ON THE SKELETON OF THE SNOUT OF THE MAMMARY FŒTUS OF MONOTREMES.

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(Plates xxxvii.-xlii.)

At the Meeting of the Society, held March 28th, 1900, I exhibited photographs and wax-plate reconstructions illustrating the anatomy of the snout of the so-called mammary fœtus of Ornithorhynchus and Echidna. A brief preliminary account of the conclusions arrived at was published in the Proceedings of the Society (1).

The present paper aims at presenting a more ample and detailed account of the facts, accompanied by the necessary illustrations.

The material employed in the investigations which form the subject of this paper included, in addition to adult specimens of both Monotremes—(A) the snout of a "mammary fœtus" of Ornithorhynchus, whose external characters were described by me in a former communication to the Society (2), and which was originally placed at my disposal by the Trustees of the Australian Museum; (B) a "mammary fœtus" of Echidna of almost precisely the same stage of development as the younger of two specimens described and figured by Professor W. Newton Parker (3). Both Professor Parker's and my specimen were obtained by the courtesy of the Trustees of the Australian Museum, though at widely different times. (C) Another and larger "mammary fœtus" of Echidna in my possession I owe to the generosity of my colleague Professor W. A. Haswell, F.R.S. (D) Through the kindness of Mr. J. P. Hill I have had access to a series of coronal sections of the snout of a larger "mammary fœtus" of Ornithorhynchus, of almost the same size and general stage of development as that originally described and figured by Professor W. K. Parker (4), and again subsequently figured by Professor E. B. Poulton (5).

To the gentlemen who have thus assisted me with valuable material I desire to offer my grateful acknowledgments.

The investigation has been carried on chiefly by means of serial sections of the snout region. The sections were stained in hæmatoxylin and picric acid. Wax-plate reconstructions were made of the skeletal structures of the snout region of each of the specimens, with the exception of C. The scale of magnification employed for this purpose was 40 diameters. In the case of Model i., (younger Ornithorhynchus) serial photographs of the sections were traced directly, with thin manifolding carbon paper, upon the surface of the wax-plates. In the case of the other two models the drawings were made by tracing the image thrown on the screen by the projection microscope, and then re-tracing with the thin carbon paper directly upon the surface of the wax. This has been found very convenient and greatly preferable to the inclusion of the paper basis of the drawing in the wax-plate according to Born's later method.

For the figures illustrating this paper I am indebted to my wife, as also for valuable assistance in the preparation of the reconstructions. The figures representing the models have been drawn from the models themselves, after photographs reduced to a scale of about five-twelfths of the originals. The sectional anatomy of the snout of the younger Ornithorhynchus is further illustrated by the series of figures 13-21, which were drawn with the aid of the Edinger's drawing-apparatus to a scale of enlargement of 18 diameters.

I wish also to acknowledge the skilful assistance I have received from my laboratory assistant Louis Schaeffer, both in the preparation of the wax-plates and in photography of the models.

I.—The cartilaginous rostral skeleton in the Monotremes.

In 1893 an important advance towards a more correct interpretation of the cartilaginous skeleton of the anterior nasal region of Ornithorhynchus was made by Dr. C. J. Martin in collaboration with the present writer (6).

It was then shown that the "large sheet of hyaline cartilage forming the outline of the great rostrum" previously noted by Kitchen Parker (4), is continuous with the septum nasi. The latter, on being traced forwards in the adult, was found to divide into a smaller dorsal, and a more massive ventral, subdivision. It was shown that the ventral portion descends and is intercalated into the anterior part of the roof of the mouth, and, rapidly widening out, is prolonged forwards into continuity with the large rostral cartilage. This again is continuous laterally with the alinasals, and, extending forwards between the diverging premaxillary crura, spreads both forwards, outwards, and backwards to form the peculiar marginal cartilaginous support of the upper lip—the "valance of solid hyaline cartilage" described by Parker. The rostral cartilage thus described was identified with the "prenasal portion of the axis of the embryonic chondrocranium." The anatomy of the region dealt with was illustrated by a series of figures of transverse sections through the adult snout, and by a drawing (*loc. cit.*, fig. 17) showing the main outlines of the bony and cartilaginous snout-skeleton as seen from the ventral aspect.

It is now desirable to amplify, and in some measure to correct and reinterpret, the details of the description epitomised above, in the light of further observations, both upon the adult by Broom (7), and upon immature specimens of both Monotremes by the writer.

Whilst expressing his entire agreement with the interpretation of the rostral cartilage in the adult Ornithorhynchus given by Wilson and Martin, Broom contributed to the anatomical description highly important observations of his own. He found that "the rostral cartilage does not extend forward to the front of the beak as an entire sheet. Almost immediately in front of the plane passing through the anterior part of the premaxillaries, the cartilage becomes abruptly arrested in the middle line; but while this is so, the lateral parts extend forward almost to the front of the beak, where they again approach each other, meeting, or almost so, in the middle line. There is thus left in the middle an oval space entirely free from cartilage. This arrangement I have found in three different individuals (two males and one female). The lateral portions of the cartilage curve round backwards along the outer sides of the rostral crura, supporting the lip as shown by Wilson and Martin. It seems probable that this whole complicated marginal cartilage is a development of the prenasal. . ."

