PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

On the Structure of Lysorophus, as Exposed by Serial Sections

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XI.—*On the Structure of Lysorophus, as Exposed by Serial Sections.*

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(Received March 17, 1919,—Read May 22, 1919.)

[Plate 70.]

Our knowledge of Lysorophus, the most remarkable land vertebrate, according to Broom, which has been discovered for many years, begins with the description given by Cope,* in 1877, of three isolated vertebræ found in beds of probably Upper Carboniferous age in Vermillion County, Illinois. On the evidence of these vertebræ, Cope regarded Lysorophus as a reptile, and, in 1879,† he doubtfully assigned it to the Clepsydropidæ, a sub-division of the Theromorpha. Case,‡ who had redescribed the vertebræ in 1899, obtained ribs and additional vertebræ from a new locality in the State of Texas, and published an account of them in 1902.§

The same locality afterwards afforded Broili|| the fragmentary skulls of 14 individuals; and it is to his study of these that we owe our first introduction to the cranial anatomy of the organism. Influenced, unfortunately, by a mistaken interpretation of the occipital region, Broili definitely assigned Lysorophus to the Reptilia, but again misled, this time by the supposed presence of gular plates, which have no existence, he exaggerated the closeness of its alliance with the fishes, and concluded by making it the representative of a new family, which he named the Paterosauria—ancestral reptiles *par excellence.*

Case,¶ having now collected some excellent material from the Texan locality, was able to give an improved account of the structure of the skull, accompanied by excellent figures. With a true instinct, he seized upon the form of the great parasphenoid as stamping it with an indubitable Amphibian character. This contribution evoked a reply from Broili,** who, while modifying his previous

* Cope, E. D., "Description of Extinct Vertebrata from the Permian and Triassic Formations of the United States," 'Proc. Am. Phil. Soc.,' vol. 17, pp. 182–193 (1877).

† Cope, E. D., "Systematic Catalogue of the Species of Vertebrates found in the Beds of the Permian Epoch of North America," 'Trans. Am. Phil. Soc.,' vol. 16, p. 287 (1886).

‡ Case, E. C., "The Vertebrates from the Bone-bed of Vermillion County, Illinois," 'Journ. Geology,' vol. 7, p. 698 (1899).

§ Case, E. C., "Palæontological Notes," 'Journ. Geology,' vol. 10, p. 256 (1902).

|| Broili, F., "Permische Stegocephalien und Reptilien aus Texas," 'Paläontographica,' vol. 51, pp. 94–97, Taf. XII (1904); "Stammreptilien," 'Anat. Anz.,' vol. 25, p. 579 (1904).

¶ Case, E. C., "Notes on the Skull of *Lysorophus tri-carinatus*, Cope," 'Bulletin Am. Mus. Nat. Hist.,' vol. 24, pp. 531–533, figs. (1908).

** Broili, F., "Systematische und biologische Bemerkungen zu der permischen Gattung Lysorophus," 'Anat. Anz.,' vol. 33, pp. 290–298 (1908).

 [Published March 31, 1920.]

views, still maintained that Lysorophus was a reptile, and compared it with Amphisbæna.

In the same year appeared a masterly description by WILLISTON.* Based upon a very perfect skull, this is as remarkable for the fulness as for the accuracy of its information. It definitely established the Amphibian nature of Lysorophus, and,

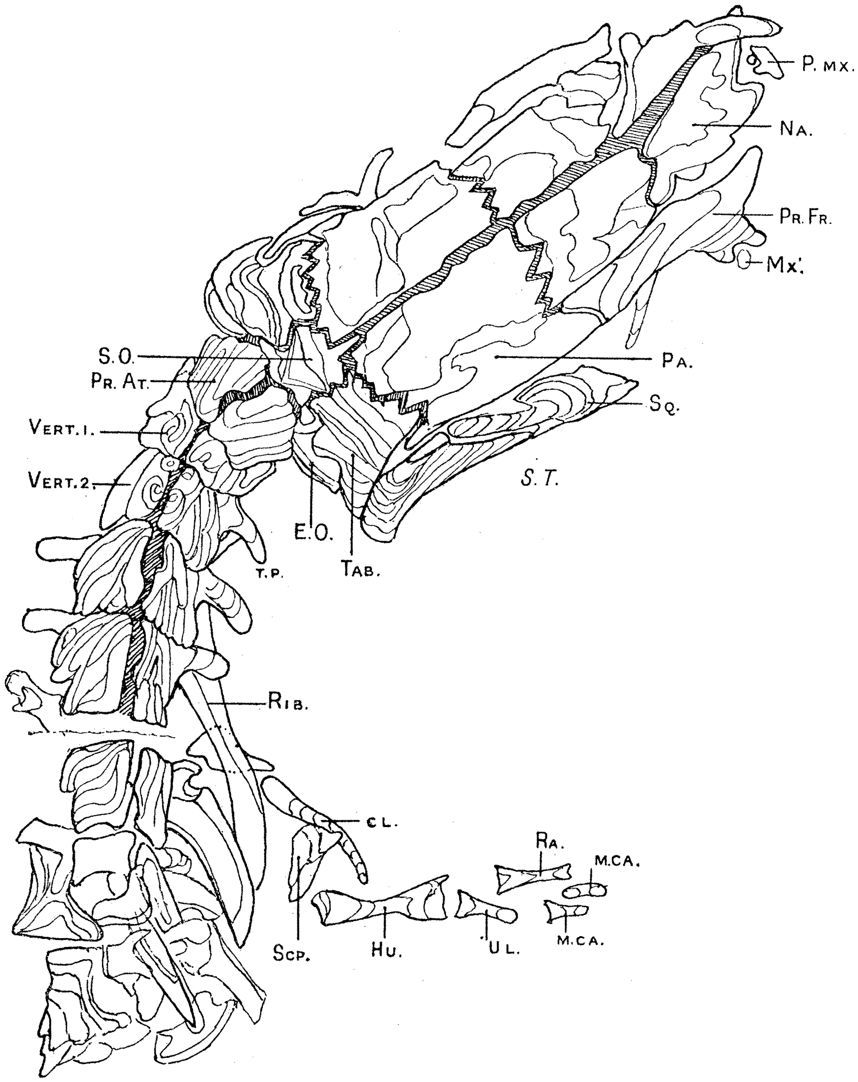

FIG. 1.—Reconstruction of Lysorophus. Dorsal surface. (×5.)

more precisely, even suggested its close alliance with the Urodela; indeed, in a closing paragraph, the author expressed the "conviction . . . that the Lysorophidæ should be included in the Ichthyoidea." A year later, MOODIE,† who has contributed

* WILLISTON, S. W., "Lysorophus, a Permian Urodile," 'Biological Bulletin,' vol. 15, pp. 229–240 (1908).

† MOODIE, ROY L., "Vertebrate Palæontology—The Lysorophidæ," 'The American Naturalist,' vol. 43, pp. 116–119 (1909).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

so largely to our knowledge of the Palæozoic Amphibia, expressed his agreement with WILLISTON on the general question, but refused to admit Lysorophus to the Urodela, chiefly on the ground of its long curved ribs, and spoke strongly in favour of its affinity with the Gymnophiona.

