

12. *On the STRUCTURE of the PLESIOSAURIAN SKULL.* By CHARLES W. ANDREWS, Esq., B.Sc., F.G.S. (Read February 26th, 1896.)

[PLATE IX.]

THE structure of the skull of the Liassic Plesiosauria has been discussed by many writers, but the various accounts that have been given of it are incomplete, and often differ one from the other in important particulars, doubtless owing to the fact that in most cases the specimens examined are much crushed, and are embedded in the matrix, so that only one aspect is visible. In the National Collection there is, however, a fine skull of *Plesiosaurus macrocephalus*, which has lately been almost completely cleared from the matrix, so that it exhibits both the upper and under surfaces; this specimen, though it has been subjected to a slight vertical compression which has caused some fractures and dislocations, gives a fairly clear idea of the general arrangement of the constituent bones, and, since it throws light on some obscure points, seemed worthy of the following brief notice. Certain other specimens, which are of assistance in some difficulties, will also be referred to.

In 1838 Owen<sup>1</sup> figured and described the upper and lateral regions of the skull of *P. macrocephalus*, and in 1881 Sollas<sup>2</sup> described under the name *P. brachycephalus* some portions of the head of a specimen probably referable to the same species. Neither of these writers had an opportunity of examining the palate, and it is this region, therefore, that is more particularly considered here; while, in the structure of the rest of the skull, only such points are noticed as seem to add to, or to be at variance with, the descriptions already published.

The specimen (Pl. IX.) under consideration is from the Lias of Lyme Regis, and was referred to *Plesiosaurus macrocephalus* by Mr. Lydekker.<sup>3</sup> The occipital surface is still somewhat obscured by adherent matrix, and has the anterior cervical vertebræ attached to it, although the atlas has been dislocated from its articulation with the occipital condyle.

The bones of the palate (Pl. IX. fig. 1), though somewhat displaced from their natural positions, are, with the exception of the transverse bone, fairly well preserved and distinct, so that their form and relations can easily be made out.

The basioccipital (*b.oc.*) bears the whole of the nearly hemispherical occipital condyle, and carries on either side a stout, outwardly-directed tuberosity, the truncated end of which looks outward. In the Plesiosauria the whole of these tuberosities is formed by the basioccipital, but in most reptiles the basisphenoid enters into their composition.

<sup>1</sup> Trans. Geol. Soc. ser. 2, vol. v. pt. iii. (1840) pl. xlv.

<sup>2</sup> Quart. Journ. Geol. Soc. vol. xxxvii. (1881) pl. xxiv. fig. 1.

<sup>3</sup> Cat. Foss. Rept. Brit. Mus. pt. ii. (1889) p. 268, no. 49202.

The palatal surface of the basisphenoid (*b.sph.*) rises abruptly from the basioccipital; it is slightly concave from side to side, and is sharply separated from the lateral surfaces, which make an angle of from  $100^{\circ}$  to  $120^{\circ}$  with it. The posterior portion of these lateral surfaces forms a facet, looking outward and downward, with which the pterygoid articulates. The basisphenoid seems to have been overlapped by a parasphenoid (*pas.*), but the hinder border of that bone is indistinguishable; anteriorly it expands into a thin, spearhead-shaped plate, the outer angles of which in the present specimen overlap the ventral surface of the pterygoids, and with them limit the posterior palatine foramina (*post.pal.vac.*),<sup>1</sup> which open between the *basis cranii* and the pterygoids, as in *Peloneustes*. In this latter, however, the parasphenoid is slightly overlapped on its ventral surface by the pterygoids; this difference in the relative position of the bones in the two genera may be due to displacement in the present specimen.

The pterygoids (*pt.*) are triradiate bones, like those of *Peloneustes*, but differ from them in not meeting in the median line over the basisphenoid, and remaining separated by the whole palatal width of that bone. Anteriorly they have been dislocated from their junctions with one another and the surrounding bones, but there can be no doubt that in their natural position they met anteriorly and, together with the parasphenoid, closed the palate in the middle line.

Their anterior rami are thin triangular plates, the apices of which meet the vomers, while their inner borders form a median suture with one another in front, and are overlapped by the parasphenoid behind. In the uncrushed skull their outer edges united with the palatines.