Broom's interpretation of his facts is worthy of special remark, since its correctness is largely borne out by the facts of development as shown by the reconstructions of the fœtal snout now figured. Referring to the dorsal subdivision of the nasal septum, he says:—"Though in the region of the anterior nares it is considerably removed from the prenasal plate" [which is continuous with the ventral moiety of the septum nasi] "on passing forwards it approaches the latter, and ends in close connection with it, at the point where the prenasal becomes arrested in the middle line. This point" [marked with an asterisk in his fig. 1, which should be consulted] "probably represents the anterior end of the beak in the ancestor of the Platypus, as not only do the two cartilages here end together, but this is practically where the two premaxillaries would meet if they came together. Connected with it, moreover, there is a further feature of importance. On the upper side of the beak in the middle line is a small thickened area of epithelium (*c* in fig. 1) unlike that of the rest of the beak. This is probably the remains of the caruncle. If it be so, and it is quite perceptible to the naked eye, it corrects the statement of Owen's that no trace of the caruncle can be found in the adult. Whatever be its signification, it is evidently closely related to the supposed apical point of the primitive beak, as a series of fibrous bands pass from it to the latter."

It will presently be shown that the actual condition as seen in the developing snout very nearly corresponds to this interpretation.

The solution of the problem of the snout-cartilage at once appears when it is realised by aid of the wax-plate models that the supposed bifurcation of the septum nasi into dorsal and ventral subdivisions is no genuine bifurcation of the structure, the appearance of such being due to a fenestration of the septum. In point of fact, the dorsal and ventral portions do not merely "end in close connection with one another" anteriorly, "where the prenasal plate becomes arrested in the middle line," but they are actually continuous with one another, and it is this, their point of fusion in front of a somewhat spacious fenestra, which constitutes the true anterior border of the septum nasi—the extreme anterior limit of the strictly axial portion of the embryonic chondrocranium.

Further, in his figure 1, Broom represents the two halves of the marginal cartilage of the lip meeting and uniting in front of the oval gap he discovered; and he speaks (p. 558, line 27) of "their anterior union." But previously (p. 557, line 22) he has used the expression "meeting, or almost so, in the middle line." It is the latter alternative which is correct. The marginal strips of opposite sides do not meet in front, though in the adult they may possibly touch. Thus, in front of what has now been discovered to be the proper anterior edge of the septum nasi there is strictly no cartilaginous tissue present in the mesial plane The anterior edge of the septum is here, as in other mammals, the strict limit of the mesial chondrocranial axis.

Full demonstration of the correctness of these views is afforded by the study of the wax-plate reconstructions upon which this paper is based.

A view of the lateral aspect of the septum nasi in Model i., representing the anterior region of the snout of the younger fœtal Ornithorhynchus, is given in fig. 1. The internasal fenestra above referred to perforates it so close to its anterior end that only a slender median bar of cartilage forms the extreme anterior portion of the septum. A section across the snout in this plane is represented in fig. 15. The posterior border of the fenestra lies slightly in front of the plane at which the lower edge of the cartilaginous septum intercalates itself into the nasal floor to constitute the "prenasal plate." Fig. 17 shows a coronal section immediately behind the posterior edge of the fenestra, whilst the section shown in fig. 16 passes through the fenestra.

A corresponding view of Model ii., representing the same region of the snout in the larger "fœtal" Ornithorhynchus is shown in fig. 5. Here the fenestra is less regularly oval than in the earlier stage. It is becoming vertically more compressed in front.

The same region in the "fœtal" Echidna is illustrated by fig. 9 from Model iii. In its stage of development this specimen corresponds fairly closely to the younger of the Ornithorhynchus specimens. Both as regards the condition of the septum and of the prerostral notch, Echidna at this stage deviates less from the ordinary mammalian condition than does Ornithorhynchus, though there is no essential difference between the two Monotremes.

It was long ago noted by the late Professor W. K. Parker (8) that an internasal fenestra like that now described in the Monotremes is a common feature in low Eutheria. He suggests that it is the posterior margin of such a fenestra which represents the true anterior limit of the septum nasi. We therefore see that it is the specialisation of a not uncommon mammalian character which accounts for much that seems highly peculiar in the Monotreme snout.

I need hardly say that the septal cartilaginous fenestra above described has nothing whatever to do with the internasal defect in the septum of the living Monotreme. The latter is situated altogether posterior to the plane region represented by the present Models.