In the same paper, MOODIE adds some important information on the age of the

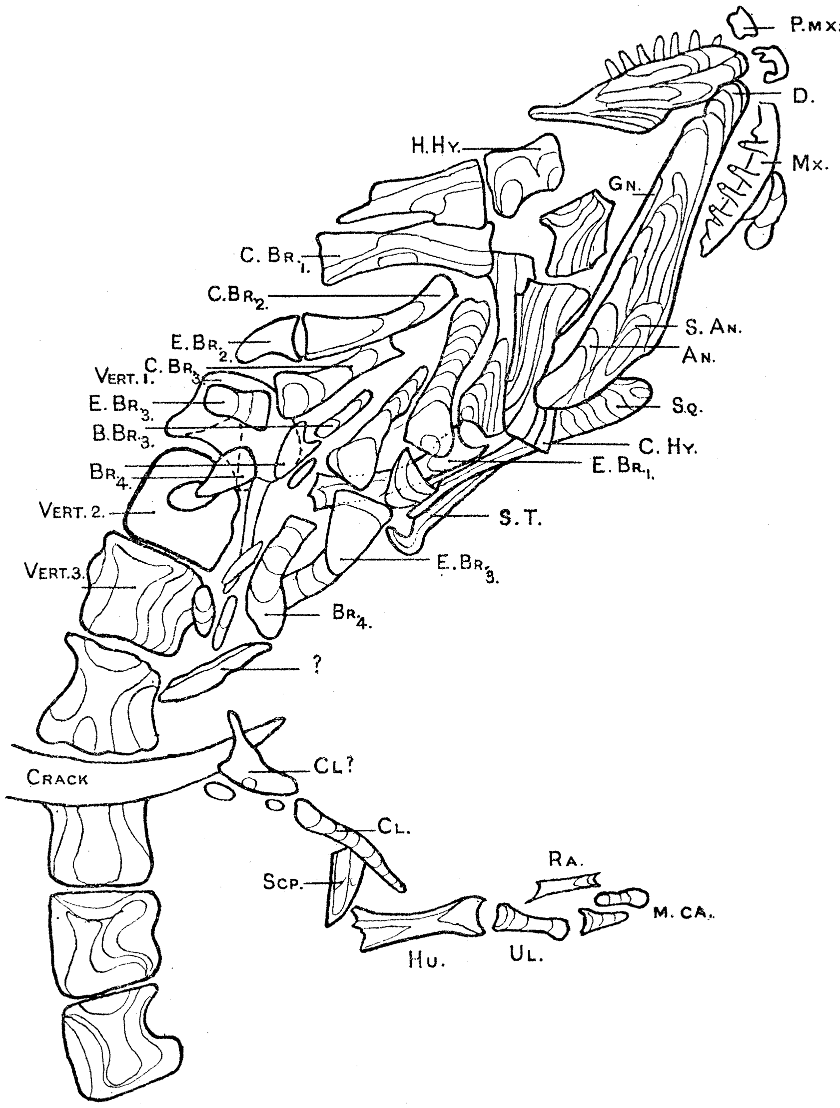

FIG. 2.—Reconstruction of Lysorophus. Vertical surface. (×5.)

fossil. It appears that the Texan deposits in which Lysorophus occurs are not Permian, as was originally supposed, but Pennsylvanian, probably Upper Pennsylvanian ; thus, Lysorophus would seem to have inhabited North America during Coal Measure times.

Notwithstanding the arguments brought forward by WILLISTON, BROILI*

* KARL A. VON ZITTEL, "Grundzüge der Paläontologie." Neu arbeitet von F. BROILI, E. KOKEN, M. SCHLOSSER. II. Abtheilung, 'Vertebrata,' p. 218. Munich and Berlin, 1911.

evidently remained unconvinced, for, in the edition of ZITTEL'S 'Palæontology,' published in 1911, we find Lysorophus included among the reptiles as a member of the "Paterosauridæ," which is attached to the Squamata. It is illustrated by CASE'S early figures of the skull, with the tabulare interpreted as the squamosal and the anterior cranial walls as the interorbital septum.

In the same year, MOODIE* again expressed his objections to the inclusion of Lysorophus among the Urodeles, alleging that even the presence of limbs, should they be discovered, would not affect his opinion on this important point. He thus met by anticipation the force of the discovery made soon afterwards by Miss MARIAN FINNEY,† to whom we are indebted for a full description of several femurs and other isolated bones of the leg, which were found in association with the now well-known vertebræ.

After a short summary,‡ with an added note retracting a previous statement, WILLISTON returned to the subject in 1912.§ The fact that in this communication Lysorophus is discussed under the heading of "Primitive Reptiles," suggests a change of view, and some conclusions are reached which leave the impression that the author is no longer prepared to maintain his original position intact. Thus, after enumerating its characters, he remarks that, should his account prove to be correct, then "it will necessarily follow that, if Lysorophus is a real reptile, it must occupy a place all by itself as a separate sub-class, without descendants or antecedents." On the other hand, "Lysorophus has no direct ancestral relationships with any modern vertebrates. That the Urodela, or even the Gymnophiona, began in such extremely Amphiuma-like forms in the Carboniferous would be contrary to all . . . experience."

This is far, however, from asserting that Lysophorus is a reptile or that it is not an Amphibian, yet it is easy to understand how a foreigner, like VON HUENE, unacquainted with the niceties of our language, should have interpreted the statement in that sense.

Fortunately, in a later paper, WILLISTON|| leaves us in no doubt of his views, and definitely places Lysorophus with the Amphibians, as an early offshoot from the Urodele stem.

In 1913, VON HUENE¶ redescribed the skull from specimens in Tübingen and the

* MOODIE, ROY L., "Recent Contributions to a Knowledge of the Extinct Amphibia," 'Am. Nat.,' vol. 45, p. 382 (1911).

† FINNEY, MARIAN, "The Limbs of Lysorophus," 'Journ. Morphology,' vol. 23, pp. 664–667 (1912).

‡ WILLISTON, S. W., "New Permian Reptiles, Rachitomous Vertebræ," 'Journ. Geology,' vol. 18, p. 600 (1910).

§ WILLISTON, S. W., "Primitive Reptiles," 'Journ. Morphology,' vol. 23, p. 640 (1912).

|| WILLISTON. S. W., "The Phylogeny and Classification of Reptiles," 'Journ. Geology,' vol. 25, p. 411 (1917).

¶ FRIEDRICH VON HUENE, "The Skull Elements of the Permian Tetrapoda in the American Museum of Natural History, New York," 'Bulletin Am. Mus. Nat. Hist.,' vol. 32, pp. 315–386, in particular

American Museum ; to new and valuable observations he added some new errors, but recognised, correctly as I believe, its affinity with the Urodeles.

In 1914, my friend, Dr. BROOM, who had seen and appreciated the results already obtained by the employment of serial sections in the elucidation of fossil remains, obtained through the kindness of Dr. MATTHEW, of the American Museum, two specimens of Lysorophus, which he generously presented to me for investigation ; and, still more generously, he placed in my hands at the same time, to dispose of as I might think fit, the MS. of a paper he had himself prepared on the cranial anatomy of this organism. After sections had been prepared of one of the specimens, I found that they confirmed in so striking a manner the most important conclusions in Dr. BROOM'S paper that I took immediate steps for its publication.*

Out of much that is new in this communication, we may select for special attention the interpretation of certain deep-seated elements of the skull as ossifications in the cranial cartilage, resembling, at least superficially, the sphenethmoid and alisphenoid or epipterygoid. Dr. BROOM concludes his account with the statement that the skull is "fundamentally Amphibian," with closer alliances to the Urodela than the Anura or Gynophiona.

Finally, my friend Dr. WATSON, who has made several fresh observations as yet unpublished, informs me that he is convinced from the study of a remarkably well preserved skull in his possession that the Amphibia are the only group to which Lysorophus can be assigned. Dr. WATSON has taken great interest in my work of reconstruction and I am indebted to him for several valuable suggestions. His last visit to Oxford, made when this account was on the verge of completion, had indeed some unexpected consequences, necessitating a change in the nomenclature of the parts associated with the suspensorium. Thus the bone which I, in common with previous investigators, had regarded as the quadrate (fig. 3) was supposed by Dr. WATSON to be completed below on the inner side by a process which is identical with the upper part of a separate bone, identified by me with the articulare of the lower jaw. This led to a re-investigation of the supposed articulare; it is distinguished by a very narrow "waist" and in one specimen the "waist" has disappeared, so that the upper is no longer continuous with the lower part. Dr. WATSON therefore suggested that the supposed articulare is not a single bone but consists of one bone above the "waist"—the true quadrate, and another below—the true articulare. This was a rather startling interpretation, especially as the identifications already made corresponded very closely with the disposition of the parts as they occur in Amblystoma. It is supported, however, by convincing evidence. Thus, the head of my supposed articulare never articulates with my supposed quadrate but lies between

pp. 322 *et seq.*, and "Ueber Lysorophus aus dem Perm von Texas," 'Anat. Anz.,' vol. 43, pp. 389–396, figs. (1913).

* BROOM, R., "On the Genus Lysorophus, COPE," 'Annals and Magazine of Natural History,' ser. 9, vol. 2, pp. 232–240 (1918). (With a Note by W. J. SOLLAS.)

that bone and the pterygoid, a relation which I had attributed to dislocation. It obtains, however, in all my specimens and in Dr. WATSON's as well and thus seems too constant to be the result of accident. Further, on a re-examination of sections we found the pterygoid and the false "quadrate" so precisely adapted to the sides of the head of the "articulare" (fig. 20) that such an explanation became impossible and it was necessary to admit that all three bones still retain their original position.

