inner face of the processus alaris, which indeed is closed in Skull *B.* This skull is illustrated in three aspects on Plate I.

Specimen E. 80 mm. in length. This is the young adult skull briefly described by Watson (1916). The full adult condition is reached in nearly all the bones; most of the sutures, though closed, are clearly discernible.

Specimen F. An adult skull 102 mm. long.

Specimen G. A partly prepared skull measuring 112 mm. from tip of cartilaginous snout to occiput. This is apparently a little younger than the last. Both these last two were loaned to us by Dr Anderson.

Specimen H. Over 100 mm. in length, it is the skull of an old adult and was cut about and opened up very completely before it was thought to measure it.

Specimen J. An adult head in the flesh. It was divided along its length just to one side of the mid-sagittal plane. One half was then dissected clean, and both halves were decalcified. The other half was now cut by hand into thick slices and both halves were then rendered transparent. These transparent preparations enabled us to check the course of nerves and vessels, and the position of the cavities of the otic labyrinth.

The last two specimens are the property of the senior author.

A comparison of our 48 and 50 mm. skulls with Prof. Wilson's older foetus, as described by Watson, indicates that there has not been much advance in ossification in the intervening stages. We have therefore a very complete series by which to connect the earlier development of the skull with the adult features.

Particular attention has been paid to this aspect of the work and, as a result, we have been able to correct one or two misinterpretations of the adult skull, notably the origin, extent and situation of the presphenoid and ethmoid ossifications and the discovery that the squamosal bone is excluded from sharing in the formation of the inner wall of the cranial cavity.

We believe that an independent lachrymal bone is present as an independent entity in the youngest skull (25 mm.) and is still recognisable in the 48, 50 and 65 mm. skulls, but on this point we are not able to make a definite statement.

As there is no complete description of the *Ornithorhynchus* skull in the English literature we have extended our work to fill this want.

A discussion on the significance of the alisphenoid lamina of the periotic bone, for which the senior author alone is responsible, forms the concluding portion of this communication.

REGIO OCCIPITALIS

The occipital segment is composed of four separate ossifications.

The *Basioccipital bone* viewed from the ventral aspect in the young adult skull *E* is seen forming the postero-medial part of the basis cranii, and for descriptive purposes it may be said to consist of an anterior and a posterior portion separated, or joined, by a neck which is formed by the encroachment of the two jugular foramina. The anterior portion forms a straight transverse suture with the basisphenoid bone. In the adult skull this suture is bridged in the mid-line by a posterior prolongation of the vomer. Laterally the anterior portion of the bone forms sutures, which diverge posteriorly, with the petrosal bone. The posterior portion of the basioccipital is a stout curved bar of bone

with the concavity of the curve open at the foramen magnum. On either side this bar forms a short straight suture with the exoccipital.

In the 48 and 50 mm. skulls the basioccipital bone is isosceles triangular in outline, but with all three angles truncated. The truncated apex of the triangle is anterior and sutures with the basisphenoid. The straight suture line with the periotic bone commences in front at the side of this truncated apex and extends backward and outward to the jugular foramen. In these young skulls this foramen does not constrict the bone appreciably, and it is of interest to note that in the older skulls, measuring 65 and 80 mm., the basioccipital is actually narrower here than in the younger skulls. One cannot therefore, in the younger skulls, describe the bone as being composed of anterior and posterior portions. The truncated lateral corners provide the face for suture with the exoccipital bones (fig. 1).

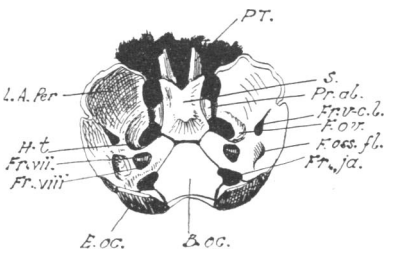

Fig. 1.

In all four mature skulls the basioccipital bone is fenestrated on either side of the mid-line immediately behind the basioccipito-basisphenoid suture. In Skull *F* there are two fenestrae on the left side and two semi-transparent areas of the bone in corresponding situations on the right. The anterior of the fenestrae is situated actually in the line of the suture, and has resulted as much, or nearly as much, from the absorption of the hinder end of the basisphenoid as from absorption of the front of the basioccipital. In Skull *G* the fenestrae are symmetrical and, besides having coalesced on each side, have been extended forward through the basisphenoid to the hinder edge of the carotid foramina. In Skull *H* they have not been run together but the anterior pair extend forward right to the carotid foramina, which in consequence have to be sought on the upper surface of the basisphenoid, where they are found tunnelling forward through the dorsum sella.

The *Exoccipital bones* are irregularly quadrilateral in shape. Each presents an inferior border, much thickened to form the occipital condyle. Situated almost in the coronal plane, the condyles diverge from the sagittal plane at an angle of approximately 45°, the outer ends being the higher. Above the outer end of the condyle the lateral border of the bone forms a straight, nearly vertical suture with the mastoid region of the petrosal bone. The superior border forms another straight suture, with the horizontal lower border of the supraoccipital bone.

The *Supraoccipital bone* is roughly half-moon shaped, with its long axis transverse. It covers, in the posterior portion of the cranial cavity above, the foramen magnum across nearly the whole width of the skull. Dorsal and lateral margins merge in one full sweep, though the parietal border is slightly straightened out, forming a transverse suture with the posterior border of the

parietal bone. The inferior margin sutures with the exoccipital on each side, and lateral to this with the parietal lamina of the petrosal; sweeping round to the side of the skull, this margin also sutures, outside the parietal lamina just mentioned, with the dorsal lamina of the squamosal bone.

The *Foramen Magnum* is bounded below by the basioccipital bone in the median one-third of its extent, and by the lower portions of the occipital condyles, on the exoccipital bones, for the other two-thirds. The lateral margins, formed by the exoccipital bones, converge towards one another dorsally, but do not meet, there being a gap in the mid-line above, this gap extending upward as a notch into the inferior margin of the supraoccipital. In the flesh it is made good by a sheet of fascial tissue.

REGIO SPHENOIDALIS

In this region there are the basisphenoid bone below and the parietal above, with the posterior portion of the composite periotic bone between them. The vestigeal alisphenoid bone is described with the facial skeleton.

The *Parietal* is a large, single bone which forms the vaulted dome of the cranial cavity, extending almost the whole width of the dorsal surface of the cranium from the supraoccipital to the frontal bones. As we have seen, its posterior border forms a transverse, serrated suture with the supraoccipital. The postero-lateral angle is overlapped by the anterior part of the expanded dorsal limb of the squamosal. Anteriorly the bone is produced on each side into a pointed process which overlies the postero-lateral corner of the frontal of its side. In the mid-line, between these larger processes, are two other, smaller, processes which underlie the posterior border of the frontal bones on either side of the sagittal suture. The lateral border of the parietal bone forms sutures with the dorsal margin of the orbitosphenoid and behind this with the dorsal edge of the alisphenoid lamina of the periotic bone.

The *Basisphenoid bone* is to a large extent hidden inferiorly by the palatine. It does not lie in the same plane as the basioccipital bone, but inclines dorsally as it extends forward. It is a quadrilateral bone with two short processes on each side. Posteriorly it sutures with the basioccipital medially and with the cochlear portion of the periotic on each side. Anteriorly it sutures with the presphenoid. The posterior of the two pairs of lateral processes have, in previous descriptions of this skull, been termed the two alae temporales, but inasmuch as it has been demonstrated that the alisphenoid is always developed from a true ala temporalis and that there is no alisphenoid developed in relation to the processes in this skull, it would appear more correct to designate this pair the *processes alares*. Each processus alaris is a short broad expansion of the bone, which sutures in the adult skull with the inferior edge of the alisphenoid lamina of the periotic. The anterior processes are narrower but of equal length, and they also form a suture with the same lamina of the periotic bone, at its antero-inferior angle. Inferiorly each processus alaris is intimately fused with the pterygoid bone and below this it forms a suture with the lateral edge of the