In fig. 2 we have a view of Model i., from the front (the "os carunculæ" has been removed from the model in order to allow a view of the anterior parts of the snout-cartilage). On either side the lower part of the anterior margin of the septum is seen to expand and to become continuous ventrally with the great cartilaginous sheet prolonged from the nasal floor into the marginal cartilage of the upper lip. As far back as the plane of the anterior end of the cartilaginous capsule of the organ of Jacobson (about level of *s.n'*. in fig. 3), th emarginal cartilage is directly continuous with the cartilage of the nasal floor, of which, indeed, it forms the lateral and anterior expansion. Behind that plane, however, it is severed from the nasal floor cartilage—the maxilla and premaxilla coming to intervene between the two—and is prolonged backwards as a free marginal strip to a point which at this stage is considerably posterior of the plane of the anterior border of the maxillary palate (fig. 3). In front, the marginal cartilage projects forwards on each side into the lip, considerably in front of the plane of the free anterior margin of the septum nasi—*i.e.*, of the primitive anterior end of the snout.

There is thus formed a deep notch between the marginal cartilages of opposite sides. This prerostral notch is the original representative of the oval gap which Broom (7) found in the adult arresting the rostral or prenasal cartilage in the middle line in front. At this stage in development the notch lodges the slender anterior continuations of the premaxillæ which connect the latter with the "os carunculæ" (*v. infra*). The fibrous bands which Broom discovered passing from this region to the vestigial caruncle of the adult can be nothing else but vestiges of these lost premaxillary trabeculæ, together with (and perhaps chiefly) remains of the os carunculæ itself.

Only one of the two premaxillary trabeculæ is shown in this figure occupying the prerostral notch, for the sake of clearness. The ventral view of the model in fig. 3 may be consulted in this connection, in which both the prerostral premaxillary bars are shown, whilst, also for greater clearness, the prerostral extension of the marginal cartilage on the right of the figure has been removed.

The complete cartilaginous ring surrounding the external narial aperture and the upper of the two osseous splints representing the body of the premaxilla are both well seen in fig. 2. Compare figs. 4 (Model i.), 7 and 9 (Model ii.), and figs. 11 and 13 (Model iii.). It will be seen that in the Echidna the cartilage of the aperture is incomplete.

The earlier processes by which the definitive palate of Echidna is constituted have been described in detail by Seydel (9) and illustrated by him from wax-plate reconstructions of this region, in stages considerably earlier to those now under consideration. His fig. 8, taf. xv., may be advantageously compared with figs. 3 and 12 of our Models i. and iii., bearing in mind that the latter represent the skeletal structures isolated. On p. 466 Seydel describes the descent of the nasal septum into the plane of the secondary palate :—" Der vorderste Theil der oralen Fläche des Septums welcher bei Embryo 46 dem Gaumenloch entspricht, hat sich abwärts in das Niveau der oralen Fläche des secundären Gaumens gesenkt, er verschmilzt mit der hinteren Umrandung des Gaumenloches und verschliesst letzteres bis auf die Oeffnungen der beiden Canales naso-palatini." The present models show, however, that in later stages the cartilaginous skeleton of the septum is intercalated in the plane of the secondary palate some little distance in front of the region of the "Gaumenloch," viz., at the triangular depression visible in the figures illustrating the ventral aspect of each of the three models.

In treating of the formation of the permanent septum nasi, Seydel refers to Newton Parker's observation of an internasal communication in the young of Echidna (3), and he remarks upon this—"Vielleicht erhält sich diese Communication auch noch bei der erwachsenen Echidna." It is perfectly evident from Parker's own words that he had ascertained this actually to be the case not only in Echidna but in Ornithorhynchus. Seydel is also unaware of the detailed description of this communication in both Monotremes given independently of, and almost simultaneously with Parker, by the present writer (10).

II.—The prevomer (dumb-bell bone) and the palatine process of the premaxilla.

In a paper read before the Society in 1894 (10) the writer has recorded a number of observations on the anatomy and relations of the so-called "dumb-bell-shaped bone" in Ornithorhynchus.

It was there suggested that this bone is morphologically an anterior vomerine element. Its homology to at least a portion of the palatine process of the premaxilla of other mammals was also discussed, and was considered by no means incompatible with the vomerine theory propounded by the writer.

In a paper subsequently published in these Proceedings (11), Dr. R. Broom further discussed the homology of the palatine process of the premaxilla in the mammalia generally.

In this paper he summarised the arguments of the present writer in favour of the essentially vomerine nature of the dumb-bell-shaped bone, and held that "these arguments afford conclusive proof that the dumb-bell-shaped bone belongs to the vomerine category and is no part of the premaxilla." He further suggested the term "prevomer" as preferable to that of "anterior vomer," which the present writer, following the nomenclature of W. K. Parker, had already applied to it. He then proceeded to advocate the view, already contemplated by the writer, that the palatine process of the premaxilla in other mammals "is itself a distinct vomerine element, ankylosed or formed in connection with the premaxilla."