We are thus led to conclude that Dr. WATSON's view is correct. The bone which had every appearance of being the articulare is in fact two bones, the articulare and the quadrate, which in one of our specimens retain their natural position and articulate with each other.

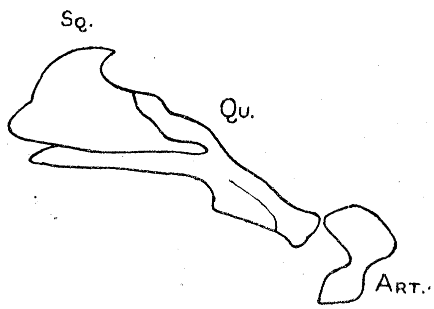

FIG. 3.

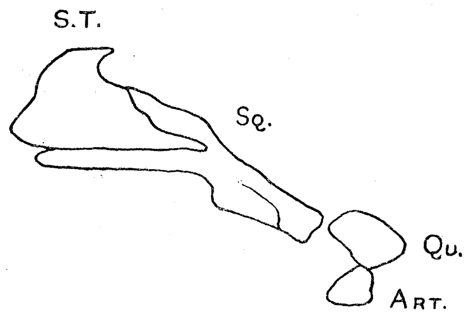

FIG. 4.

FIG. 3.—Original interpretation of the suspensorial region. The "articulare" is displaced towards the right: in its natural position it would be partly concealed by the "quadrate." (× 5.)

FIG. 4.—Interpretation now proposed for the suspensorial region. (× 5.)

This renders necessary a renewed identification of the bones previously named quadrate and squamosal. Dr. WATSON proposed to call the "quadrate," which bounds the true quadrate on the outer side, quadrato-jugal and for this there may be, no doubt, much to be said. On the other hand the numerous and important features which connect Lysorophus with the Urodeles suggest the squamosal; for in that group it is the squamosal which in all its relations most recalls the bone in question. But if this be admitted then the bone which has hitherto been called "squamosal" becomes the supra-temporal (fig. 4) and in support of this interpretation it may be re-called that PARKER and BETTANY* in their account of the skull of Amblystoma make mention of the fact that on the right side of the specimen which they figure "the postero-superior angle of the squamosal is converted into a distinct small supra-temporal bone."

Lysorophus would thus appear to furnish us with an additional instance of that overlap of the squamosal by the supra-temporal which is so marked a feature in Ichthyosaurus.

Before closing this part of my subject I should like to express my deep sense of the obligations I am under to my friend and colleague, Mr. GOODRICH. In

* PARKER and BETTANY, 'The Morphology of the Skull,' London, p. 126, § 301 (1877).

endeavouring to find my way through the difficulties of this investigation I have constantly sought his advice and never in vain. How often he has diverted my steps from deceptive by-paths and concealed pitfalls will be known only to myself.

The specimens presented me by Dr. BROOM had not a very promising appearance: they consisted of two nodules with some of the roofing bones of the skull exposed on the surface. The matrix consisted of a fine red limestone traversed by a network of winding canals. It looked as though the coils of the snake-like creature had been invested with a thick coating of calcareous and ferruginous mud which had subsequently been cemented together by a deposit of calcite.

The nodule which contained the largest head was selected for treatment and in spite of its apparently imperfect consolidation no difficulty was experienced in grinding it down. A complete series of 156 sections were obtained at intervals of 0·1 mm. and these were photographed under an enlargement of 4 diameters. The skull, as well as a series of dorsal vertebræ associated with it, was then reconstructed, first by tracing the sections on glass plates, a very useful preliminary, and afterwards by building it up in plaster.

The results exceeded my expectations and I proceeded to a description of this material with the intention of confining myself to its evidence and so dispensing with the labour of preparing the second specimen. When, however, it appeared necessary to clear up some obscure points, I had to relinquish this intention and obtained a series of 46 sections from the second specimen. These were cut at intervals of 0·2 mm. and photographed under an enlargement of 5 diameters. They exposed the skull, a series of "cervical" and dorsal vertebræ, the right shoulder girdle, and bones of the right fore limb.

These sections proved so much superior to the first, especially by the comparative absence of distortion, that abandoning the figures I had already drawn, I commenced anew and based my description on the reconstruction of the second specimen, using the first merely for confirmation and supplementary information.

Now that we can handle the skull and other parts of the skeleton and examine them on all sides, free from adventitious matter, it is difficult to repress a feeling of æsthetic satisfaction. Every detail of structure is revealed, the several bones are displayed in their original relations as clearly as in a macerated and mounted skeleton, and accidents of fossilization, when they exist, proclaim as a rule their true nature.

There is, I am convinced, a great future for this method, which is bound to add largely to our knowledge of fossils, rendering the study of palæontology more exact and inspiring greater confidence in its results. Many of the mistaken interpretations made by distinguished palæontologists would have been impossible if they had been able to avail themselves of this means.

The drawbacks are more apparent than real. The loss of the original specimen is of little account, for all that can be known of its form and structure is preserved on photographic plates which can be multiplied at will; thus, like the art of printing, rendering possible a permanent existence which can be ensured by no other means.

The laboriousness of the process has been exaggerated, partly, I fear, by myself, but when owing to the war I had on one occasion to perform all the work of grinding down, photographing, and reconstructing the second specimen without assistance, I was astonished to find that the whole series of operations from start to finish occupied less than three weeks. When it is considered that this single specimen affords all the information that has been accumulated by the repeated study of rich collections by numerous observers, and has even disclosed new and important facts, it becomes clear that the method is not so laborious as it seems. Further, the greater part of the work can be performed by comparatively unskilled labour, and finally the labour expended is recompensed by a certainty which is well worth the pains.

The Skull.—The skull may be compared to a wedge-shaped box, broader and deeper behind than in front, and with several apertures in the sides. In specimen No. 1, the length is 20 mm.; the height, 9·5 mm.; and the breadth where broadest, *i.e.*, between the posterior angles formed by the supra-temporal bones, 14 mm.; in specimen No. 2 these numbers become respectively 16 mm., 7 mm., and 9 mm. If the roof be regarded as horizontal then the base rises gently forwards from the basi-occipital bone to the premaxillæ.

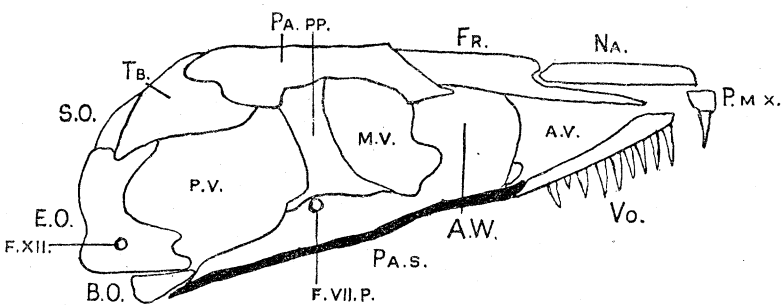

FIG. 5.—Lateral view of the skull with the side bones removed. The symbols which are the same throughout the illustrations are explained on p. 527. (×5.)

The roof is composed of the nasal, frontal and parietal bones, together with the dorsal part of the supra-occipital and tabulares. It is extended in a kind of eaves over the orbito-temporal region by the prefrontal bone and a lateral process of the parietal.

The floor is formed by the basi-occipital, parasphenoid, and vomers.

The roof is supported from the floor by the following structures taken in order from behind forwards: (i) First by the back of the skull, which is vertical below, where it is constituted by the exoccipital bones, but rounded off above by the forward curvature of the supra-occipital and tabulares. (ii) Next by a pair of pillars (fig. 5, *P.P.*) which rising from a long base on each side of the parasphenoid, and sloping slightly backwards, pass into the parietals. Homologous perhaps with alisphenoids, these are, in a true sense, "*columellæ cranii.*" (iii) Then come a pair of laminæ (fig. 5, *A. W.*), which rise like two walls above the parasphenoid; on the whole bowed slightly outwards, they curl inwards below over the parasphenoid, but remain distinct and separate from it: above they reach the frontals with which they seem to be confluent. They are analogous at least to orbitosphenoids. (iv) Finally, the vomers pass upwards from the ventral face of the anterior extremity of the parasphenoid to end just behind the premaxillæ by which they are linked on to the nasal bones.