The lateral rami run outward opposite the anterior end of the posterior palatine foramina; their outer ends are much thickened and in the present specimen have been partly broken away. In the skull of *P. dolichodeirus* noticed below (fig. 1, p. 248), the outer ends of these lateral rami are joined to the maxillary region by a transverse bone (*trs.*), and the same is the case in *Peloneustes* and *Pliosaurus*.

In front the posterior rami are narrow bars of bone forming the outer border of the posterior palatine foramina. Behind these openings they widen a little, and bear on their inner side facets for articulation with the corresponding surfaces on the sides of the basisphenoid. Posteriorly they run outward and backward as thin vertical plates to the quadrates, which do not appear to send forward to meet them plates of bone such as are seen in *Sphenodon*.

The *columella cranii* (Pl. IX. fig. 4, *col.*) or epipterygoid is well

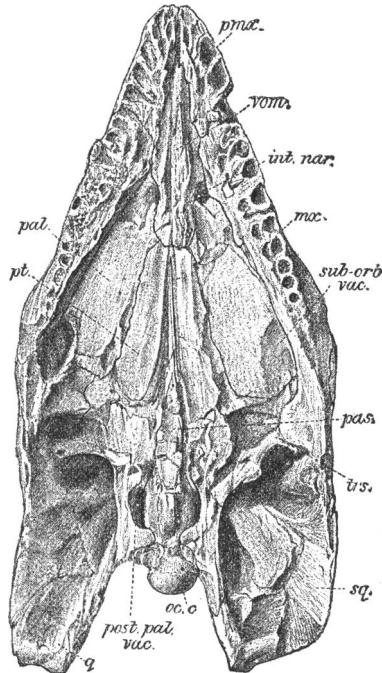
<sup>1</sup> In this paper, as well as in that on the skull of *Peloneustes* (Ann. Mag. Nat. Hist. ser. 6, vol. xvi. 1895, p. 242), the term 'post-palatine foramen' is used in a different sense from that in which it is sometimes employed (for example, by E. T. Newton in his papers on the Reptilia of the Elgin Sandstones), and is applied to the pair of foramina which result from the division of the median interpterygoid foramen by the basisphenoid and parasphenoid. Newton employs the term for the aperture which lies in front of the transpalatine, and is here called the 'suborbital foramen.'

shown in this specimen. It rises from the upper surface of the pterygoids about opposite their junction with the basisphenoid; its base of attachment is very long from before backward, so that it extends for a considerable distance along the upper edge of the quadrate process of the pterygoid. In its middle portion it contracts in width, and is an elongate oval in section. On both sides of the skull the upper portion of this bone has unfortunately been broken away, so that the junction with the parietals is not clear, but it evidently joined their lower edge at about their middle point.

The palatines (*pal.*) are elongated plates of bone, of which the anterior edges form the hinder margin of the nares; on the inner side they unite in front with the vomers, and behind with the pterygoids, while on the outer they join the maxillæ. In the present specimen the relations of the hinder border of the palatine are not clear, though it is evident that internally it joined the lateral ramus of the pterygoids; but in a skull of *P. dolichodeirus* (B.M. Coll. 41101) it can be seen (fig. 1) that externally the hinder border of the palatine joined the transpalatine for a short distance, and was then separated from it by a small suborbital foramen (*sub-orb. vac.*) which appears to be closed on its outer side by the maxilla. Mr. Lydekker<sup>1</sup> first called attention to these foramina in this specimen (fig. 1), in which also he first observed the fact that the pterygoids extend forward to meet the vomers.

The vomers (*vom.*) are not well preserved; they are long narrow bones which unite, and perhaps ankylose, in the middle line. Posteriorly they join the pterygoids, and in front of these, the palatines. About the middle of their length they form the division between the internal nares, and anterior to these apertures they run forward between the maxillæ and premaxillæ.

Fig. 1.—Palatal surface of the Skull of *Plesiosaurus dolichodeirus*. (About  $\frac{1}{2}$  natural size.)



<sup>1</sup> Cat. Foss. Rept. Brit. Mus. pt. ii. (1889) p. 257, no. 41101.