A further important view is, however, also put forward, viz., that the so-called vomers of the Lacertilia, which are topographically related to the organ of Jacobson in these forms, are in reality the homologues of the mammalian anterior or prevomers, and not of the mammalian vomer. In support of this doctrine he invokes the authority of W. K. Parker, who would seem to have arrived at a similar conviction.

These views of the nature of the dumb-bell-shaped bone elicited a reply in 1896 from Professor Symington (12), who had previously (13) upheld the theory that the dumb-bell-shaped bone represented neither more nor less than the detached palatine processes of the premaxilla. The paper was written before Dr. Broom's latest contribution reached Europe, though this writer's views were already to some extent known to Dr. Symington through a previous paper by Dr. Broom dealing with the organ of Jacobson in the Monotremata (14).

It is now unnecessary to enter into any detailed criticism of Symington's objections to the theory of the vomerine nature of the dumb-bell bone, as the present writer is of opinion that the definite prevomerine homology of at least the greater part, if not of the whole, of the palatine process of the mammalian premaxilla, may now be taken as sufficiently established, and this position practically conserves that view of the homology of the bone for which Symington contended. Indeed in a letter to the writer Professor Symington says, with reference to the dumb-bell bone, that he "does not think there is now much difference of opinion between us as to its homology."

The question of whether the entire palatine process of the premaxilla in mammals is prevomerine, as Broom is disposed to believe, cannot yet be regarded as finally decided. Reason will now be adduced for the belief that the anterior part of this process may originate as a direct backward extension from the body of the premaxilla, whilst the posterior part arises as a distinct prevomerine element. Such a view is very strongly supported by W. K. Parker's investigations on various Eutheria. The figures illustrative of the present paper prove conclusively that it holds good for Ornithorhynchus, provided we accept the homology of the dumb-bell bone to *any* portion of the palatine process of the premaxilla in other mammals.

In both specimens of the young of Ornithorhynchus, and also in the young Echidna the main body of the premaxilla is completely divided into dorsal and ventral plates grafted as splints upon the dorsal and ventral surfaces of the wide-spreading cartilaginous plate which forms the chief skeletal element of the snout extending into the lip. These dorsal and ventral parts of the premaxilla are quite distinct from one another, as was surmised to be the case in young stages, in the earlier paper on the snout, contained in the Macleay Memorial Volume (6).

The ventral plate of the body of the premaxilla appears from below as an elongated and curved strip of bone applied to the ventral surface of the cartilaginous plate aforesaid. As seen in Model i., (fig. 3) it tapers away posteriorly, and is there lodged in a sulcus in the ventral aspect of the antero-lateral extension of the maxilla. Anteriorly it bends mesially and then sends backwards paramesially a pointed palatine process which reaches a point exactly opposite the anterior blind extremity of the cartilaginous capsule of the organ of Jacobson (fig. 1).

The hinder end of this palatine process closely skirts the margin of a triangular mesial depression or fovea, which is due to the descent of the nasal septum and its appearance in the roof of the mouth (*s.n'*), where it merges in the great cartilaginous plate of the snout. This same triangular area is faintly indicated in fig. 17, plate xxiii., of Macleay Memorial Vol., illustrating the adult condition of the cartilaginous skeleton as then conceived. In that adult figure it is seen to lie immediately in front of the dumb-bell bone.

Thus in the young stage under consideration, the palatine process of the premaxilla extends precisely throughout that region where, in the adult, there is no representative whatever of a palatine process of the premaxilla. That this true palatine process of the premaxilla has nothing whatever to do with the production of the dumb-bell-shaped bone is made certain by the examination of the later stage of development illustrated in fig. 7 of Model ii. In this the palatine process of the premaxilla still persists, and is of almost exactly the same length as in the previous stage, not having shared in the considerable growth of the surrounding structures. One result of this is that its position has shifted, relative to the cartilaginous roof of the mouth, so that it now no longer extends as far back as the triangular fovea where the septum first appears in the roof of the mouth. It now also falls considerably short of the anterior end of the capsule of Jacobson's organ. This bony process has thus become arrested in development, and no trace whatever of it is to be found in the adult. But already in this stage (Model ii.) the development of the dumb-bell bone has begun in the shape of two small bony splints applied, one on each side, to the ventral aspect of the cartilaginous capsule of Jacobson's organ. These are visible in fig. 17, plate iii., of W. N. Parker's paper in P.Z.S., 1894 (3), which represents a section through the snout of a young Ornithorhynchus of precisely the same stage of development as that illustrated by Model ii. The section there figured is somewhat posterior of the region represented by Model ii.