palatine towards the posterior end thereof, and with the vestigeal alisphenoid bone. On the inferior surface it is grooved along the mid-line for the reception of the dorsal margin of the vomer, this groove being flanked on each side by a low ridge. On either side of the groove a little way from the posterior limit of the bone there are to be seen the two external apertures of the carotid canals. Viewed from above the body of the bone is convex, with the processes alares appearing to stand out from the inferior edge of the convexity of the body. The sella is defined by lateral ridges and by a post-clinoid transverse wad. Viewed from below, the body is flat, with the alary processes standing down and out at an angle of about 45°. The pterygoid bones are plastered to the sloping lower surfaces of the processes, the slightly prominent inferior edge of the pterygoid forming with the alary process to its outer side a groove for the reception of the palatine. The inferior extremity of each alary process is somewhat thickened and is perforated along its length by the canal for the internal maxillary artery and a small nerve from the otic ganglion. The Vidian canal perforates the fused pterygoid bone and process obliquely just in front of and above the fore end of the canal for these structures. None of our skulls is young enough to allow us to speak definitely on the relation of the Vidian canal to the pterygoid bone. Watson (1916, p. 320) quotes Gaupp as stating that the pterygoid is not perforated by the nerve. In our Skull *B*, disarticulated, the canal is found above the posterior portion of the pterygoid bone, which is definable as such by reason of the fact that its ventral border is free, with a nearly obliterated suture line between it and the alary process, commencing just in front of and above the nerve where it enters the bone, and extending thence dorsally and forward across the inner side of the process till it reaches the body of the basisphenoid; this suture then becomes quite distinct and passes directly forward. It would appear from the conditions found that the canal lies between the process and the pterygoid bone throughout its length. This is practically as Watson (*l.c.* p. 331) describes the course of the nerve. This description of the basisphenoid is based on the bone in the little disarticulated 48 mm. skull, but it is actually applicable equally well to the bone in the adult skulls. Our youngest skull enables us to state that the bone ossifies from three centres, one median, and two lateral, these latter situated in the processes alares medial to the canal for the artery.

The *Periotic bone* covers in the greater part of the side of the cranium as well as forming part of the posterior wall lateral to the exoccipital and supra-occipital bones, and in the otic region is covered to a great extent by the squamosal bone. On the inferior surface of the bone, the crista parotica supplies a landmark that may well serve as a starting-point from which to describe the bone.

The crista parotica is wedge-shaped, the thick truncated end of the wedge being posterior, and the thin end of the wedge is produced forward like a flying buttress to the posterior edge of the foramen ovale by a ridge. The inner side of the truncated posterior end is notched and its point (processus styloideus)

gives attachment to the hyoid arch; in the very young skull it has been shown to be in cartilaginous continuity with Reichert's cartilage. The notch is continued forward along the inner side of the process and its buttress as the sulcus stylomastoideus. The vestibular and cochlear portions of the bone lie immediately to the inner side of the process, the labyrinthine portion of the bone is directly above it, the processus anterior, or as we would prefer to designate it, the alisphenoidal lamina, extends forward of and above it, whilst the crista parotica and a small area of the bone behind it may be regarded as constituting the mastoid portion of the bone. A parietal lamina is present above the labyrinthine portion of the bone.

The fenestra ovalis (*seu* vestibuli) lies immediately to the inner side of the anterior end of the stylomastoid sulcus on the inferior surface of the vestibular portion of the bone. The fenestra rotunda (seu cochleae) is situated further back on the vertical posterior margin of the bone in line with the posterior margin of the foramen jugulare. The cochlear portion of the bone medial to these apertures is roughly oblong; its long axis extending forwards and medially; it sutures with the lateral border of the basioccipital and the postero-lateral corner of the basisphenoid. Immediately above and behind the crista parotica there is to be seen in young skulls a prominence due to the conjoined ends of the horizontal and posterior semicircular canals, in older skulls this prominence is obscured by the greater development of the root of the crista parotica.

The stylomastoid sulcus burrows further under the crista parotica as it is followed forward until it reaches the flying buttress formed by the hinder end of the alisphenoid lamina; this is perforated for the transmission of branches of the vena capitis lateralis and of the external carotid artery, and it is this perforation which leads us to describe it as a "flying" buttress. On the anterior wall of the tunnel thus formed under the buttress the external aperture of the Fallopian canal (stylomastoid foramen) opens on to the sulcus. Looking into the Fallopian canal from here one is able to see right through into the hinder angle of the foramen rotundum owing to the fact that the hiatus Fallopii opens on to the hinder wall thereof in direct line with this lower segment of the canal. The inner aperture of the canal is within the internal auditory meatus near its anterior margin, from here it takes a short course forward, downward and slightly outward, to very nearly perforate the hinder wall of the foramen rotundum, and at this point an actual perforation results from the departure of the very short hiatus Fallopii. At the point of departure of the hiatus the canal turns abruptly backwards and with a slight downward trend reaches the external aperture situated as described. In two of our skulls there is on one side a small canal parallel with and just to the outer side of the lower segment of the Fallopian, and from the fact that it is of inconstant occurrence we conclude that it transmits blood vessels. In our Skulls *B* and *C* (48 and 50 mm.) the proximal portion of the Fallopian canal, i.e. the portion between the internal auditory meatus and the hiatus Fallopii, presents the

embryonic condition, and it is enclosed by the ossified commissura suprafacialis only. Doubtless the geniculate ganglion at this stage was lying uncovered against the posterior wall of the foramen rotundum. And moreover in the 48 mm. skull (*B*) the lower segment is not enclosed by bone below, and is only a forward continuation of the stylomastoid sulcus. There is little doubt that the geniculate ganglion in the adult skull lies in the canal at the point of departure of the hiatus and not, as Watson (*l.c.* p. 331) states, at its lower end. Watson's description is based on serial sections of a head little older than our youngest and a good deal younger than our Skull *B*. The hiatus Fallopii was correctly identified by van Bemmelen (1901).

It is of interest to note that there is a striking resemblance between the course of the canalis Fallopii of the *Platypus* and that of man and other mammals; the course is from the internal auditory meatus, above and in front of the foramina for the eighth nerve, forward and outward, and downward in *Platypus*, to the hiatus Fallopii, thence downward and backward. The two segments have, moreover, in both cases similar origins. The proximal is formed below the cartilaginous commissura suprafacialis, the geniculate ganglion lies immediately beyond the commissure. The distal segment is enclosed by extension of ossification beyond the cartilage, this extension reaching a variable distance towards the styloid process. There is no doubt that what Watson (p. 331) regarded as the outer end of the Fallopian canal is in verity the hiatus Fallopii. Actually the roof of the "sulcus facialis" is the posterior portion of an incompletely enclosed Fallopian canal. The attachment of Reichert's cartilage indicates that the apex of the "crista parotica" may be aptly termed "styloid process" to impress the homology of the part, and hence our designation "sulcus stylomastoideus" in preference to "sulcus facialis."

A comparison of the early condition of the Fallopian canal of *Platypus* with those of *Xerus* (Fawcett, 1923), *Miniopterus* (Fawcett, 1919) and *Tatusia* (Fawcett, 1921) as well as that of man (Macklin, 1921), discovers a remarkable general similarity, and, in view of the diversity of the forms mentioned, it would appear that this is the fundamental mammalian condition. There is, moreover, a general similarity to this disposition in the birds and some reptiles (Kesteven, 1925 A).

Returning again to the tunnel under the flying buttress (which, it will be remembered, lodges the vena capitis lateralis, the facial nerve and the superficial temporal branch of the external carotid artery) the external aperture of the canalis vena capitis lateralis will be found to the outer side of the stylomastoid foramen. The course of this canal is upward and slightly outward and forward through the bone just in front of the ampulla of the anterior semicircular canal, but near the top of the curve of this canal it opens into the cranial cavity, and the main branch of the vessel passes backward above the arcuate fossa in a well-marked groove. Watson describes another branch, which, he states, "splits up and seems to send branches both above and below the ganglion semilunare in the sinus cavernosus" (*l.c.* p. 336).

The mastoid portion of the bone behind and above the crista parotica sutures with the exoccipital bone. Viewed from the lateral aspect the otic capsule proper is almost entirely covered by the body and lower expansion of the squamosal bone, whilst above the capsule the dorsal expansion of the same bone covers the parietal lamina of the periotic bone. The alisphenoid lamina of the bone is very extensive. In shape it is approximately oval, the fore end of the oval being narrower than the hinder. It may be said to spring from the front of the otic capsule by a narrow neck. To the inner side of this neck is the outer angle of the foramen rotundum, to its outer side is the inner aperture of the canalis venae capitis lateralis. Above this latter point on the inner surface of the bone a groove curving forward as it rises marks approximately the fusing-point of the ossification in the membrana spheno-obturatoria and that which extends upward and forward from the processus perioticus superior. The groove in question actually lodges a forward-reaching branch of the vena capitis lateralis in the dura. It may be said then that the alisphenoid lamina of the periotic is fused to the parietal lamina above its origin from the capsule. Above the line of fusion it is in sutural contact, slightly overlapped, with the lower margin of the parietal; in front of this it forms an irregular, nearly horizontal, suture with the lower margin of the orbitosphenoid, and this suture terminates at the sphenoptic fissure. Following down the posterior margin of this fissure the lamina next forms a short suture with the anterior lateral process of the basisphenoid, it next arches over the foramen ovale to form a suture with the upper edge of the lateral margin of the processus alaris, and at the posterior end of this last process it arches over the foramen rotundum and reaches the otic capsule with which we started.