Between these supports are three great lateral apertures, the most posterior (fig. 5, *P. V.*) which is the largest lies between the back of the skull and the posterior pillars; save for some minor openings it is completely closed by the pro-otic, opisthotic, stapes, the lateral wing of the tabulare, the supra-temporal, and to a slight extent also by the squamosal (figs. 6, 7).

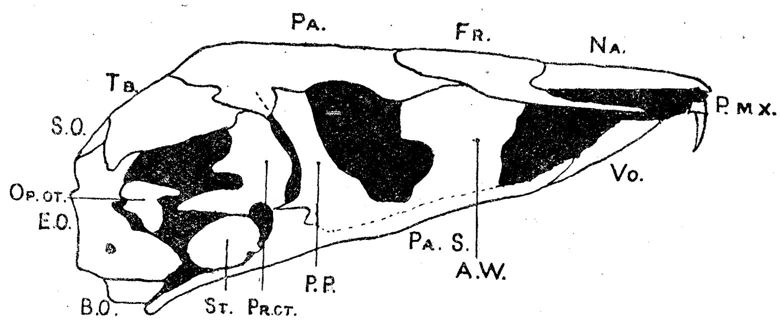

FIG. 6.—Lateral view of the skull showing the ear bones in place. (×5.)

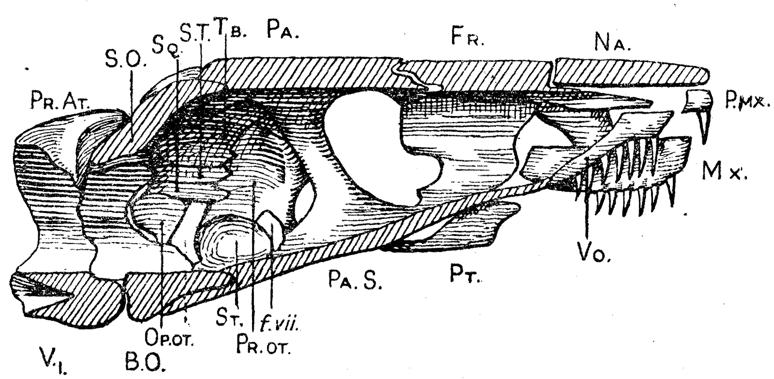

FIG. 7.—The structure of the skull seen from within as exposed by a sagittal section. (×5.)

The middle aperture (*M. V.*) between the posterior pillars and the anterior walls is vacant. It is of considerable size, and was doubtless occupied during life by cartilage, through which passed the optic and other nerves to the eye.

The anterior aperture (fig. 5, *A. V.*) is very incompletely closed by the ascending wall of the maxilla, and is bridged over by an arch formed by the union of a descending process of the prefrontal and an ascending process of the maxilla.

The occipital segment (fig. 12) presents a large foramen magnum, to the boundary of which the supra-occipital contributes. Above the foramen a small post-temporal fossa occurs on each side, bounded by the supra-occipital, tabulare and exoccipital. The exoccipitals are perforated by a foramen for the twelfth nerve and its associates.

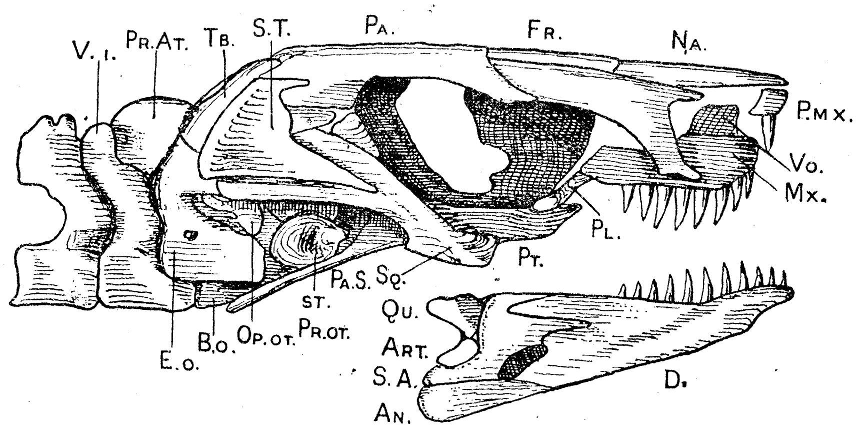

FIG. 8.—Right side of the skull seen from without. (×5.)

Between the exoccipital and the opisthotic is the jugular foramen, which no doubt gave passage to the tenth nerve.

Between the pro-otic and stapes is an aperture which corresponds to the foramen pro-oticum commune for the fifth and seventh nerves.

The posterior pillars are perforated near the base by a foramen for the palatine branch of the facial nerve.

The space outside the middle aperture was probably the seat of the eye.

The open space of the incompletely closed anterior aperture, in particular that part of it which lies in front of the maxilla, between that bone, the premaxilla, nasal and prefrontal probably included the outer nostril. It is continued downwards and backwards to open between the vomer, maxilla and palatine in a large oval space within which the inner naris was probably situated. That a well-defined external nostril is not expressed in the skeleton is only what we might expect, for in living Urodeles the boundary of this aperture is furnished by the soft parts, and on their disappearance disappears with them.

The curious feature presented by the maxillary prefrontal arch suggests the existence of a tentacular organ, such as occurs in Ichthyophis and is said to be present as a rudiment in Amblystoma,* as well as in the larva of Necturus (PLATT). The opening of the space within the arch seems to have been observed by WILLISTON, who suggests that it may have lodged the eye.

The maxilla does not present the free posterior termination so characteristic of the Urodeles, but joins the palatine bone, which is also connected with the posterior end of the vomer and the anterior end of the pterygoid.

* A. DAVISON, 'Am. Nat.,' vol. 30, p. 648.

Between the posterior third of the pterygoid and the thickened anterior end of the squamosal is lodged the quadrate bone.

The lower jaw consists of the dentary, surangulare, angulare and goniale, all comparatively large bones, and a small articulare.

There is a large hyoid; and the branchial arches, which are at least three in number, more probably four, are well developed, and extend as far back as the middle of the third vertebra.

Basi-occipital (figs. 5–9).—This is a comparatively large separate bone, shaped rather like a wedge, broader than long (3·5 mm. by 2 mm.).

Its dorsal surface is horizontal and approximately flat, with a shallow depression at each side for the reception of the heel of the exoccipital.

The ventral surface (fig. 7) shares in the general slope of the base of the skull, *i.e.*, forwards and upwards, and is produced along the middle line into a sharp ridge (measuring 0·8 mm. from base to summit), which is bounded on each side by a wide groove. The ridge projects into and even through the parasphenoid, which fills the channels on each side and completely invests all the rest of the ventral face.

The posterior surface, which is vertical and 1·6 mm. in height, is almost flat, but with a faint though evident depression in the middle, where it is in contact with the "odontoid" of the first vertebra.

The sides of the basi-occipital meet the back in a well marked but rounded angle over the ventral half, but as they continue upwards they flow smoothly into the rounded outline which distinguishes the summit.

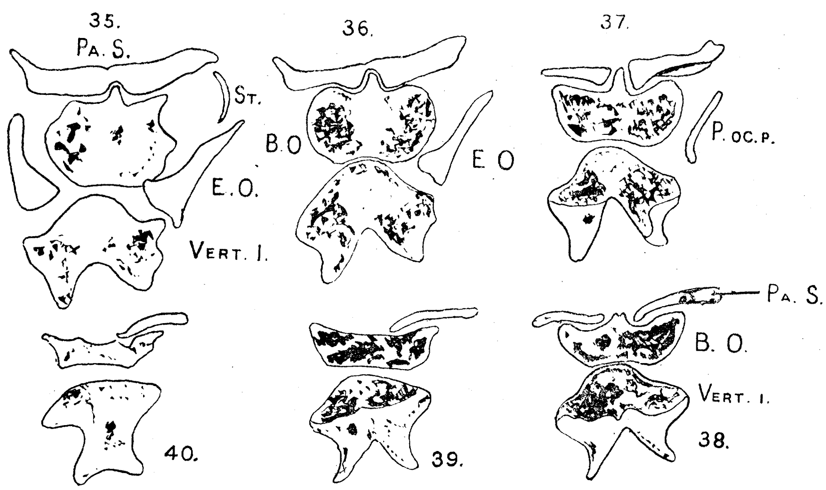

Fig. 9.—A series of horizontal sections through the basi-occipital, the end of the parasphenoid, the first vertebra, the paroccipital process of the exoccipital and the base of the stapes. (× 5.)