These osseous prevomerine splints (= paired rudiments of dumb-bell bone) extend in the specimen itself from about 1 mm. behind the hinder extremity of the true palatine process of the premaxilla, backwards for a distance of 2·6 mm. They begin in front in the plane of the anterior end of the capsule of Jacobson's organ about 1·89 mm. anterior to the anterior margin of Stenson's duct, and end about 0·49 mm. behind its posterior margin. Here their posterior extremities are slightly overlapped by the anterior margin of the transverse cartilaginous lamina which corresponds to that visible in Model i. (fig. 3, *s.p.c.*). This lamina is the same as that transverse strip of cartilage figured in the adult between the dumb-bell bone and the osseous maxillary palate in fig. 17 in the paper in the Macleay Volume already cited (6). It is also shown in my figs. 8 and 9 "*nf.*" in my former paper on the dumb-bell bone (*loc. cit.*), and the relation to the bone is there further indicated by the line "d" in fig. 1 of the same paper (10). But whereas in the adult I have shown the dumb-bell bone to extend backwards into the roof of the internasal aperture there described and depicted, here, in this early stage (specimen D, Model ii.), the posterior extremities (not included in the model) of the paired prevomerine elements as yet fall short of the anterior margin of the aperture by about 0·49 mm.

From this description and from the figs. of Model ii., it is evident that the prevomerine dumb-bell arises autogenously during the interval in development between the stages illustrated by Models i. and ii., and is from the beginning separated by a wide interval from the true palatine process of the premaxilla. The latter has, indeed, obviously been receding in an anterior direction ever since the stage of Model i., in which there was no trace of the prevomerine elements. There cannot, therefore, at any time have been any connection or continuity between the prevomers and the true palatine processes of the premaxillæ. This fact serves to complete the proof originally brought forward by the writer to establish the independent prevomerine character of a much discussed skeletal element. The reconstructions now figured afford complete demonstration of the fact that, quite independent of the prevomer we find a genuine palatine process of the pre-maxilla. This entirely harmonises with the results of the extensive investigations of W. K. Parker upon the skeletal constitution of this region. The fact that Schwink (15) failed to find evidence of a compound origin of the mammalian palatine process, except in one case, may very probably be explained by the fact that in most mammals in which the premaxilla is well developed, the union of the prevomer and the palatine process proper, takes place very rapidly, so that the stage of distinct ossific centres is a very transient one, if, indeed, it can be said to occur at all as a rule. Here in Ornithorhynchus it is only the arrest in development of the palatine process proper and its progressive absorption in an anterior direction, combined with a rapid lengthening of the snout region and a probable demand for the preservation of the prevomerine element as a skeletal support in the region of Stenson's ducts, which determine the preservation of the isolated posterior element of the so-called palatine process, whilst preventing fusion with the disappearing anterior element or genuine palatine process.

III.—The os carunculæ, a specialised prenasal portion of the monotreme premaxilla.

The caruncle in the young Ornithorhynchus has been recognised since Owen first drew attention to it in 1865 (16). The original idea that it might function in some way similiar to the "egg-breaker" of some Sauropsida has finally been set aside by the more recent discovery of a true "egg-tooth" developed upon the upper lip, in younger stages of development than had previously been examined (*cf.* Seydel, *loc. cit.* (9), and also Taf. x. of Semon's illustrations of young of Echidna (17)).

In a previous paper (2) I have figured the caruncle in the younger of the two mammary fœtuses of Ornithorhynchus now under consideration, whilst Semon has figured earlier conditions of the caruncle co-existing with the "egg-tooth" in the young of Echidna (17).

So far as I am aware, no description of the skeletal basis of the caruncle is extant apart from the abstract I presented at a former meeting of the Society (1).

Seydel (9) has, however, figured without remark (other than the lettering "os incis." and "praem.," "unpaarer Fortsatz beider Zwischenkiefer" in his text-figures 10 and 11) the os carunculæ of Echidna, which is evidently at no time so well developed as it is in Ornithorhynchus.

In fig. 3 (Model i.) the premaxillæ, or rather the inferior lamellæ of them (*px.*), are traceable forwards into the prerostral region where they become attenuated and turn up dorsally into the prerostral notch and in front of the anterior extremity of the septal cartilage. Here the two osseous trabeculæ (*px.*) fuse to constitute a remarkable nodule of bone (*o.c.*) which forms a skeletal foundation for the caruncle. This latter structure, as is evident both from Semon's figures of young Echidna and from similar stages of Platypus, as yet undescribed, which I have had the opportunity of examining, attains a relatively large size and must possess some definite physiological significance, perhaps for the function of lactation, as yet undetermined. In the specimen represented by Model i., the os carunculæ, as I have ventured to name it, has probably already passed the zenith of its development. In the older specimen it is undergoing active resorption and is represented by only partially-connected bony nodules, and is permeated by osteoclasts. In the Echidna specimen represented by Model iii., the os carunculæ is still more rudimentary, although the stage is otherwise almost parallel to the younger of the two Ornithorhynchus. Its original connection with the premaxilla has entirely disappeared, and it itself constitutes only an insignificant oval nodule of bone placed dorsally in front of the upper part of the anterior margin of the septum, remote from the rest of the premaxilla (figs. 9 and 10, *o.c.*).