The parietal lamina is largely covered externally by the dorsal expansion of the squamosal bone. It extends dorsally and posteriorly from the superior border of the labyrinthine portion of the bone, and it is in sutural relation behind with the supraoccipital and above with the parietal.

In our two youngest skulls this last lamina is not yet developed, the whole of the dorsal expansion of the squamosal bone rests upon a thin sheet of membrane which completes the side wall of the cranium between the labyrinthine portion of the periotic bone below and the lateral edge of the parietal bone above, and also between the posterior margin of the dorsal expansion of the squamosal and the lateral margin of the supraoccipital bone on the posterior aspect of the skull. This extensive sheet is apparently an extension from the processus superior periotici and it occupies the situation of the parietal lamina of the bone in older skulls. In the young skulls in question the processus superior is ossified as a low ridge along the dorsal margin of the labyrinthine portion of the bone, the alisphenoidal lamina on the other hand is well developed, and presents the features of the adult bone on a reduced scale, the postero-dorsal margin corresponding very nearly to the vascular groove above mentioned as the line of fusion of the two laminae in the adult skull.

Before leaving the periotic bone there remains to be mentioned a small foramen close to the inner edge of the foramen rotundum at its anterior angle. In one of our skulls this appears as a notch in the margin of the foramen rotundum on the right side and as a foramen on the left, in the two youngest skulls it is represented by a notch on both sides. This foramen (foramen vasculosum innominatum) has been described as transmitting a deep temporal artery. There is a very definite vascular (?) groove extending upward and forward from it on adult skulls.

The *Squamosal bone* has been described as entering into the formation of the side wall of the cranium by its dorsal lamina; this, however, is an error which the material we have enables us to correct. The disarticulated bone in Skull *B* presents a zygomatic process, a body, a dorsal and a ventral lamina, the latter divided into anterior and posterior portions (fig. 2). The zygomatic process is grooved along its length inferiorly for the reception of the zygomatic process of the maxilla. The body, approximately square in outline, is no thicker

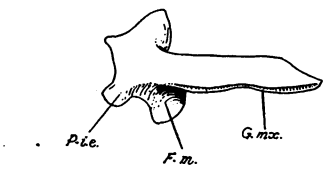

Fig. 2.

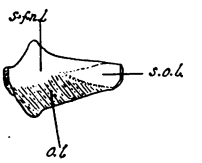

Fig. 3.

For explanation see text.

than the rest of the bone, though appearing more solid when in position owing to the fact that it is broadly grooved antero-posteriorly to form the outer wall of the post-temporal canal between itself and the outer wall of the otic capsule. The form of dorsal and ventral expansions is plainly shown in the figure and calls for no description.

In Skull *C* the bone is of almost precisely the same size and shape as that in Skull *B*. The inferior or ventral lamina lies directly against the outer aspect of the labyrinthine portion of the periotic bone, the little bay between the anterior and posterior portions of the lamina clasping a prominence on that bone which is due to the underlying posterior vertical semicircular canal. The lower half of the inner wall of the post-temporal canal is formed by the ossified processus superior periotici, the upper half by a sheet of membrane directly implanted on its dorsal free margin. This sheet of membrane finds attachment behind to the lateral margin of the supraoccipital bone, in front it is continued forward along the dorsal free margin of the alisphenoid lamina of the periotic and gains attachment to the posterior angle of the orbitosphenoid bone. Superiorly the membrane is attached to the lateral margin of the parietal just within its actual edge. In this dried partially disarticulated skull there is a definite gap between the dorsal lamina of the squamosal bone and the membranous sheet. Quite certainly then the dorsal lamina was not developing in this membrane but external to it. On placing the parietal bone

in place it is found to be overlapped at its postero-inferior corner by the dorsal lamina of the squamosal bone.

In Skull *D*, though very little larger, the squamosal bone has assumed the full adult form and relations. There is very little actual enlargement of the bone in any of its parts, but it is now in sutural relation to the supraoccipital bone. This latter has expanded, doubtless by ossification of the sheet of membrane, so that there is now no interval between it and the periotic bone below and the dorsal arm of the squamosal in front. An examination of the inner wall of the cranium fails to discover anything that may be regarded as a suture between the old level of the ossified processus superior periotici and the margins of the parietal and supraoccipital bones. An examination of the cross-section of the fractured suture between the dorsal arm of the squamosal and the parietal and of the dorsal arm itself and the bones in front and behind it, parietal and supraoccipital, reveals that there are very clearly two fused layers of bone along the section of the dorsal arm and only one along the sections of the other bones.

There is no longer any division of the ventral arm of the squamosal into anterior and posterior portions, the little bay has been filled in and the prominence of the inferior end of the semicircular canal masked by a general thickening of the bones of the skull in this region.

In the young adult skull *E* the only differences are of size.

It is concluded that the squamosal bone does not enter into the formation of the cranial wall, but is excluded therefrom by the parietal lamina of the periotic bone which underlies it and with which very early in adult life it becomes intimately fused.

In the *presphenoid* and *ethmoid regions* the axis of the skull is ossified by extension from the orbitosphenoid bones. In Skull *B* the orbitosphenoid bones have the form shown in fig. 3. The long axis of this little bone is directed antero-posteriorly, and the broader end is the front, the ventral margin having the larger expansion. Actually the two lateral expansions of the bone anteriorly lie in planes nearly at right angles to one another. In Skull *C* the orbitosphenoid has almost precisely the same shape and size as that of Skull *B*. It lies in place with the dorsal anterior expansion almost entirely overlapped by the hinder end of the frontal bone, and behind this bone the dorsal margin is in contact with the lateral edge of the parietal. The thickened posterior end gives attachment to the anterior edge of that sheet of membrane above described as being later ossified from the two processes of the periotic bone. The lower margin of the bone behind the anterior lateral or ventral expansion is in contact with the anterior part of the superior margin of the alisphenoid lamina of the periotic. The lateral expansion (ala orbitalis) of the orbitosphenoid reaches down in the vertical plane to the level of the skull base, and its ventral edge or corner is attached to a sheet of cartilage which extends across the cranial floor to become attached in similar manner to the opposite orbitosphenoid. This sheet of cartilage is of particular interest. In front of the

orbitosphenoid bones it continues forward for a short distance and then is split into three narrow bands. Of these the median rises in the sagittal plane in the mid-line, and is the cartilaginous septum nasi; it is interrupted almost at once by the internarial hiatus which persists in the bony septum of the adult. The lateral bands pass forward from the outer corners of the main sheet, attached to the upper border of the orbital plate of the palatine bone and in front of this to the inner aspect of the maxilla, below the level of the naso-lachrymal and infraorbital canals and above the ophthalmic nerve. In front of the foramen ophthalmicus posterior this lateral band of cartilage gains attachment to the nasal bone above and to the inner side of the canalis ophthalmicus, and to the maxilla below that canal, continuing forward with these attachments to the foramen ophthalmicus anterior at the forward limit of the palatine plate of the maxilla. Throughout its length it spreads out over the inner face of the maxilla below the actual line of attachment, so that it supplies a lining to the lateral wall of the nasal cavity from the roof thereof almost to the floor.

Behind the ventral processes of orbitosphenoid bones the sheet of cartilage is attached to the upper margins of the pterygoid bones and by them is carried back to gain attachment to the fore end of the basisphenoid bone across the mid-line. It is noteworthy that this sheet of cartilage, which forms the floor of the cranial cavity and roof of the naso-pharyngeal cavity in the presphenoidal and ethmoidal regions, is absolutely devoid of any trace of centres of ossification, at a time when every bone in the skull except the ethmoid and the presphenoid is assuming the form of the bones of the adult skull.

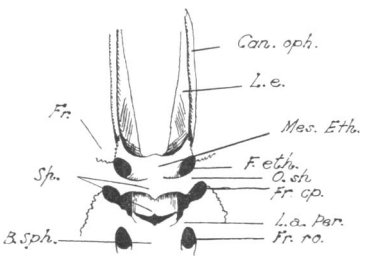

Fig. 4. Semi-schematic drawing of presphenoid and ethmoid of *Platypus*. For explanation see text.

In our next stage, Skull *D*, which, it will be remembered, is very little larger than *C*, the whole of this sheet of cartilage has been ossified (fig. 4).