The lower surface of the maxillæ and premaxillæ is largely concealed by the mandible, which is tightly closed upon them. The inner border of the palatal plate of the maxilla is, however, visible for some distance both in front of and behind the internal nares, the outer border of which it forms. In its anterior region there are one or two pits which probably mark the points of eruption of successional teeth. The palatal portion of the premaxillæ is almost completely concealed by the symphyseal region of the mandible; but the anterior ends of the vomers appear to run forward some distance between these bones; in the above-mentioned skull of *P. dolichodeirus* this is certainly the case (fig. 1, p. 248).

The general structure of the Plesiosaurian palate is shown diagrammatically in fig. 2 (p. 251).

The structure of the temporal arcade (Pl. IX. fig. 3) is, in all essential respects, similar to that in *Plesiosaurus brachycephalus* (figured by Sollas),<sup>1</sup> *P. dolichodeirus*, and *P. Hawkinsi* (figured by Owen),<sup>2</sup> and also to that of *Peloneustes*<sup>3</sup>: the only important difference being that in the present species the postorbital sends back a long thin strip along the anterior ramus of the squamosal nearly to its origin. The supra-jugal which Sollas observed in *P. brachycephalus* cannot be detected, but, if I understand the description of that bone (it is not figured), it corresponds to the lower portion of the postorbital. The thin posterior extension of the maxilla along the lower edge of the jugal is concealed by the mandible, the pressure of which has driven it inwards.

The wall of bone described by Sollas, which separates the orbit from the temporal fossa, is well shown in this specimen. It appears to be mainly formed by the postfrontal and postorbital, each of which thus consists of an external facial and an internal postorbital portion, which meet in the angle forming the anterior rim of the temporal fossa. I cannot make out what share in the formation of this postorbital wall is taken by the jugal; according to Sollas it is an important one.

The upper ramus of the triradiate 'squamosal' is in this specimen indistinguishably fused with the remainder of that bone; but in the younger skull described by Owen it is separated by a distinct suture, which is figured by him.<sup>4</sup> He calls this upper portion the 'mastoid,' while the remainder of the bone, consisting of the inferior and anterior rami, is designated the 'squamosal.' It is clear that these two elements are equivalent to the supra-temporal and squamosal of lizards, according to the terminology of Parker & Bettany and many other writers, or to the squamosal and prosquamosal, according to Baur. Their arrangement is similar to that occurring in the Rhynchocephalia, the fused elements of the older individuals having almost exactly the form and relations of the so-called 'squamosal.'

<sup>1</sup> Quart. Journ. Geol. Soc. vol. xxxvii. (1881) pl. xxiv. fig. 2.

<sup>2</sup> Trans. Geol. Soc. ser. 2, vol. v. pt. iii. (1840) pl. xlv.

<sup>3</sup> Ann. Mag. Nat. Hist. ser. 6, vol. xvi. (1895) p. 251, fig. 2.

<sup>4</sup> Trans. Geol. Soc. ser. 2, vol. v. pt. iii. (1840) pl. xlv.

of *Sphenodon*. Koken<sup>1</sup> has expressed the same opinion as to the constitution of the 'squamosal' in the *Nothosauria*. In several Plesiosaurian skulls in the British Museum the suture between these elements is distinct.

The quadrate (*q*) is a long, stout bone; posteriorly it is convex from side to side, anteriorly concave. It projects downward and backward, and the condyle for the mandible lies somewhat below the level of the alveolar border of the maxilla. On its outer side the inferior ramus of the squamosal is closely adherent to it, and extends nearly down to the condyle.

In *Cimoliosaurus* Cope<sup>2</sup> has figured a small quadrato-jugal, and Koken<sup>3</sup> has recorded the probable occurrence of this bone in *Nothosaurus*; it therefore seems possible that the Plesiosaurian quadrate may be a fusion of the quadrate and quadrato-jugal, a view which derives some support from the fact that the relations of the squamosal to the 'quadrate' are almost exactly similar to those existing between the squamosal and the quadrato-jugal in *Sphenodon*.