Even in the younger Ornithorhynchus the interior of the os carunculæ (fig. 22) is in part hollowed away by osteoclastic absorption. Towards the dorsal portion of its interior there appears in successive sections a patch which shows on high power examination a structural character indistinguishable from that of hyaline cartilage, partially calcified, it may be, but which has not yet undergone neoplastic ossification. What the significance of this small and apparently cartilaginous vestige may be, I am unable to determine. Whilst embedded in, it appears tolerably sharply distinguishable from, the rest of the osseous tissue of the caruncle.

The further details of the anatomy of the snout-skeleton of the fœtal Monotreme will best receive elucidation in the course of a description of the plates.

DESCRIPTION OF PLATES.

Plate xxxvii.

Fig. 1 represents a view of the left side of the septum nasi and mesial aspect of the interior of the cartilaginous capsule of Jacobson's organ (*J.c.*), as exposed by a sagittal section of through Model i., to the left of the median plane. The cartilaginous septal fenestra and the profile outline of the os carunculæ (*o.c.*) are well seen. Note also the anterior extremity of the true vomer (*vo.*) and the cross section of the transverse cartilaginous lamina (*s.p.c.*) of the secondary palate.

Fig. 2 gives a view of Model i., from front, foreshortened, with the os carunculæ removed in order to show more clearly the cartilaginous skeleton of the front of the snout. Only one, the right, of the two premaxillary trabeculæ which are continued into the os carunculæ, is figured, and that is cut across at the level of the prerostral notch in which it is lodged.

m.c., marginal cartilage of upper lip, continued behind into the cartilage of the nasal floor, *n.f.*; *s.n.*, anterior margin of septum nasi, forming anterior boundary of cartilaginous fenestra; *al.n.*, cartilaginous roof of nasal cavity formed by alinasal; *px'.*, premaxillary trabecula; *px''.*, dorsal lamina of body of premaxilla.

Fig. 3. Ventral aspect of Model i. The os carunculæ (*o.c.*) is seen in front connected by the slender premaxillary trabeculæ (the left one being cut short) (*px'.*) with the ventral lamina of the body of the premaxilla (*px.*) and with the palatine process of the premaxilla (*p.px.*). These latter lie on the ventral

aspect of the cartilaginous nasal floor (*n.f.*) and (*al.n.*), which are continuous in front and laterally with the marginal cartilage (*m.c.*).

s.n′., septum nasi where it descends and is intercalated into and continuous with the cartilage of the nasal floor; *n.p.c.*, naso-palatine foramen (Stenson's duct); *J.c.*, cartilaginous capsule of Jacobson's organ, and *J.c′.*, its posterior extremity; *s.n″.*, edge of ventral border of septum nasi which is largely hidden by the anterior extremity of the vomer, *vo.*; *al.n.t.*, alinasal turbinal ridge projecting into the cartilaginous nasal cavity; *n.d.*, nasal duct proceeding along outer surface of alinasal wall of nasal cavity; *n.d′.*, nasal duct passing inwards and piercing alinasal near its ventral border; *mx.*, anterior prolongation of maxilla forming a trough which lodges the posterior end of the ventral lamina of the body of the premaxilla; *mx′.*, palatine plate of maxilla; *s.p.c.*, transverse cartilaginous lamina developed in the secondary palate, its anterior margin forming the true anterior limit of the skeleton of the latter.

Fig. 4. Right lateral aspect of Model i.

o.c., os carunculæ; *s.n.*, septum nasi, anterior border bounding septal fenestra (*fen.*) in front; *c.ap.*, cartilaginous boundary of anterior narial aperture; *al.n.*, alinasal wall of nasal cavity; *n.f.*, nasal floor; *m.c.*, marginal cartilage of snout; *px″.*, dorsal lamina of body of premaxilla; *n.*, nasal bone; *mx.*, maxilla; *n.n.*, nasal nerve; *n.d.n.*, notch in anterior margin of alinasal in which nasal duct turns inwards to open into anterior part of nasal cavity.

Fig. 5. Sagittal section close to left side of septum of Model ii. (snout of larger fœtal Ornithorhynchus).

al.n., alinasals of right and left sides (cut edge of left); *c.ap.*, cartilage of narial aperture; *s.n.*, septum nasi where it forms median bar bounding septal fenestra (*fen.*) in front; *s.n′.*, more posterior portion of septum nasi; *n.f.*, nasal floor, the more vertical dotted line leads to the place where the septum nasi descends to be intercalated into the nasal floor; *J.c.*, cartilaginous capsule of Jacobson's organ; *p.vo.*, prevomer or dumb-bell bone; *p.px.*, palatine process of premaxilla; *px.*, cut surface where ventral lamina of body of premaxilla is continuous with rest of bone; *px′.*, trabecula of left premaxilla, continuous through prerostral notch with degenerating os carunculæ, *o.c.*; *m.c.*, rostral ends of left and right marginal cartilages of snout.