Exoccipital (figs. 1, 5–8, 10–12).—The exoccipital consists of a short vertical stem which expands above in the plane of the occiput into a plate resembling an inverted triangle—the superior lamina—and below, just before its termination, into a horizontal plate—the "foot." Its continuation for a short distance further downwards may be termed the "heel."

The stem presents itself in transverse sections as a spherical triangle with one side concave, so that its edges fore and aft are well marked. This concave side forms a large part of the parietes of the foramen magnum which is thus sharply defined before and behind.

The superior lamina is cleft near the summit by the post-temporal fossa into two lateral lobes, one mediad or inner, the other outer.

The inner lobe, which is the narrower, articulates with the supra-occipital, adapting itself on the outside of the skull to an angular incision in the lower margin of this bone, and on the inside to the under surface, which it follows close to the outer edge for a considerable distance forwards.

The outer—or since it articulates with the tabulare—the "tabular" lobe crowns the lamina like a little parapet. It is curved forwards from side to side, thus providing a rounded recess behind to receive the descending termination of the tabulare.

The foot is formed by the expansion of the stem at the front and sides into a horizontal plate; behind there is no noticeable expansion, the back of the stem being continued downwards into the heel.

On each side the foot is produced into a long prong-like process, which is directed forwards. The inner of the two prongs, as well as that part of the plate which lies in front of the stem, is closely applied to the upper surface of the basi-occipital, and the front end of the prong extends beyond the basi-occipital to end against the parasphenoid.

This prong makes the terminal sweep of a well-marked curve, which is continued upwards from it along the front edge of the stem and inner lobe of the exoccipital, and still onwards along the outer margin of the supra-occipital, as exposed on the interior of the skull, up to its termination against the parietal. It probably marks the limit between the brain and the auditory chamber.

The outer prong, a lamelliform process which is applied to the side of the basi-occipital, extends forwards as far as the posterior margin of the fenestra ovalis, to form part of the side of the skull. It also contributes to the support of the opisthotic, and hence may be distinguished as the paroccipital process.

The heel of the exoccipital is applied on its inner side to the posterior upper corner of the basi-occipital, and projecting beyond the back of that bone overlies the interspace between the basi-occipital and the centrum of the first vertebra (fig. 11). It bears a facet which looks downwards and inwards, and articulates with the centrum of the first vertebra, which is excavated at its antero-lateral corner to receive it.

Just above the origin of the foot a slight recess is visible on the inner side of the stem, and at the bottom of this a minute foramen about 0·2 mm. in diameter. This, which is present in all four of the exoccipitals provided by my two specimens, has been unhesitatingly attributed to the tenth nerve. This interpretation rested, no doubt, on the assumption, now known to be erroneous, that the exoccipital included an opisthotic element. The foramen for the vagus is to be looked for between the exoccipital and the opisthotic, and it is precisely in this position that a large foramen, the jugulare or lacerum posticum, is displayed in our reconstructions. It follows, therefore, that the foramen in the exoccipital itself should be assigned not to the tenth nerve but to the twelfth.

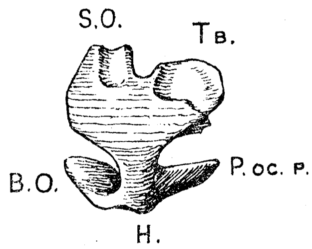

Fig. 10.

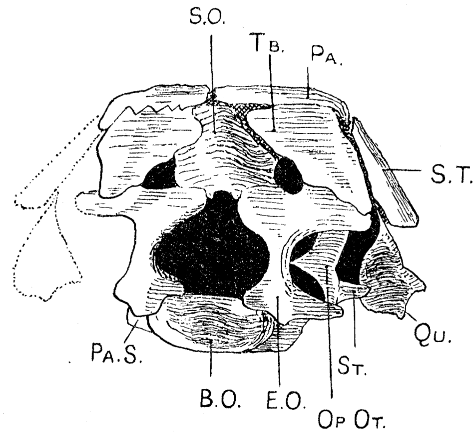

Fig. 12.

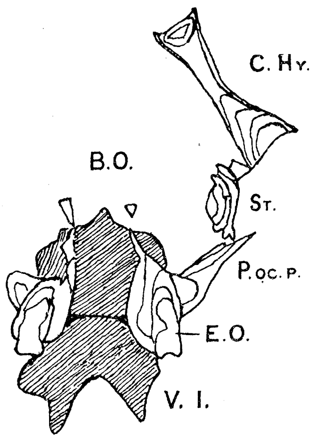

Fig. 11.

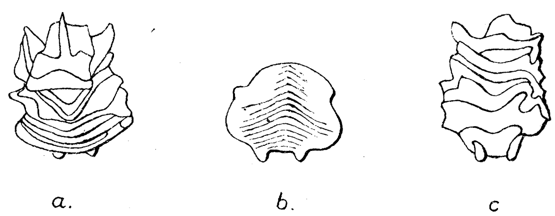

Fig. 13.

Fig. 10.—Exoccipital (specimen 1) seen from behind. *H.* the heel; *P.oc. P.* paroccipital process; *B.O.*, *S.O.*, *Tb.* point to the articular facets made by the exoccipital with the bones indicated by these letters. (× 4.)

Fig. 11.—The exoccipitals seated between the basi-occipital and first vertebra. The paroccipital process of the right exoccipital extends as far as the stapes and the stapes is in contact with the ceratohyoid. (× 5.)

Fig. 12.—The back of the skull. (× 5.)

Fig. 13.—The supra-occipital bone. *a*, posterior and superior; *b*, posterior; *c*, anterior surface. (× 5.)

It would seem that the attachment of the exoccipitals to the basi-occipital was not very secure, for in specimen 1 both the exoccipitals are displaced, with a shift to the left, that on the right being at the same time carried forwards, so that its heel now lies over the middle of the basi-occipital. From this specimen alone, it would have been impossible to determine with certainty the true relations of these bones; in specimen 2, however, which is much less distorted, both exoccipitals are in place, and afford harmonious testimony.

Supra-occipital (figs. 5–7, 12, 13).—This is a fairly large curved plate, broadest in the middle, where it measures 4 mm. across. The outer surface, except at the summit, which is flat, is curved from side to side, and rather sharply so in the middle, or, as WILLISTON remarks, it possesses a "median sagittal crest." This crest corresponds with the line along which the two members of the paired pro-atlas meet one another, and its sides are in close apposition with those bones. It is also bounded above by the medial margin of the tabulares.

The inner surface is excavated by a widely open longitudinal channel.

The bone slopes rather rapidly forwards as it ascends, so that its height (2·4 mm.), taken vertically, is less than half its true length (5·5 mm.). Its maximum thickness is about 1 mm.

The lower margin is notched in the middle by the summit of the foramen magnum, and excised on each side for articulation with the exoccipital bones, which extend forwards beneath it.

Above the exoccipitals the margin of the bone bounds the post-temporal fossa, and above this it articulates with the tabulare by a simple serrate suture.

At the summit it articulates with the parietals, also by a serrate suture, one large median tooth being thrust forwards along the sagittal line, while a smaller one on each side enters the parietal bone itself.

The *tabulare* (figs. 1, 5–8, 12, 14) bounds the upper posterior angle of the cranial cavity, and roughly resembles the corner of a shallow box, with the angles inside, filled up and well rounded off.

The "top" articulates in front with the parietal by a serrate suture, and then extends forwards below the suture in a long pointed process, which is received by a groove on the under surface of the parietal.

The "back" curves downwards, overlapping the side of the supra-occipital, with which it articulates, for the first half of its course; it is then notched by the post-temporal vacuity; beyond this it rapidly diminishes in breadth by the retreat of its mediad margin from the middle line, and articulates with the exoccipital, overlapping the tabular lobe of that bone. Its outer margin is comparatively straight, and is bounded by the supra-temporal.

Parietals.—The *parietal* (figs. 1, 5–8, 12, 15), which is the largest of the roofing bones, may be described as consisting of a body and its processes. The body, as seen from above, is a roughly rectangular plate, 6·5 mm. long by 4·0 mm. broad in specimen 1, and 5 mm. long by 3·5 mm. broad in specimen 2; in front it articulates by a coarsely serrate suture with the frontal, and by a similar suture with the tabulare behind, as well as with the supra-occipital, which thrusts a long tooth into the sagittal suture. On its outer side the body extends beyond the cranial cavity, roofing over the orbito-temporal region. On its under surface it is thickened immediately in front of the supra-occipital and tabulare, and adapts itself to their margins.