Seen from the lateral aspect, the orbitosphenoid now extends further back below the parietal bone and above the alisphenoid lamina of the periotic. The amount of this extension is not as great as it appears to be. In Skull *C* the posterior limit of the bone is vertically above the hinder margin of the foramen ovale, in Skull *D* the posterior limit is a little further back, but the alisphenoidal lamina has extended forward and below it. In front of the sphenoptic fissure the orbitosphenoid bone is seen extending down to suture with the fore end of the pterygoid, the upper margin of the orbital lamina of the palatine and the postero-inferior corner of the orbital plate of the frontal bone. Above these sutures the bone is grooved to form the sulcus pro nervi ophthalmici. This sulcus may be described as being terminated by the foramen ophthalmicum. Looking into this foramen it will be found that there is an hiatus in the side wall of the skull immediately to its inner side; this is the

fenestra ethmoidale. The suture between the orbitosphenoid bone and the orbital plate of the frontal runs vertically upward from the ethmoid fenestra and is interrupted just below the supraorbital margin by a foramen which transmits an ethmoid artery. Within the foramen the artery apparently breaks up into a posterior diploic branch and an anterior larger branch, which splits again into branches to the canal for the nervus ophthalmicus and the posterior region of the nasal chamber in the neighbourhood of the turbinate bones; at least it may be stated confidently that the foramen in question has communications suggestive of this division of the transmitted vessel, and it may be designated foramen ethmoidale superius.

Turning now to the interior of the cranium it will be seen that the two ventral processes of the orbitosphenoid bones are joined across the mid-line by a narrow bar of bone. This bar of bone is incorporated into the plate of bone which has replaced the sheet of cartilage that in Skull *C* here formed the floor of the skull and roof of the naso-pharyngeal passage. No trace of suture is discernible anywhere in this fusion.

The conjoined ends of the ventral processes of the orbitosphenoid bones are, in this skull, flush with the plane of the plate of bone forming the skull floor, but at their point of attachment on either side, coming down as they do from above, they clearly mark a "step up" that, in the next stage, is developed right across the floor. The portion of the plate behind and that beneath the "step" may be regarded as presphenoidal topographically, whilst that in front of it is ethmoidal, in the same sense. The extent of the horizontal portion of this plate anteriorly is greater than was that of the sheet of cartilage which it has replaced, and it has been extended upward as well as forward so that the vertical bar which is the posterior end of the septum nasi is shorter than was the cartilaginous bar. This piece of the bone is nearly in contact with a low ridge developed on the under side of the fore end of the frontal bones along the sagittal suture. The lateral processes, too, are shorter, as viewed from behind, than were their cartilaginous precursors; they are in contact with the inner face of the maxilla, separating the fenestra olfactorius from the canal of the ophthalmic nerve. Laterally the plate is attached to the inner face of the maxilla, roofing the infraorbital canal, and to the nasal bone, forming the inner wall of the ophthalmic canal.

In Skull *E* the adult conditions are nearly approached.

There is a small hiatus between the hinder end of the presphenoidal plate and the fore end of the basisphenoid bone. On either side of this hiatus the dorsal edges of the pterygoid bones appear. In front of the hiatus the ophthalmic sulci appear as though encroaching on the cranial floor. Where these sulci pass under the ventral plates of the orbitosphenoid bones the cranial floor is markedly stepped up, and from here forward there is a steady even rise to the point of contact with the frontal bones. Owing to the presence of the fenestrae ethmoidalia and the fact that the sulci for the ophthalmic nerves lie beneath the cranial floor it appears as though there were four apertures in the fore end

of the cranial cavity; those on either side of the mid-line are the fenestrae olfactorii, the outer pair are the canals for the ophthalmic nerves seen through the ethmoidal fenestrae. The constriction of the cranial cavity initiated at the posterior margin of the ventral processes of the orbitosphenoid bones becomes accentuated at their anterior margins; here a very definite ridge takes origin on each side and swings upward and slightly forward across the processes to the roof of the cavity, and these constitute a very definite boundary line between the cranial cavity proper and a true *sphenoidal cavity* in front (Kesteven, 1925 B, p. 280).

That process of the frontal bones, which in the last stage was nearly in contact with the fore end of the ethmoidal plate, has in this stage developed further down and is now in contact. We have carefully opened the roof along one side of the sagittal suture and cannot persuade ourselves that this little *ethmoidal process of the frontal bones* is other than that name implies.

The fenestra ethmoidale is still present, as already noted above.

Forward of the olfactory fenestrae the inner walls of the canal for the ophthalmic nerve, and of the infraorbital canal below it and a little further from the mid-line, together constitute the outer wall of the nasal cavity. There are here three sets of turbinate bones. The upper set is much the smaller and is placed high up on the wall just in front of the olfactory fenestra. The middle set is placed at a lower level just in front of the fore end of the first set and extends forward to about the junction of the posterior and middle thirds of the length of the snout, or nearly half-way to the position of the external nares. The lower set is small with one element extending forward to the anterior olfactory foramen.

In the old adult skull *F* there is a general resemblance to Skull *E*. One notes the closure of the fenestra ethmoidale and a general increase in thickness of the bones, as well as the complete closure of all the sutures except that between the fore end of the ethmoidal plate and the ethmoidal process of the frontal bones.

Reviewing now the features observed it is apparent that the presphenoid and ethmoidal regions have been ossified by extension from the orbitosphenoid bones and that these bones cannot be defined genetically. It is, however, quite open to us to define not only the orbitosphenoid bones but also the presphenoid and ethmoid on a topographical basis.

The extent of the orbitosphenoid bones has been correctly determined by previous authors. The presphenoid may be regarded as constituting the cranial floor from the fore end of the basisphenoid to the posterior boundary of the sphenoidal cavity.

The ethmoid is a much more extensive bone. It forms the floor of the sphenoidal cavity and supplies the side walls of the nasal cavity as far forward as the anterior opening of the canal of the ophthalmic nerve.

The persistence of the suture between the fore end of the ethmoidal plate and the ethmoidal process of the frontal bones, taken in conjunction with

the situation of the anterior continuations of the ethmoidal cartilage, together clearly indicate that van Bemmelen erred in his interpretation of this region of the *Platypus* skull. His sections (1901, p. 744) indicate an ethmoid continuous across the roof of the nasal cavity just in front of the hiatus in the septum nasi. Our material enables us to state quite emphatically that this is not so, and we have endeavoured to convey the situation and relations of the ethmoid in the drawings of the nasal region of the skull in a later section of this paper (see also Watson's fig. 19, p. 336).

The *Frontal bone* develops very early, even in our youngest skull it presents in miniature most of the features of the adult bone. The dorsal and orbital plates are well developed, the connecting isthmus being largely covered by the antero-lateral corner of the parietal just as in the adult skull.

In the adult the dorsal lamina sutures in front with the nasal bone and behind and laterally with the parietal bone. In the 48, 50 and 65 mm. skulls the antero-lateral corner of the parietal bone reaches the postero-lateral corner of the nasal of each side, covering the outer portion of the dorsal lamina of the frontal and the isthmus connecting this latter to the orbital plate. In the 80 mm. skull, and, as far as one can judge, in the adult skulls as well, though a portion of the dorsal lamina is similarly covered, the isthmus is freely exposed on the surface of the skull. The orbital plate is situated on the inner wall of the orbit in front of, and below, the hinder margin of the isthmus. Its superior margin sutures with the lateral margin of the nasal, and its anterior border forms a short suture with the orbital process of the maxilla. Inferiorly this short suture is interrupted by the lachrymal foramen. Immediately below this foramen the orbital plate forms an even shorter suture with the dorsal edge of the lachrymal bone, and behind this the inferior margin sutures with the dorsal margin of the orbital plate of the palatine bone. The posterior margin of the orbital plate sutures with the anterior margin of the ala orbitalis of the orbitosphenoid bone. This suture is interrupted by the foramen sphenoidale superius immediately below the orbital margin and a little lower it is more drastically interrupted by the foramen ophthalmicum (foramen ethmoidale of van Bemmelen), and below this latter the inferior margin sutures with the outer edge of the presphenoid bone. The portion of the plate interposed between the presphenoid above and to the inner side and the orbital plate of the palatine below appears as a little backward-projecting tongue; the tip of this tongue is in sutural contact with the anterior tip of the pterygoid bone, and just where these meet, between them and the presphenoid, to the inner side, there is fairly constantly a vascular foramen (foramen sphenoidale inferius). It should be noted that the orbital plate of the frontal bone does not enter into the formation of the cranial wall, but forms the outer wall of the ophthalmic canal and a portion of the inner wall of the orbit, separating the former from the latter.