Fig. 6. Anterior view of Model ii. There is a considerable amount of necessary foreshortening. The ragged and irregular outline of the degenerating os carunculæ (*o.c.*) is seen continuous with the rest of the premaxilla only through the right trabecula in the prerostral notch, the left having already been absorbed. The nasal duct (*n.d.*) is seen to turn inwards in the notch in front of the alinasal cartilage (*al.n′.*), to reach the nasal cavity; (*m.c′.*), edge of right marginal cartilage. The rest of the lettering as in previous figures.

Plate xxxviii.

Fig. 7. Ventral view of Model ii.

pr.n., prerostral notch, between rostral prolongations of marginal cartilages, *r.m.c.*; *px'*., anterior trabeculæ of premaxillæ, fused here; *p.px.*, palatine processes of premaxilla; *px.l.*, cut surface of continuity with ventral lamina of left premaxilla; *px.*, ventral lamina of right premaxilla; *n.f.*, nasal floor; *s.n'*., ventral edge of nasal septum where it enters into constitution of nasal floor; *J.c.*, cartilaginous floor of capsule of Jacobson's organ; *p.vo.*, bilateral prevomerine elements (anterior portions only) representing the dumb-bell ossification.

Fig. 8. Dorsal view of Model ii.

al.n'., anterior border of alinasal cartilage, with nasal duct (*n.d.*) turning inwards in front of it to enter the nasal cavity. Rest of lettering as in other figures.

Fig. 9. Sagittal section close to right of septum in anterior two-thirds, and lateral view of posterior third of Model iii. (fœtal Echidna). Here the os carunculæ is seen as a very small bony nodule (*o.c.*); the premaxillary trabeculæ (*px'*.) extend into, but not through, the shallow prerostral notch, of which only the left boundary (*r.m.c.*), formed by the rostral prolongation of the left marginal cartilage, is seen.

f.J.c., opening in anterior part of capsule of Jacobson's organ; *c.p.*, cartilaginous process prolonged backwards from alinasal wall behind and below narial aperture. Other letters as in other figures.

Fig. 10. Anterior view of Model iii., the right anterior part of the model being cut away.

al.n., cut edge of alinasal continued ventrally into cartilage behind anterior narial aperture; *c.ap.a.*, anterior cartilaginous margin of anterior narial aperture; *c.ap.p.*, the posterior cartilaginous margin of narial aperture. Other letters as elsewhere.

Plate xxxix.

Fig. 11. Ventral view of Model iii.

pr.n., shallow prerostral notch; *px'*., short and abruptly truncated premaxillary trabecula; *p.px.*, short palatine process of premaxilla; *px.*, ventral lamella of body of premaxilla; *n.p.c.*, cartilaginous gap corresponding to naso-palatine canal; *p.p.c.*, short and isolated cartilaginous rod forming skeletal basis of papilla palatina (*cf.* Broom, 11, "*p.c.*"). This corresponds with the palatine cartilage described by Broom in the papilla palatina of various Marsupials, and figured by him in Perameles (7, fig. 6, "*p.c.*"); *s.p.c.*, is the transverse cartilaginous lamella which develops as the skeletal basis of the secondary palate, and is to be compared with the corresponding lamella in Ornithorhynchus as seen in fig. 3, *s.p.c.*; *al.n.f.*, nasal floor formed by the ventral extension of the alinasal cartilage; *s.n'*., triangular depressed area formed by the ventral edge of the septum nasi where it descends to become intercalated into the nasal floor.

Fig. 12. Left lateral aspect of Model iii. The interrupted character of the cartilaginous boundary of the anterior narial aperture is apparent. The posterior aperture-cartilage (*c.ap.p.*) is continuous behind and internally with the alinasal, and just behind this attachment the alinasal is continued backwards for some distance as a tapering conical cartilage visible in fig. 9 (*c.p.*), but hidden here under cover of the premaxillary splint, *px″*. Other letters as elsewhere.

Plate xl.

Figs. 13-21 represent a series of coronal sections through the region of the snout of the younger fœtal Ornithorhynchus. They may be collated with the figures of Model i.

Fig. 13 represents the 20th section of the series, the os carunculæ having first appeared in the 12th section. The section cuts the tips of the rostral prolongations of the marginal expansions of the great plate of cartilage which behind forms the nasal floor. The prerostral notch lies between the tips of the cartilages.

In fig. 14 the premaxillary trabeculæ continuous above with the os carunculæ are passing ventrally through the prerostral notch to join the rest of the premaxillæ.

In fig. 15 we reach the plane of continuity of the median septal bar (*s.n.*) and the cartilage of the nasal floor, the section passing just in front of the septal fenestra. The os carunculæ is now tapering away posteriorly. In figs. 14-16 the epidermis over the caruncle is somewhat thickened, though not excessively. It is stained yellow by the picric acid which was used as a counter-stain with the hæmatoxylin. A study of sections in front of those here figured shows that the cornification is most intense in the epidermal layers which correspond to the stratum lucidum.