The processes are three in number, one at the antero-lateral angle, one at the postero-lateral angle, and one descending from the middle of the under surface.

The antero-lateral process, which extends forwards, continuing the lateral margin of the body, parallel to the side of the skull, presents two regions: (i) a shorter outer part, which runs forwards and downwards beneath the prefrontal, articulating with that bone by an overlapping suture; and (ii) an inner part, which begins as a forward extension of the body below its serrated union with the frontal—the suture, which is serrate above, thus becoming squamous below—and then continues as a narrow wedge thrust far in between the frontal and prefrontal.

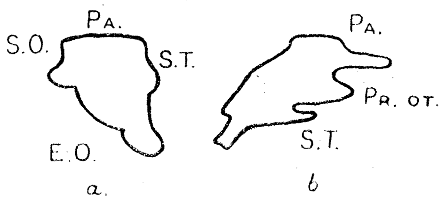

FIG. 14.

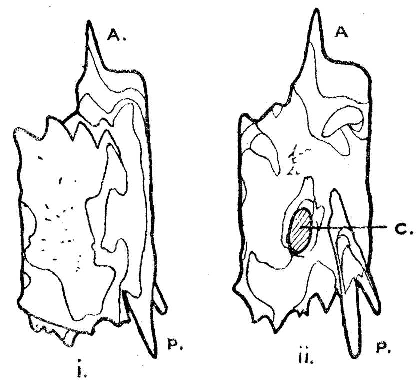

FIG. 15.

FIG. 14.—Right tabulare. *a*, from behind; *b*, from the side. (×5.)

FIG. 15.—Right parietal bone. i, dorsal; ii, ventral surface. *A*, antero-lateral; *P*, postero-lateral; and *C*, central process. (×5.)

The posterior process, which extends downwards and backwards, forks into two prongs, one of which is inserted between the tabulare and supra-temporal, while the other adapts itself to the outer edge of the supra-temporal and the summit of the pro-otic.

The central process is continued downwards from the under surface of the body, to form, or contribute to form, a posterior pillar of the skull.

The total length of the parietal, when the processes are included, is 10·5 mm. in specimen 1 and 9 mm. in specimen 2. The thickness of the body is 2 mm. and 1 mm. respectively.

The substance of the bone is traversed by a radiate system of fine canals.

As stated by WILLISTON and others, there is no parietal foramen.

Frontals (figs. 1, 5–8, 16).—The frontal as exposed on the surface is also a roughly rectangular bone, 6·3 mm. long, 2·2 mm. broad, and 1·5 mm. thick in specimen 1, and 4 mm. long, 2 mm. broad, 1·2 mm. thick in specimen 2. It articulates with the nasal by a digitate suture above, which extends obliquely downwards and forwards, and is finally replaced by simple overlap. By this anterior extension the length of the bone is increased in specimen 1 to 9 mm.

The outer lateral margin articulates by a simple suture with the prefrontal, and for a short distance with the antero-lateral process of the parietal.

The under surface, near the outer margin, appears to be continued downwards into the anterior wall of the skull.

Nasals (figs. 1, 5–8, 17).—In specimen 2 these bones are displaced and not so well preserved as in specimen 1. In the latter they measure 5 mm. in length and 2 mm. in breadth, but only 0·9 mm. in thickness. In front they immediately overlie the premaxillæ, and behind they first overlap the frontals and then articulate with them by a serrate suture (fig. 17).

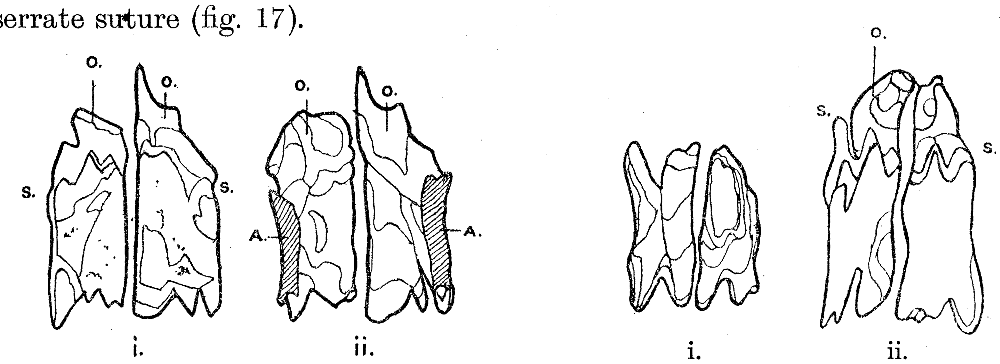

Fig. 16. Fig. 17.

Fig. 16.—Frontal bones of specimen 2. i, dorsal; ii, ventral surface. *S.S.*, sutures with nasal bones; *o.o.*, anterior region overlapped by the nasals; *A.A.*, anterior walls of skull. (× 5.)

Fig. 17.—i. Nasal and ii, frontal bones of specimen 1, dorsal surface. *S.S.*, serrate sutures of frontal; *o*, region overlapped by nasals. (× 4.)

Prefrontal (figs. 1, 7, 8, 18).—This bone variously named prefrontal, postfrontal, and lacrimal by investigators of Lysorophus corresponds precisely with that named ectethmoid or lateral ethmoid by Parker in all his work on the Amphibia, but as Parker has identified the ectethmoid with the prefrontal of the higher Tetrapods, we may adopt the latter term as most in accordance with established usage.

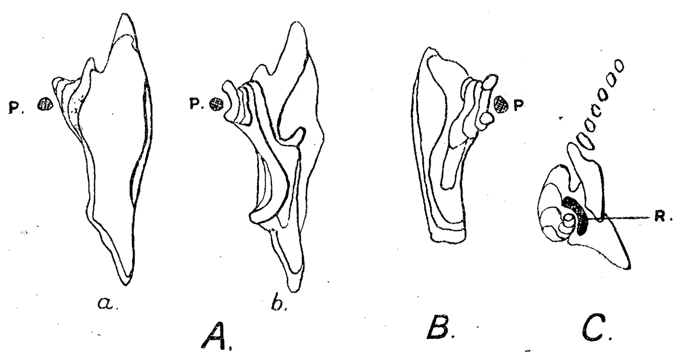

Fig. 18.—A. Left prefrontal bone of specimen 1. *a*, seen from above; *b*, from below (reversed); *p*, articulating process of the maxilla. (× 4.) B. Right prefrontal of specimen 2, seen from below (reversed). (× 5.) C. Left maxilla of specimen 1; *r*, articular process of prefrontal. (× 4.)

The prefrontal (figs. 1, 8, 18), forms a considerable part of the roof or eaves of the skull; articulating behind by overlap with the anterior lateral process of the parietal, it extends forwards along the whole of the outer margin of the frontal, with which it articulates by a simple straight suture, and then continuing still further flanks the nasal for more than half its length. The anterior rather pointed termination of the prefrontal lies over the suture of the premaxilla with the maxilla.

The under surface (fig. 18, *b*), is excavated by a long shallow sinus and thickened by a longitudinal curved ridge, the anterior end of which is produced downwards into a strong process. This curves outwards as it descends, diminishes in breadth, and is grooved on its outer face for the reception of the attenuated rod-like end of a process which arises from the maxilla to meet it. In specimen 1 the suture so effected extends through 11 sections, *i.e.*, for 1·1 mm., or about three-quarters of the total height of the C-shaped bar formed by the united processes.

Parasphenoid (figs. 5–8, 12, 19, 20).—The general form of this bone is shown in fig. 19. In specimen 1 it measures 13 mm., and in specimen 2 11 mm. in length. Its broadest part lies between the basi-occipital and the cranial pillars* (6·2 mm. in specimen 1 and 5·6 mm. in specimen 2); beyond the pillars it becomes rapidly narrower and then maintains a fairly uniform breadth (4 mm. in specimen 1, 3 mm. in specimen 2) till it diminishes to a pointed extremity. The broader part is dentate or notched as in some modern Urodeles, giving it an appearance which in those forms is described by PARKER as "foliaceous."