THE FACIAL REGION

The *Nasals* are elongated flat bones which roof in the major portion of the nasal cavity and form part of the side wall thereof as well. They overlap the frontals behind and suture with the maxillae and premaxillae laterally, meeting one another in a long median suture. Anteriorly they become narrower and diverge. In the disarticulated skull it is seen that the bones are deeply grooved to form the greater part of the length of the ophthalmic canal. There are two exits from this canal, the *foramen ophthalmicum superius* interrupts the naso-maxillary suture a little way in front of the orbit, the *foramen ophthalmicum anterius* appears as an elongated sulcus at the fore end of the nasal bone lateral to the prevomer or dumb-bell bone. Though it would appear so to do the nasal bone does not actually supply a side wall to the nasal cavity except near the fore end, because the delicate ethmoid is plastered to it almost as far forward as the posterior end of the prevomer. In front of the prevomer the nasal bones extend forward to fit against the posterior border of the inturned ends of the premaxillae, and for the greater part of this length they appear on the inner side of the premaxillae on the inferior aspect of the skull. Between the diverging ends of the nasal bones the dorsal surface of the anterior point of the palatine plates of the maxilla is visible covered by cartilage and with the prevomer just a little further forward embedded in the cartilage.

The *Lachrymal bone* is apparently present as an independent entity in our youngest specimens. Here we find a trihedral piece of bone placed in the angle of the maxilla formed by the junction of the malar process and the body. The little bone lies just within the antorbital ridge below and behind the orbital process of the maxilla and rides on the dorsal edge of the root of the malar process, forming the roof of the posterior infraorbital foramen. The bone sutures with the root of the malar process on the outer side and with the anterior edge of the orbital plate of the frontal on the inner side. Where these two sutures meet the lachrymal foramen is to be found, and from this the suture between the orbital plate of the frontal and the orbital process of the maxilla passes directly upward.

The suture across the roof of the infraorbital canal is not so evident. Though we feel confident on the point we do not care to speak dogmatically thereon, and therefore make the announcement of this discovery with a little reservation. The suture between the lachrymal and the orbital plate of the frontal is the most persistent and has, in the past, been regarded as being between the orbital process of the maxilla and the plate of the frontal. The condition, as we describe it, is similar to that of *Aelurus* and *Ursus* (Gregory, 1920, pp. 148 and 151, figs. 81 and 82).

With rather more hesitation we express the opinion that future investigation will demonstrate an original independence for the little piece of bone which in *Echidna* is found between the lachrymal foramen and the posterior

infraorbital foramen, attached to the root of the malar process but sutured to the orbital plate of the frontal.

The *Maxilla* may, for descriptive purposes, be said to be composed of a body and palatine and malar processes. The body is situated in the side of the face in front of the orbit, it sutures above with the nasal and premaxilla, both to its inner side, and below with the premaxilla. The body is thinner from above downward in front than it is behind, where it is tunnelled by the infraorbital canal; actually this canal tunnels nearly the full length of the bone, but it is very much reduced forward of the infraorbital foramen, which is a large opening situated on the side of the bone a little in front of and below the superior ophthalmic foramen. The anterior infraorbital foramen will be found at the extreme anterior tip of the body of the maxilla on the inferior aspect of the skull. The postero-dorsal corner of the body forms part of the anterior boundary of the orbit and has been referred to above as the orbital process of the bone. The palatine process of the maxilla is a long narrow lamina attached to the infero-medial border of the body, but leaving it in front to permit of the insertion of the palatine process of the premaxilla. At about the centre of the length of the palatine process the line of attachment to the body is interrupted by the inferior infraorbital foramen. The anterior extremity of each palatine process is deeply notched, and it is the common projection of the two processes between these notches which appears between the diverging anterior ends of the nasal bones when the skull is viewed from above. The posterior margins of the palatine processes suture with the anterior margins of the palatine bones.

The malar process springs from the postero-lateral corner of the body, and immediately spreads out below into the wide, spoon-like dental fossa. No trace of this fossa is visible in our youngest skull and it is little more than indicated in the 48 mm. skull. Behind the fossa the malar process continues as a laterally compressed splint bevelled on the inner side superiorly for suture with the forward-extending malar process of the squamosal bone.

The *Jugal* is a little triangular splint of bone which is perched on the dorsal edge of the zygoma, just above the anterior end of the squamosal component thereof. This little bone marks the boundary between the orbital and temporal fossae. In old adult skulls it becomes completely merged with the other components of the zygoma, and its dorsal edge bears backward and inward, very clearly indicating the outer one-third of the posterior boundary of the orbit. Beyond this there is nothing in the skull to indicate the boundary between the two fossae.

The *Premaxillae* are elongated bones which, for the greater part of their length, fit in between the nasal bone and maxilla on the upper aspect of the skull. Inferiorly the same relations are maintained forward of where the bone fits between the palatine process and the body of the maxilla.

The body of the *Palatine bone* is oblong in outline, it sutures in front with the hinder margin of the palatine plate of the maxilla, laterally it sutures with

the dental plate of the same bone and behind this its lateral margin is free for about one-third of the total length of the bone. Behind the free margin the bone sutures with the inferior edge of the processus alaris above it and with the vestigeal alisphenoid below it. The posterior margin of the bone is free, lying below the posterior choanae. The orbital lamina of the palatine bone is a thin plate of bone, broader in front than behind, which rises in the vertical plane from the dorsal surface of the bone near its lateral edge. Anteriorly this lamina is in sutural contact with that part of the posterior end of the body of the maxilla which forms the inner wall of the infraorbital canal. Above this there is a point of suture with the lachrymal, and then the dorsal margin of the lamina sutures with the ala orbitalis of the frontal and behind this with the inferior edge of the anterior end of the pterygoid bone. In our 48 and 50 mm. skulls there is on the dorsal surfaces of the palatine bones close to their medial borders a pair of para-vomerine laminae, which together form a trough into which the vomer is fitted when, at a later stage of development, it is formed from the cartilaginous septum which at this stage occupies its place. It is noted that the palatine bone extends almost to the posterior end of the processus alaris and well beyond the posterior limit of the pterygoid bone.

The *Alisphenoid bone* is represented by the tympanic wing only in the Prototheria; in the past this little bone has been designated "Echidna-pterygoid," following the lead of Gaupp (1905 and 1910), but in conformity with the conclusions of the senior author (Kesteven, 1918) that term is discarded in this paper.

The bone in the *Platypus* is an elongated spathulate splint, broader and thinner in front, quite loosely sutured to the inferior aspect of the suture between the processus alaris and the palatine. The anterior end stands out freely lateral to the palatine bone below the foramen rotundum. The posterior end of the bone stands beyond the palatine and is produced into a small hook which lies in the same plane as the rest of the bone and therefore is inclined downward and away from the mid-line of the skull. This hook is attached along its posterior edge to the anterior extremity of the curved tympanic bone by a ribbon of connective tissue.

Although this bone presents few of the relations detailed for the so-called Echidna-pterygoid in *Echidna* by the senior author in the communication above referred to, and on which the conclusions therein arrived at were based, still its position is such as to leave no room for doubt as to its complete homology with that bone and also justifies our use of the designation "tympanic wing of the alisphenoid bone."

The *Pterygoid bone* has been described above in the course of the description of the basisphenoid.

The *Prevomer* has been so frequently and so fully described that it is not necessary to discuss it here, and the same holds true for the vomer.

THE NERVE AND VASCULAR CANALS AND FORAMINA, AND OTHER FENESTRATIONS

The *Foramen Magnum* is bounded below by the basioccipital only in the young skulls, but in adult skulls the foramen is relatively much enlarged by absorption of the lamina of the exoccipital bone on each side above the condyles, which latter come thus to bound the adult foramen magnum inferiorly. The lateral boundaries are supplied by the exoccipital bones, and these, converging, nearly meet above. There is a gap above the foramen, between the exoccipital bones and the supraoccipital above them; this is filled, in the flesh, by a strange fascial membrane.

The *Foramen Jugulare* is bounded medially by the basioccipital, and in front by the periotic and behind by the exoccipital, these two latter bones meet at the outer angle of the foramen. It would appear that all the cranial nerves behind the eighth leave the cranium through this foramen.

The Fallopian canal and hiatus, the internal acoustic and the external acoustic apertures have already been sufficiently described.

The *Foramen Ovale* lies between the vestibular portion of the periotic and the hinder angle of the basisphenoid to the inner side, and the lower margin of the alisphenoid lamina of the periotic to the outer side; it transmits the third branch only of the fifth nerve.