Fig. 16 passes through the plane of the anterior nares and the septal cartilaginous fenestra. Here we can distinguish dorsal and ventral lamellæ of the body of the premaxilla as well as the true palatine processes.

Fig. 17 passes behind the cartilaginous septal fenestra, and shows the continuity of the wide ventral portion of the septum nasi with the cartilage of the nasal floor. The section is slightly in front of *s.n′.* in fig. 3. The upper and lower valvular folds are here cut across.

Fig. 18 is a little in front of the plane of the partial coronal section of Model i., seen in fig. 3 in the right side of the figure. The anterior end of the cartilaginous capsule of Jacobson's organ is cut across. The marginal expansions of the nasal floor cartilage are now no longer continuous medially with the alinasal.

Fig. 19 is practically in the plane marked by *n.p.c.* in fig. 3. It passes through the naso-palatine canal and the opening into the latter of the efferent duct of Jacobson's organ. The neuro-epithelium of the latter is well shown (*J.o.e.*).

Plate xli.

Fig. 20 represents a coronal section at about the plane of the posterior margin of the lamella marked *s.p.c.* in fig. 3. It passes through the internasal aperture (*i.a.*) below the septum nasi, and shows the now tapering posterior ends of Jacobson's cartilages.

Fig. 21 is immediately behind the plane of the internasal aperture; the tip of Jacobson's cartilage on one side is still present, whilst the vomer has appeared as a splint on the ventral border of the cartilaginous septum nasi. Instead of the cartilaginous lamella (*s.p.c.*) seen in fig. 20, we now have, as skeletal basis of the secondary palate, the palatine plates of the maxillæ (*mx'.*). Note here, as well as on one side of the previous figure, the compact bundle of nerve-fibres from the olfactory bulb passing towards the hinder extremity of Jacobson's organ to supply its neuro-epithelium.

Plate xlii.

Fig. 22. Portion of coronal section of snout of specimen "A" of fœtal Ornithorhynchus. Section No. 23, of series. Hæmatoxylin and picric acid staining. Magnification of 100 diameters. The most dorsal portion of the os carunculæ exhibits an area of apparently cartilaginous character. Its cells are larger, vesicular, and have very distinct capsules around them.

General list of reference letters,

al.n., alinasal; *al.n'.*, free anterior margin of alinasal; *al.n.f.*, alinasal forming nasal floor; *al.n.t.*, alinasal turbinal; *ant.nar.*, anterior nares; *c.ap.*, cartilage of narial aperture; *c.ap.a.*, cartilage of narial aperture, anterior moiety; *c.ap.p.*, cartilage of narial aperture, posterior moiety; *fen.*, fenestra of cartilaginous septum nasi; *gl.*, glandular tissue; *i.a.*, internasal aperture above secondary palate; *J.c.*, cartilaginous capsule of Jacobson's organ; *f.J.c.*, foramen in cartilaginous capsule of Jacobson's organ; *J.o.e.*, epithelium of Jacobson's organ; *J.ol.*, olfactory nerve-bundle for Jacobson's organ; *m.c.*, marginal cartilage of snout, expansion from nasal floor cartilage; *r.m.c.*, rostral continuation of above by side of prerostral notch; *mx.*, maxilla; *mx'.*, palatine plate of maxilla; *n.*, nasal bone; *n.n.*, nasal nerve; *n.d.*, nasal duct; *n.f.*, nasal floor; *n.v.*, narial valves; *n.p.c.*, naso-palatine canal; *o.c.*, os carunculæ; *pr.n.*, prerostral notch; *p.p.c.*, cartilage of papilla palatina; *p.vo.*, prevomer (dumb-bell ossification); *px.*, ventral lamella of body of premaxilla; *px'.*, trabecula connecting os carunculæ with rest of premaxilla; *px''.*, dorsal lamella of body of premaxilla; *p.px.*, palatine process of premaxilla; *s.n.*, septum nasi; *s.n'.*, septum nasi where it descends into the floor of the mouth; *s.p.c.*, cartilaginous lamina forming skeleton of anterior part of secondary palate; *st.c.car.*, cornified strata of epidermis covering caruncle; *T.*, tongue; *vo.*, vomer.

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Addendum.

Since the above paper was read I have received through the courtesy of Dr. J. F. van Bemmelen, a copy of his recently published contribution to Semon's Zoologische Forschungsreisen in Australien, &c., on the subject of the Monotreme skull (der Schädelbau der Monotremen). The author deals at some length with both adult, immature adult, and young conditions of the snout skeleton, summarising and discussing the views of previous writers. He adopts the designation of praevomer for the dumb-bell-shaped bone, and defends the vomerine theory of its homology from certain recent criticisms of Gegenbaur, which would seem to rest on a misconception. The paper is a comprehensive one, and may be consulted in connection with the present publication, although dealing with substantially older stages than those I have been privileged to work with.