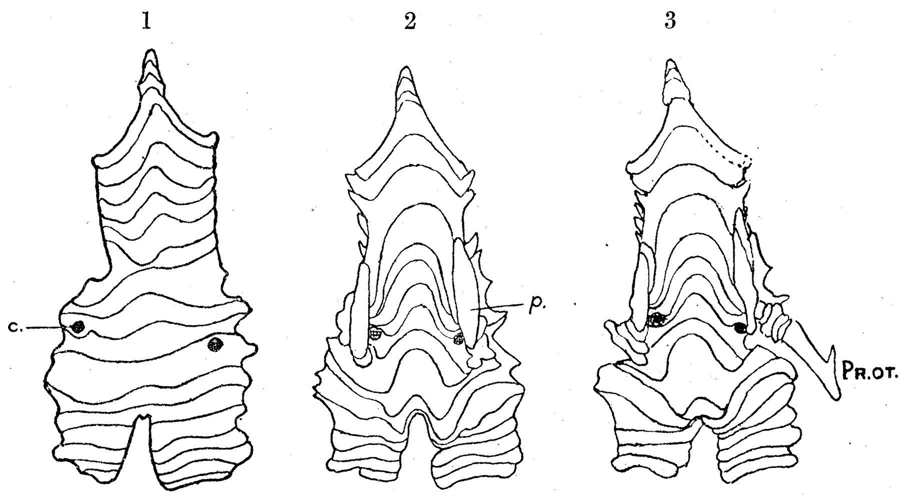

FIG. 19.—The Parasphenoid. i, ventral; ii, dorsal surface; iii, dorsal surface with the basal process of the pro-otic; *c.c.*, foramina for carotid artery; *p.*, base of posterior pillars. (×5.)

The broader moiety of the ventral surface is fairly flat, but as it passes into the narrower moiety it rises into a median longitudinal ridge, bounded on each side by a gentle depression; as these features are continued forward they become slightly more accentuated.

Posteriorly the parasphenoid overlaps the whole of the ventral surface of the basi-occipital except the central ridge and the region immediately behind this. It is thus divided here into two lobes the outer margins of which extend beyond the sides of the invested bone.

* See fig. 20, p. 499.

The dorsal surface is also fairly flat over the posterior moiety, but as it passes forwards between the pillars it takes the form of a shallow median trough as shown in the transverse section (fig. 24) obtained from specimen 1.

The trough is continued forward without much change till it flattens out in front; the anterior walls which are based upon its sides may be clearly distinguished from it. Traced backwards from here its sides gradually rise to pass into the posterior pillars. My sections show no trace of a suture, but on pointing this out to Dr. WATSON he made a close examination of a very perfect specimen of his own, which he has developed by skilful chiselling, and succeeded in discovering one. By his kindness I am able to represent this in fig. 23.

Two openings (0·3 mm. in diameter) are visible on the ventral surface, just in front of its greatest breadth, one on each side and not far from the margin. Their course as they traverse the bone is slightly forwards and a little inwards and they reach the dorsal surface close to the sides of the median trough. These are evidently the foramina for the internal carotid arteries.

In Amia and the Frog they occupy much the same position but lie outside the parasphenoid, just in front of the "guard" of that dagger-shaped bone.

Nothing that could be construed as a basisphenoid or a presphenoid or a depression for the pituitary body exists above the parasphenoid.

The Anterior Walls (figs. 5–8, 20, 21).—On each side of the skull a bony wall rises from above the anterior third of the parasphenoid and extends to the frontal above.

At its base each wall is 3 mm. in length, about a third of the way up it is reduced to 2 mm. by a notch in the posterior margin and then increases to 4 mm. before passing into the frontal. It is from 2·4 to 2·8 mm. in height and 0·75 mm. in thickness. The posterior notch was probably occupied in the living animal by the cartilage which completed the cranial wall and was perforated in this region by the optic nerve.

The outer side of the wall is a nearly plane surface, leaning only a little out of the perpendicular or bowed outwards as it ascends. The inner side is curved and with the frontals and its fellow wall bounds a tubular cavity narrow at the base and much wider at the summit.

The foot of each wall is produced in front and on the inner side into a horizontal plate which curves inwards and downwards towards the middle line till the two feet nearly meet. In specimen 1 they extend beyond it, overlapping each other, but this is clearly due to displacement.

The shallow cavity of the parasphenoidal trough, originally no doubt occupied by cartilage, is roofed over by these plates, which were evidently not directly connected with the parasphenoid bone.

The relation of the wall to the frontal is less clear; the existence of a suture can neither be asserted nor denied, but in any case the two bones are closely connected.

The walls certainly occupy the region of the sphenethmoid or orbitosphenoid, but it would be rash to identify them with either of these two bones, especially as WIEDERSHEIM* has described similar structures in *Amphiuma tridactylum* as mere downward processes of the frontal, and the figure which he gives in illustration (fig. 22)

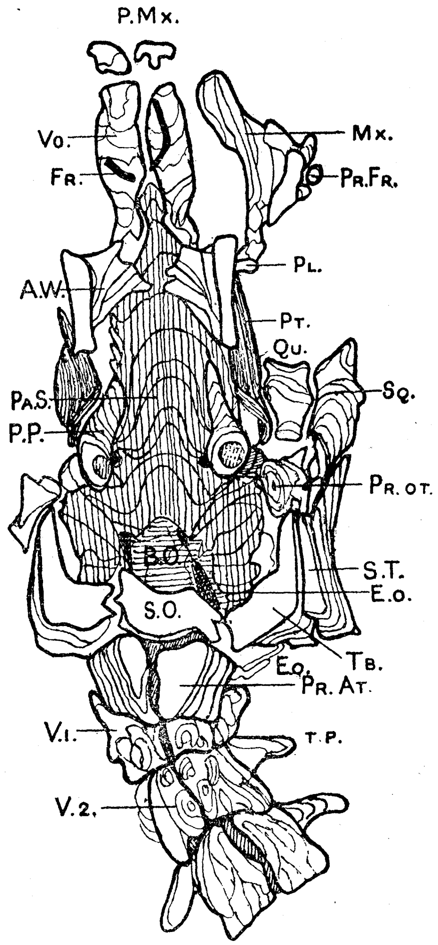

FIG. 20.

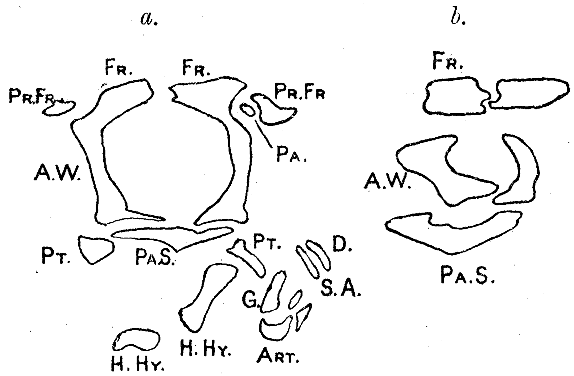

FIG. 21.

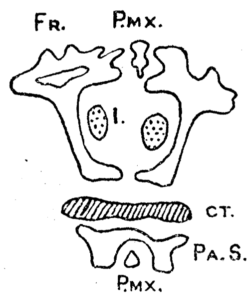

FIG. 22.

FIG. 20.—The skull seen from above with the roofing bones removed. (×5.)

FIG. 21.—Transverse section of the skull. *a*, of specimen 2 through the anterior walls. (×5.) *b*, of specimen 1. (×4.)

FIG. 22.—Transverse section of the skull of Amphiuma after WIEDERSHEIM. I, olfactory nerves; *CT.*, cartilage.

might almost serve for Lysorophus. In Amphiuma, however, the walls as they continue forward shift their origin from the middle of the frontal to its inner edge and thus becoming approximated give rise to an inter-nasal septum. Nothing corresponding to this exists in Lysorophus.

* WIEDERSHEIM, R., "Das Kopfskelet der Urodelen," 'Morphologisches Jahrbuch,' vol. 3, p. 403, Plate XXII, fig. 60 (1877).

We know very little about the embryological development of the processes in Amphiuma. HAY,* who has studied some early stages of Amphiuma, describes the frontals in larvæ (45 mm. in length) extracted from the egg capsule as mere splints; but in a young specimen (6 inches in length) the processes were found to be already well developed and in continuity with the frontals. So far as it goes this would indicate that the processes are of the nature ascribed to them and not independent elements. As the skull of this young specimen was already, however, almost as well ossified as in the adult the evidence is not conclusive and we must await the investigation of intermediate stages to determine this question.