The general structure of the upper surface of the skull is shown in Pl. IX. fig. 2. It will be seen that between the anterior halves of the temporal fossæ the parietals form a high, sharp crest, but that posteriorly they widen out into a broad triangular plate, convex from side to side, which apparently roofs in the brain-case. The outer angles of this plate are overlapped by the upper rami of the squamosals, these forming the hinder border of the temporal fossæ. In front, opposite the anterior end of these fossæ, the parietals enclose the pineal foramen, which does not extend into the frontals, and laterally they widen out and take part in the formation of the postorbital wall. There is clearly a distinct post-temporal fossa, closed above by the lateral process of the parietal and the upper ramus of the squamosal. The frontals extend much farther forward than in *Peloneustes*, and separate the external nares. I can find no clear evidence of the existence of distinct nasals and lachrymals.

Comparison of the palatal portion of this skull with that of *Peloneustes* shows that the chief difference between them is that in the latter the pterygoids, instead of merely articulating with the sides of the basisphenoid, overlap it, and form a median suture with one another on its ventral surface. In *Peloneustes*, also, the form of the parasphenoid is different, and it is very uncertain whether there is any suborbital vacuity.

In *Nothosaurus* the pterygoids meet in the middle line from end to end, and there is no suborbital vacuity, so that the palate is completely closed; this appears to be a more specialized condition than occurs in either *Plesiosaurus* or *Peloneustes*, although both these genera are of a later date.

<sup>1</sup> 'Beiträge zur Kenntniss der Gattung *Nothosaurus*,' Zeitschr. deutsch. geol. Gesellsch. vol. xlv. (1893) p. 363.

<sup>2</sup> 'On the Structure of the Skull in the Plesiosaurian Reptilia,' Proc. Amer. Phil. Soc. Philadelphia, vol. xxxiii. (1894) p. 110.

<sup>3</sup> *Op. supra cit.*

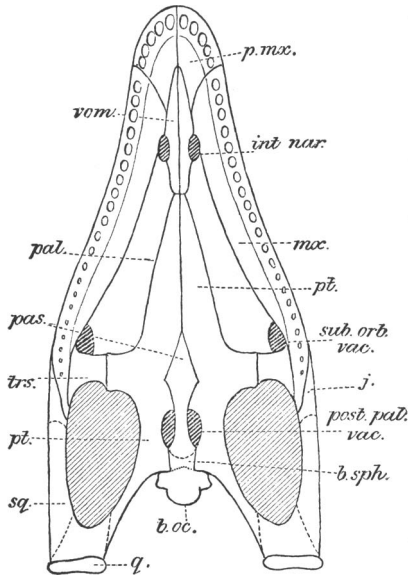
In *Lariosaurus*<sup>1</sup> the palate is essentially similar to that of *Plesiosaurus*, but here again the pterygoids completely shut in the *basis cranii*. The suborbital vacuity is very large, and the pterygoids bear teeth, both probably primitive characters. The palate of *Neusticosaurus* is doubtless similarly constructed, but the suborbital vacuities are still larger.

In *Pistosaurus* the pterygoids appear to leave the *basis cranii* exposed for some distance, and in this respect the palate in this genus is more Plesiosaurian in form than is that of any other Triassic Sauropterygian.

Among reptiles other than the Sauropterygia the palate most similar to that under consideration is found in *Sphenodon*. In this reptile the form and the relations of the bones of the palate to one another and to the internal nares are almost identical with those above described. The only difference of importance is that the pterygoids, instead of articulating directly with the sides of the basisphenoid, are borne off from it by downwardly-directed basi-ptyergoid processes, so that they come to lie at a lower level than the *basis cranii*. The consequence of this arrangement is that the parasphenoid, here very small, does not run forward between them dividing the interptyergoid vacuity into two post-palatine foramina.

Too much importance must not be attached to the similarity existing between the palates of these two forms, since the Rhynchocephalian type of palatal structure occurs in a more or less modified form in many widely divergent reptilian groups, and probably therefore approaches the primitive type of structure common to the ancestors of those various groups. For instance, the Ichthyosaurian palate, except that the lateral wing of the pterygoid is reduced, and the transverse bone consequently absent, is very like that of *Sphenodon*. Again, among the Anomodonts, *Procolophon* is, so far as the palate is concerned, Rhynchocephalian; the presence of teeth

Fig. 2.—Diagrammatic figure of the Plesiosaurian palate.