The *Foramen Rotundum* is bounded to the inner side by the body of the basisphenoid, in front by the antero-lateral process and behind by the processus alaris of the same bone. Its outer boundary is the lower margin of the alisphenoid lamina of the periotic bone. The second branch of the fifth nerve finds its exit from the cavity through this foramen.

The *Sphenoptic Fissure* (Kesteven, 1918, p. 466) is bounded below and behind by the anterior corner and antero-lateral process of the basisphenoid; in front of these its inferior boundary is the edge of the body of the presphenoid and the dorsal margin of the pterygoid meeting in sutural contact. The antero-superior margin is the descending process of the orbitosphenoid. The postero-superior margin is the antero-inferior corner of the alisphenoid lamina of periotic bone. Between these two latter there is, in all but fully adult skulls, a deficiency (fenestra sphenoidale, fig. 5, *F.sp.*) in the side wall of the skull, made good by the remnant of the membrana spheno-obturatoria.

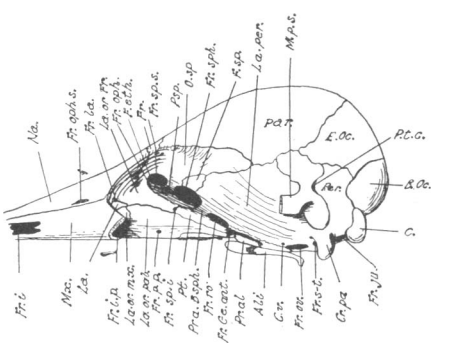

Fig. 5. The letters *Fr.oph.* point to the anterior end of the sulcus ophthalmicus. The nerve leaves the brain case in the lower angle of the foramen sphenopticum.

The sphenoptic fissure transmits the optic, the third, fourth and sixth nerves and the first branch of the fifth nerve.

It may be noted that Watson (p. 334) states that the "ophthalmic and maxillary branches of the trigeminus leave by the anterior part of the sphenoparietal fissure." The statement is, of course, based upon the conditions in a young individual before the junction of the anterior corner of the alisphenoid lamina of the periotic and the antero-lateral process of the basisphenoid divided the sphenoparietal fissure into foramen rotundum and sphenoptic fissure. (This division is referred to at greater length further on, in a note on the fate of the Taenia clino-orbitalis.) A little further on Watson states of the first branch of the fifth nerve that it passes through the orbito-nasal fissure and immediately enters a canal in the paries nasi, and his fig. 19 shows it passing forward surrounded by cartilage. Our older, but still young, skulls would seem to demonstrate that the cartilage intervening between the nerve and the nasal bone is absorbed; we have been unable to find any cartilaginous lining to the ophthalmic sulcus along the nasal bone.

The *Olfactory Foramina* lie close together at the front of the sphenoidal cavity, separated by the little spur of the ethmoid which sutures with the two frontal bones. The lateral boundary of each is the short lateral process of the ethmoid which joins the nasal lamina thereof to the body of the bone.

The positions of the foramen for the internal carotid artery, and for the superficial temporal and internal maxillary branches of the external carotid, have already been described, as also has the course of the vena capitis lateralis through the periotic bone.

The side wall of the naso-pharynx is perforated by two apparently constant vascular foramina. One of these, the foramen sphenoidale inferius, has been described in the course of the description of the frontal bone. The other, situated lower down and a little further forward, passes straight through the palatine bone to the palatine foramen, which latter interrupts the maxillo-palatine suture near the anterior end thereof. This posterior aperture of the palatine foramen may be designated *foramen palatinum posterius*. It should be mentioned that though the palatine foramen appears to interrupt the maxillo-palatine suture it is really entirely surrounded by the palatine bone.

The *Fenestra Ethmoidale* is a deficiency in the wall of the sphenoidal cavity between the orbital plate of the orbitosphenoid and the body of the ethmoid, and in adult skulls it is made good by ossification of the membrane present in the younger skulls. This ossification leaves no trace of suture and, judging from the gradual reduction in size presented in our series, would seem to take place from all round the fenestra.

The *Infraorbital canal* lies entirely in the maxilla. The entrance to the canal, *foramen infraorbitale posterius*, lies immediately medial to the root of the malar process of the bone. Of the three exits two have already been described, the third, *foramen infraorbitale inferius*, will be found as a large foramen continued forward as a fairly deep groove along the under surface of the palatine plate of the maxilla close to its junction with the body of the bone about the middle of its length.

The *Foramen Ophthalmicum*, which van Bemmelen designated foramen ethmoidale[1], is bounded laterally by the orbital plate of the frontal bone, below, medially and above it is bounded by the body and short lateral process of the ethmoid. From here the ophthalmic canal continues forward, first against the facial lamina of the maxilla and then in the groove in the nasal bone already described. Through its length the inner wall, beyond the actual opening, is formed by the delicate nasal lamina of the ethmoid. The exits from this canal have been described in connection with the description of the nasal bone.

THE FATE OF THE TAENIA CLINO-ORBITALIS

Wilson (1906) has already described in detail the fate of this interesting little bar of cartilage in both *Echidna* and in the *Platypus*, but, although he has pointed out that van Bemmelen is correct in his designations foramen rotundum and foramen spheno-orbitale opticum, he has not quite clearly indicated the relation of these to the fissurae parietale and pseudo-optica of the primordial cranium.

The fissura pseudo-optica persists entire in the adult skull of *Echidna*, or at least it so persists in the young adult, as evidenced by one in the possession of the senior author.

In this skull the sella is bounded laterally by two sharp ridges which become higher as they pass forward; diverging along the sides of the sella, the angle of divergence increases at the forward limit thereof. These ridges, which van Bemmelen termed middle clinoid processes and which Wilson has shown to be the ossified taeniae clino-orbitales, now slope downward (ventrally) and pass along the side of the presphenoid bone, to terminate at the inner corner of the ala orbitalis of the orbitosphenoid bone. Just in front of the anterior limit of the sella each ridge is lifted free of the presphenoid bone for a short distance, and the resulting foramen is the fissura pseudo-optica. To the outer side of and below the anterior end of the ossified taenia, on each side, there is formed a more or less complete pseudo-optic canal whose external aperture, if the canal be complete, is to be found within the antero-medial angle of the sphenoptic fissure. The large spheno-parietal fissure lateral to the pseudo-optic fissure is divided into foramen rotundum behind and sphenoptic fissure in front.

In none of our *Ornithorhynchus* skulls is there any remnant of the taeniae clino-orbitales, but Wilson has described their situation in the adult skull. Here also it will be found, on reference to his description, that the fissura pseudo-optica persists, completed by fibrous tissue, in the adult skull, and that it is situated in a precisely similar position to that of *Echidna*.

The fissura pseudo-optica, then, in the adult skull, is situated immediately above the suture between the body of the basisphenoid and the body of the

[1] Van Bemmelen's designation is discarded because it describes neither the situation nor the content of the foramen.

presphenoid on the floor of the cranial cavity, and is entirely distinct from the fissures and foramina in the side wall of the skull.

The foramen sphenopticum (spheno-orbitale opticum of van Bemmelen) is the anterior portion of the spheno-parietal fissure and although it does not include the pseudo-optic it transmits the two nerves which pass through that fissure as well as the fourth, sixth and first branch of the fifth nerves.

The foramen rotundum is the posterior portion of the spheno-parietal fissure, separated from the remainder by the union of the alisphenoid lamina of the periotic with the antero-lateral process of the basisphenoid bone.

THE CONSTITUTION OF THE NASAL CAVITY AND BONY NASO-PHARYNX

A complete bony palate extends from the anterior extremity of the maxilla right back to below the middle of the length of the basisphenoid. Of this, the nasal floor is that portion extending back to the level of the posterior boundary of the dental fossa, behind where the palate forms the floor of the post-nasal passage.

The floor of the nasal passage is formed by the palatine plates of the maxillae and by the anterior one-third of the palatine plates of the palatine bones. The roof is formed entirely by the nasal bones. The lateral walls are formed by the lateral, nasal, laminae of the ethmoid behind and by the nasal bones in front. The septum is constituted by the short mesethmoid behind the hiatus and by the vomer in front thereof.

The floor of the naso-pharynx is formed entirely by the palatine laminae of the palatine bone, the roof by the ethmoid, presphenoid and the body of the basisphenoid. The lateral walls are formed by the orbital laminae of the palatines, the pterygoid bones and the inner face of the processus alaris of the basisphenoid bone.