<sup>1</sup> For my knowledge of the structure of the palate in this genus I am indebted to Mr. Boulenger, who kindly allowed me to see a proof of his forthcoming paper on the skeleton of *Lariosaurus Balsami*.



on its pterygoids and vomers is probably a primitive character derived from its Labyrinthodont ancestors; the palate of *Pareiasaurus* is similar.

In the Theriodonts a short secondary hard palate is developed, carrying back the opening of the internal nares; but in some specimens (for example, the skull of *Galesaurus planiceps*, B.M. R. 511) the relations of the bones constituting the primitive palate are *Sphenodon*-like, the pterygoids extending forward to meet the vomers, and their lateral rami bearing a downwardly-directed process (ectopterygoid) which lies against the inner side of the closed mandible, and is no doubt partly formed by a transpalatine element. There seems to be no suborbital vacuity.

The palatal structures of the Chelonia, regarded as modifications of the same type, are easily comprehensible, and the same is the case with the Lacertilia. In the highly specialized palate of the Crocodilia, the resemblance to the primitive form is masked by the secondary hard palate formed by the palatines and pterygoids; but if this be disregarded, the same type of structure may be traced here also.

Enough has been said to show that among reptiles a certain similarity of palatal structure does not necessarily imply any close relationship, but the very great resemblances existing between the Plesiosaurian and Rhynchocephalian palates, reinforced by the numerous other points of likeness in other portions of their skeletons pointed out by Baur, lead to the conclusion that the Sauropterygia, notwithstanding their single temporal arcade and thecodont dentition, are descended from a primitive Rhynchocephalian reptile. This opinion has already been expressed by several writers, notably by Baur<sup>1</sup> and Boulenger.<sup>2</sup>

#### EXPLANATION OF PLATE IX.

Skull of *Plesiosaurus macrocephalus*, Buckland.

- Fig. 1. From below.  
2. From above.  
3. From the side.  
4. Temporal fossa seen obliquely from the side, showing the relations of the *columella*.

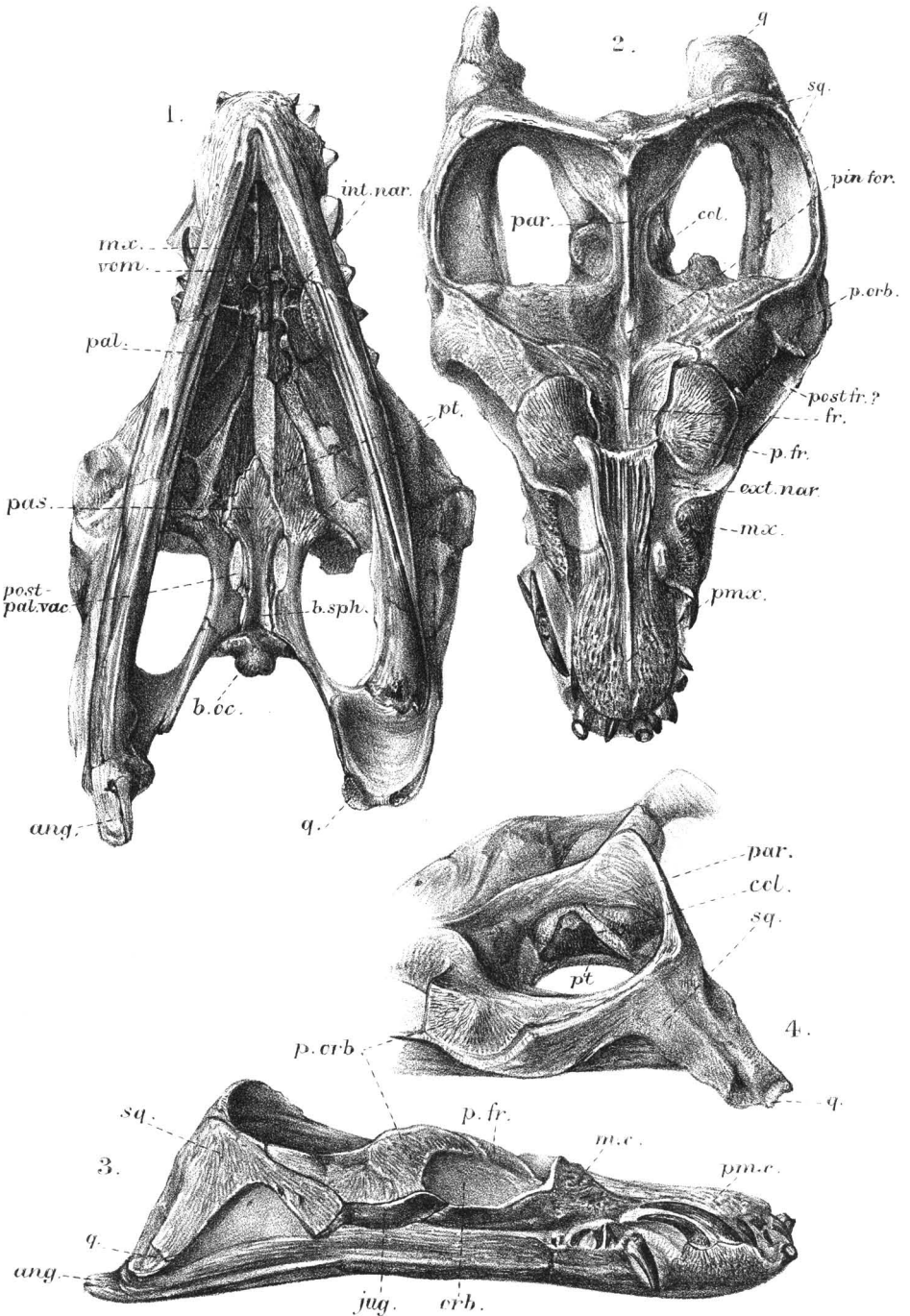
*ang.*, angular.  
*b.oc.*, basioccipital.  
*b.sph.*, basisphenoid.  
*col.*, columella cranii.  
*ext.nar.*, external nares.  
*int.nar.*, internal nares.  
*fr.*, frontal.  
*jug.*, jugal.  
*mx.*, maxilla.  
*orb.*, orbit.  
*pal.*, palatine.  
*par.*, parietal.

*pas.*, parasphenoid.  
*pin.for.*, pineal foramen  
[misprinted *pm.for.*].  
*pmx.*, premaxilla.  
*p.orb.*, post-orbital.  
*p.fr.*, pre-frontal.  
*? post.fr.*, ? separate post-frontal.  
*post.pal.vac.*, posterior palatine  
vacuities.  
*q.*, quadrate.  
*sq.*, squamosal.  
*vom.*, vomer.

All the figures are about  $\frac{1}{2}$  natural size.

<sup>1</sup> 'On the Phylogenetic Arrangement of the Sauropsida,' Journ. Morph. vol. i. p. 93.

<sup>2</sup> Cat. Chelonians, Rhynchocephalians, and Emydosaurians in the British Museum, p. 1.



J Green. del. et lith.

SKULL OF PLESIOSAURUS MACROCEPHALUS, Buckland.

Mintern Bros. imp.



DISCUSSION.

The PRESIDENT invited discussion.

Prof. HOWES, on behalf of morphologists, gave expression of gratitude to the Trustees and Staff of the British Museum of Natural History for the work now being accomplished in their Geological Department. He remarked that he had been privileged to examine the Author's specimens, and that he fully confirmed his determinations. He could not accept the idea, to which reference had been made, that *Parviasaurus* had a closed palate in the ordinary sense; that is to say, the internal nasal openings were not carried to the back of the palate by the union of the palato-pterygoid bones as they are in the Crocodilia.

In concluding, he pointed out that the Author's determinations of the bony palate of the Sauropterygia were in complete harmony with Mr. Lydekker's of that of the Ichthyopterygia, and with the best-established facts of morphology; and that, thanks to these gentlemen, we were now in a position to definitely refer the 'Enaliosauria' to an origin among the lowest reptiles.

Mr. LYDEKKER and Dr. WOODWARD also spoke.

The AUTHOR expressed his thanks to the Fellows, particularly those who had spoken, for the kind manner in which they had received his paper. He also referred to his indebtedness to Mr. Hall, one of the 'masons' at the Natural History Museum, for the skilful way in which he had cleared the specimen from its hard matrix.