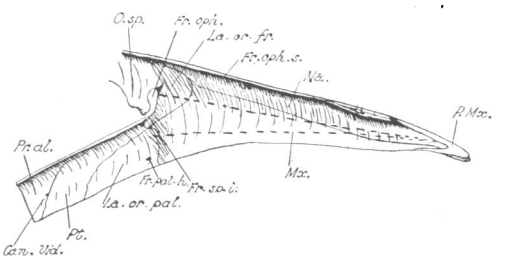

Fig. 6. The side wall of the nasal cavity and of the naso-pharynx with the cartilaginous ethmoid removed.

In fig. 6 we have illustrated, somewhat diagrammatically, the inner wall of the nasal region and of the naso-pharynx of our specimen *B*. In this specimen there is no ossification of the cartilage of the presphenoid and ethmoid regions.

The concave face of the nasal bone is exposed along the length of the nasal cavity; this is, of course, the sulcus ophthalmicus of this stage, and the foramen ophthalmicum superius is seen perforating the bone towards the hinder end well up under the roof. The premaxilla is shown embracing the fore end of the nasal bone, and behind this the inner lamina of the facial portion of the maxilla is seen to constitute the greater part of the side wall of the nasal region at this stage of development. The position of the infraorbital canal outside this

lamina is indicated by the heavy dotted lines. Behind the maxilla the orbital laminae of the frontal and palatine are seen. The former is really situated on the outer side of the ophthalmic nerve, whilst the latter forms the side wall of the anterior part of the naso-pharynx; just at this point the bones are inclined towards the observer, so that the lateral wall of the naso-pharynx is nearer the mid-line than is the lateral wall in the nasal region. The pterygoid bone is next seen, above the orbital lamina of the palatine; the posterior portion of this bone is plastered to the inner face of the processus alaris, the postero-superior corner of which is seen at the hinder end of the naso-pharynx. The suture line between the pterygoid and the processus alaris is interrupted by the posterior foramen of the Vidian canal. Though not able to speak definitely on the point, we believe that we have correctly represented the suture. The foramen sphenoidale inferius is seen at the top of the suture between the ala orbitalis of the frontal and the anterior end of the pterygoid. The foramen palatinum posterius is seen perforating the orbital plate of the palatine bone low down near its anterior border.

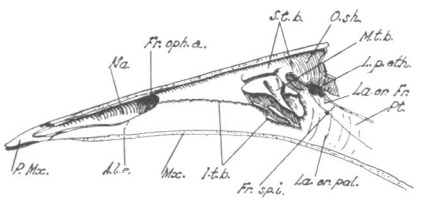

Fig. 7. The side wall of the adult nasal cavity showing the lateral ethmoid and turbinate bones.

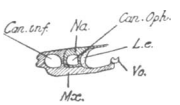

Fig. 8. A diagrammatic cross-section of the snout behind the infraorbital foramen.

In fig. 7 we have illustrated, again somewhat diagrammatically, the side wall of the nasal passage of the old adult specimen *J*. The lateral ethmoid now closes the ophthalmic canal for a little over half the length of the nasal bone, and covers the surface of the maxilla to a great extent. We have not attempted to indicate the posterior limit of the lateral ethmoid, but suggest that it is somewhere about the posterior limit of the maxilla. The anterior limit is indicated with a little more confidence by the dotted line below the ophthalmic sulcus. The lateral wall of the sphenoidal cavity is shown above the cut edge of the lateral process of the body of the ethmoid.

The superior turbinate bones are three in number. Two are but small ridges almost in line with the cut edge just mentioned, the third, a little larger, is situated further forward, above the middle turbinate. This last is more complicated, but we have endeavoured to indicate its form in the drawing. The inferior turbinate series consists of three little ridges below the middle turbinate and one, much longer, which extends right forward to the margin of the foramen ophthalmicum anterius.

In fig. 8 we have indicated, quite diagrammatically, the constitution of the snout just behind the infraorbital foramen.

THE SIGNIFICANCE OF THE ALISPHENOID LAMINA OF THE PERIOTIC

Reviewing the facts of the origin of the alisphenoid bone throughout the Craniata, in a recent contribution (Kesteven, 1926) I stated: "In every case in which its development has been studied it has been shown to develop from cartilage which is either continuous with that of the rest of the chondrocranium from its first appearance, or very early becomes continuous therewith. In the lower Craniates it has been shown that this bone is ossified indifferently from centres of ossification either in front of or behind it. In the higher forms it is seen to ossify from its own specific centre" (p. 129). I regarded the bones as always truly homologous, however arising, and proposed to recognise the difference in origin by the designations "predeterminate" as applied to those arising in continuity with other bones, and "determinate" as applied to those arising from their own specific centres of ossification (p. 121).

Throughout the communication quoted the term "lower Craniata" was used as applying to the Fishes and Amphibians, but the present study has convinced me that in the Prototheria both predeterminate and determinate alisphenoids are present. It might appear, then, that the two structures cannot be homologous, but I am of the opinion that such an appearance is deceptive, and that they are dissociated portions of the same bone.

In the first place it must be remembered that the Prototheria are truly aberrant beasts and present a very special case; it were therefore foolish to attempt to analyse the mass of evidence presented by the rest of the Craniates, using the condition in the Prototherians as the indicator, whereas the converse is only reasonable.

Briefly the position may be stated thus. Throughout the whole of the Craniata the alisphenoid, when present at all, is a bone which develops, for the most part, in membrane. In some cases the ossification of this bone is by extension from the ossifying cartilage to which the membrane is attached either in front or behind ("predeterminate alisphenoid"), in other cases the process of ossification commences in a little pellicle of cartilage which may or may not be attached to the cranial axis below ("determinate alisphenoid").

In the Marsupialia and some Insectivora the ossification in membrane is continued back below the periotic bones to form a "tympanic wing." This wing may well have been handed down from the promammalian stock, for it is well developed in certain Cynodonts.

The alisphenoid lamina of the periotic bone of the Prototheria satisfies all the conditions of the predeterminate alisphenoid, whilst the "Echidna-pterygoid" presents all the relations of the tympanic wing.

One can do little more than speculate as to the cause of the separation of the two parts of the bone, the most tempting suggestion is that the early extensive development of the palatine posteriorly resulted in the observed discontinuity. In the Insectivores and whales with an abnormal backward extension of the bony palate the formation of the posterior segment is actually

formed from the alisphenoid-pterygoid partnership, and the palatine does not extend behind the normal limit. It is an undoubted fact that the early extensive backward development of the palatine in *Echidna* and the *Platypus* has prevented the free development of the pterygoid, and one might therefore argue that, as pterygoid and alisphenoid bone are closely related at their inception, anything which interferes with the growth of one may do likewise with the other. It is obvious that, were the alisphenoid normally developed in the prototherian skull, it would not present the usual mammalian relation to the pterygoid. It may be, then, that we have here the explanation we seek.

There is another aspect of the matter that calls for comment. Is the predeterminate alisphenoid of the Prototheria to be regarded as an archaic feature or as the direct converse? These beasts present so many undoubted archaic features that one is tempted to regard the condition of the alisphenoid as another of them, but further consideration of the subject would seem to lead one to the converse conclusion.

The predeterminate alisphenoid bone of the Fishes and of the Amphibians is developed from the remnant of the complete cartilaginous cranium of the early Craniate. It should be remembered that this form of alisphenoid is found in the more archaic Fishes Crossopterygii and Holostei, which undoubtedly stand closer to the main trunk of the tree of evolution which, in its later branches, bore the Amphibians and higher Vertebrates than do the greater number of the recent Fishes. Whichever of those later branches we study we find that the primordial cranium is continuously reduced and its place taken by bones developed more and more in membrane. With the acquisition of the power of forming bone in membrane, the cartilaginous basis is more and more dispensed with. In the Fishes the alisphenoid bone develops in the cartilage of a tolerably complete primordial cranium, in the Reptiles it develops from one of the bars of an extensively fenestrated primordial cranium, whilst in the Mammals this bar has been fragmented and is represented by a mere pellicle of cartilage, the ala temporalis (Kesteven, 1926). It may well be that the Prototheria, archaic though they be in many respects, present a further stage of progression along this line and have learned to dispense with a cartilaginous centre of ossification for the alisphenoid altogether.

Should it prove that this interpretation be the correct one, the designation "predeterminate" as applied to the prototherian bone is unfortunate in a genetic sense, "postdeterminate" would be more applicable. "There are more things in heaven and earth...than are dreamed of in our philosophy." Had I been endowed with *prévoyance* I should have selected a more purely descriptive designation for the alisphenoid not developed from its own specific centre of ossification.

Future investigation may demonstrate a pellicle of cartilage related to the tympanic wing, but it appears to be quite definitely established that the cranio-mural element of this peculiar alisphenoid is developed entirely in membrane (Watson, *l.c.* p. 323).

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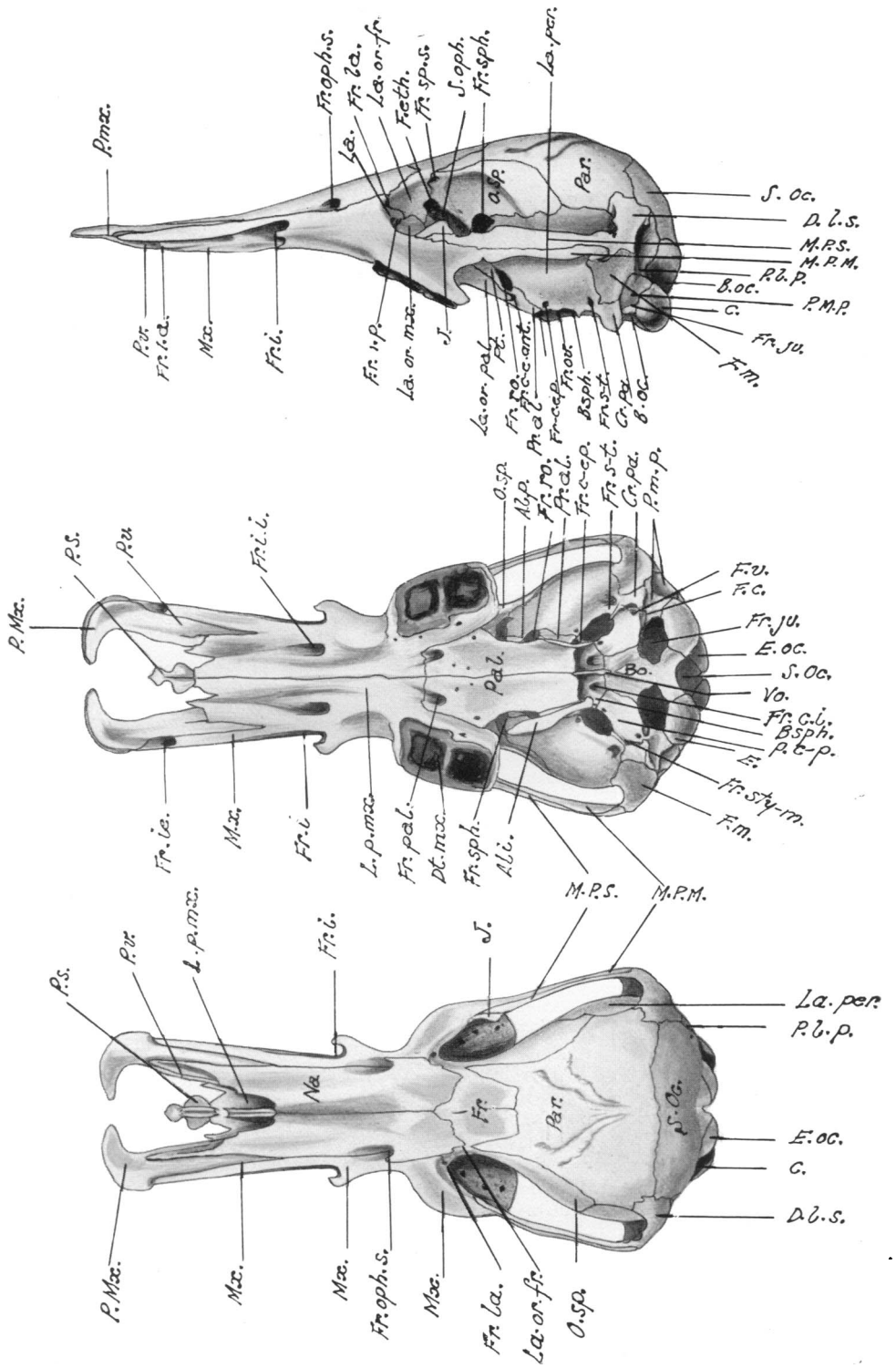
EXPLANATION OF THE ABBREVIATIONS USED IN THE FIGURES AND PLATE

A.l.e.	Margo anterior ossis ethmoidei.
Ali.	Ala tympanica ossis alisphenoidei.
A.l.p.	Processus antero-lateralis ossis basisphenoidei.
B.Oc. & *B.O.*	Os basioccipitale.
B.sph.	Os basisphenoideum.
C.	Condylus occipitalis.
Can.inf.	Canalis infraorbitalis.
Can.oph.	Canalis ophthalmicus.
Can.Vid.	Canalis Vidianus.
Cr.pa.	Crista parotica.
C.v.	Foramen vasculosum innominatum.
D.l.s.	Lamina dorsalis ossis squamosalis.
Dt.mx.	Fossa dentalis ossis maxillaris.
E.Oc. & *E.*	Os exoccipitale.
F.c.	Fenestra cochleae.
F.eth.	Fenestra ethmoidalis.
F.m.	Fossa glenoidea mandibularis.
Foss.fl.	Fossa arcuata (floccularis).
F.ov.	Foramen ovale.
Fr.	Os frontale.
Fr.c.-e.ant.	Foramen anterius canalis arteriae carotis externae.
Fr.c.-e.p.	Foramen posterius canalis arteriae carotis externae.
Fr.c.i.	Foramen arteriae carotis internae.
Fr.i.	Foramen infraorbitale.
Fr.i.a. & *Fr.ie.*	Foramen infraorbitale anterius.
Fr.i.i.	Foramen infraorbitale inferius,
Fr.i.p.	Foramen infraorbitale posterius.
Fr.ju. & *Fr.ja.*	Foramen jugulare.
Fr.la.	Foramen lachrymale.
Fr.oph. & *Fr.op.*	Foramen ophthalmicum.

Fr.oph.a.	Foramen ophthalmicum anterius.
Fr.oph.s.	Foramen ophthalmicum superius.
Fr.ov.	Foramen ovale.
Fr.pal.	Foramen palatinum.
Fr.pal.p. & *Fr.p.p.*	Foramen palatinum posterius.
Fr.ro.	Foramen rotundum.
Fr.sp. & *Fr.sph.*	Foramen sphenopticum.
Fr.sp.i.	Foramen sphenoidale inferius.
Fr.sp.s.	Foramen sphenoidale superius.
Fr.s.-t.	Foramen arteriae temporalis superficialis.
Fr.sty.-m.	Foramen stylomastoideum.
Fr.v.-c.l.	Foramen venae capitis lateralis.
Fr. VII	Foramen internum canalis Fallopii.
Fr. VIII	Meatus acusticus internus.
F.sp.	Fenestra sphenoidalis.
F.v.	Fenestra vestibuli.
G.mx.	Sulcus pro processo zygomatico ossis maxillaris.
H.t.	Hiatus Fallopii.
I.t.b.	Osses turbinata inferiores.
J.	Os jugulare.
La.	Os lachrymale.
La.or.fr.	Lamina orbitalis ossis frontalis.
La.or.mx.	Lamina orbitalis ossis maxillaris.
La.or.pal.	Lamina orbitalis ossis palatinis.
La.per.	Lamina alisphenoidea ossis periotici.
L.e.	Lamina nasalis (lateralis) ossis ethmoidei.
L.p.eth.	Processus lateralis ossis ethmoidei.
L.p.mx.	Lamina palatina ossis maxillaris.
M.p.m.	Processus zygomaticus ossis maxillaris.
M.p.s.	Processus zygomaticus ossis squamosalis.
M.t.b.	Os turbinatum medium.
Mx.	Os maxillare.
Na.	Os nasale.
O.l.	Lamina orbitalis.
O.sph. & *O.sp.*	Os orbitosphenoideum.
Pal.	Os palatinum.
Par.	Os parietale.
P.c.-p.	Pars cochlearis ossis periotici.
Per.	Os periotici.
P.i.e.	Postero-inferior lamina.
P.l.p.	Pars labyrinthinis ossis periotici.
P.m.p.	Pars mastoidea ossis periotici.
P.Mx.	Os premaxillare.
Pr.a.bsph.	Processus antero-lateralis ossis basisphenoidei.
Pr.al.	Processus alaris.
P.s.	Prevomer.
P.sp.	Os presphenoideum.
Pt.	Os pterygoideum.
P.t.c.	Canalis post-temporalis.
P.v.	Processus ventralis ossis premaxillaris.
S.	Sella turcica.
S.-f.-n.l.	Lamina subfronto-parietalis.
S.Oc.	Os supraoccipitale.
S.oph.	Sulcus ophthalmicus.
S.t.b.	Osses turbinata superiores.
Vo.	Vomer.



KESTEVEN AND FURST—THE SKULL OF *ORNITHORHYNCHUS*