It may be remarked that the absence of any coalescence of the walls with the parasphenoid is a character that the frontal processes share with the sphenethnoid of the Urodeles but not of the Anura.

A good figure of the anterior walls, as seen from the side, has been given by CASE† who mistook them, however, for an inter-orbital septum. BROOM‡ first suggested that they are ossifications in the cartilaginous brain case.

(*Postscript.*—After a re-examination of sections, I find that the anterior walls are not confluent with the frontal bones in specimen 1, but are separated from them by a considerable interval (fig. 21). It is almost certain therefore that their union with the frontals was by suture, and we may now fairly regard them as orbito-sphenoids.)

The Posterior Pillars (figs. 5–8, 20, 23, 24).—Each of these columnar bones presents a more or less cylindrical form at the summit, but as it descends it is

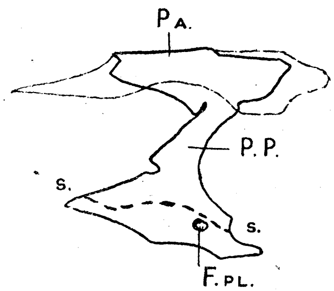

FIG. 23.

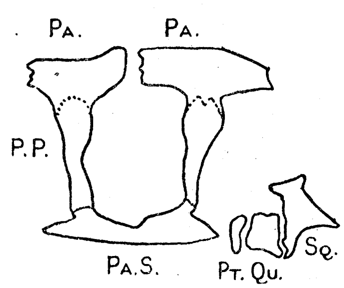

FIG. 24.

FIG. 23.—Longitudinal section through a posterior pillar. (× 5.) *S.S.*, suture observed by Dr. WATSON; *F. pl.*, foramen for palatine nerve.

FIG. 24.—Transverse section through the skull in the region of the posterior pillars. Specimen 1. (× 4.)

sharpened in front, while remaining round behind; on the inner face, in front, it is excavated by a well-marked groove, which continues downwards till the pillar, greatly compressed from side to side, passes into the wall-like region of the base.

* HAY, O. P., "The Skeletal Anatomy of Amphiuma during its Earlier Stages," 'Journ. Morphology,' vol. 4, pp. 10–34 (1891).

† CASE, E. C., 1908, *op. cit.*

‡ BROOM, R., *op. cit.*, p. 235.

Here, immediately above the entrance of the carotid canal into the cranial cavity and close to the anterior spur of the pro-otic is a rather deep recess, opening by a short canal (0·4 mm. in diameter), which runs obliquely forwards and outwards to the exterior, and is then continued as a groove along the outer margin of the parasphenoid. This must be the foramen for the palatine branch of the facial nerve, and the recess probably lodged the anterior end of the ganglion pro-oticum commune.

The pillar appears at first sight to be a simple extension downwards of the median parietal process, but an examination of sections strongly suggests the presence of a suture. For at the upper end sections transverse to the pillar reveal an outer layer of bone, which continues the wall of the pillar upwards, and surrounds an inner style which, increasing in diameter as it ascends, passes finally into the parietal. Between this style and its ensheathing wall is a vacant interval.

The union of the base of the pillar with the parasphenoid is accomplished, as Dr. WATSON has shown, by suture.

The homology of this bone is by no means clear. I have already* named it provisionally "alisphenoid," yet it certainly resembles very closely the epipterygoid of the Chelonia, both in form and its relation to the parietal. Here, however, attention may be called to the view† which would identify the epipterygoid of the reptiles with the alisphenoid of the mammals. In all three cases, Lysorophus, the mammals, and reptiles, we are concerned with a bone having similar relations with the parietal, and so far as we know with the cranial nerves. Differences arise when we pass to the base: in the mammals it articulates below with the basi-sphenoid and pterygoid, in reptiles with the pterygoid, and in Lysorophus with the parasphenoid. In this character by which the pillar of Lysorophus differs from the analogous bones of mammals and reptiles it agrees with the "alisphenoid" of the bony fishes.

On the other hand, in the bony fishes, when it articulates above, it does so not with the parietal but the frontal bone.

It is tempting to suppose that throughout the Tetrapoda we have before us the same bone, whether it is called columella or alisphenoid; that it has persisted in position between the branches of the fifth nerve owing to the important function it has to fulfil in that region as a support, and consequently that it has had to find attachment where it could. In Lysorophus where there is no basisphenoid, and the pterygoid is but feebly developed, the parasphenoid is its only resource; in the

* BROOM, R., *op. cit.* Note by W. J. SOLLAS.

† BROOM, R., 'Proc. Linn. Soc., N.S.W.,' vol. 34, p. 211 (1909); *ibid.*, "The Homology of the Mammalian Alisphenoid bone," 'Rep. S. African Assn. for the Advancement of Science,' 1907, pp. 114–115 (1908); "On the Structure of the Skull in the Cynodont Reptiles," 'Proc. Zool. Soc.,' p. 922 (1911), and in Appendix to W. K. GREGORY, "Report of the Committee on the Nomenclature of the Cranial Bones in the Permian Tetrapoda," 'Bull. Geol. Soc. Am.,' vol. 28, p. 977 (1917); W. K. GREGORY, "Critique of Recent Work on the Morphology of the Vertebrate Skull," 'Journ. Morphology,' vol. 19, p. 1 (1913).

Chelonia, where the basisphenoid is very narrow in front, it falls back upon the encroaching pterygoid.

On the other hand the embryological investigations of Dr. WATSON* have furnished weighty evidence which is opposed to the suggested identification, and as regards the posterior pillar of Lysorophus in particular, he informs me that according to observations of his own, not yet published, a cartilaginous rod is present in the original walls of the vertebrate skull, which makes its last appearance as the Tænia clina-orbitalis of the Monotremes, and is extremely persistent in some reptiles as well as in Coecilia and probably some fishes. It is as an ossification of this rod that he regards the posterior pillar.

Pro-otic (figs. 6–8, 20, 25, 26).—The upper moiety of this rather complicated bone is a stout pillar which articulates above with the under surface of the posterior descending process of the parietal, and touches the anterior edge of the lateral wall of the tabular behind.

In transverse section the pillar presents in this region a rather rounded outline,

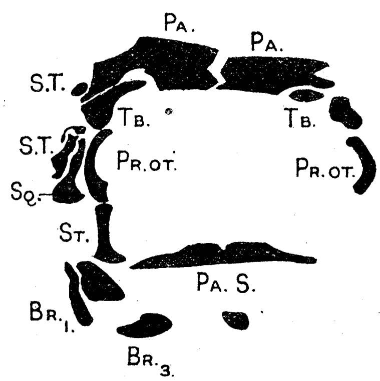

FIG. 25.—Transverse section of the skull passing through the pro-otic and the stapes. (× 5.)

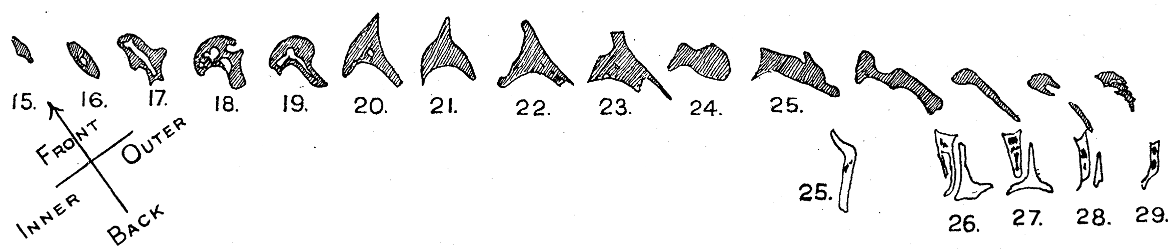

FIG. 26.—The right pro-otic and opisthotic bones in a series of transverse sections taken in order from above downwards. The pro-otic, in the upper line, is distinguished by hatching. (×5)

but as it descends it is almost immediately produced, at first posteriorly and then anteriorly as well into an alar expansion, and thus acquires a triradiate form; in other words, it becomes a triangular prism with two of its edges produced into long

* WATSON, D. M. S., in "Second Report of the Committee on the Nomenclature of the Cranial Elements in the Permian Tetrapoda," 'Bull. Geol. Soc. Am.,' vol. 28, p. 980 (1916); *ibid.*, "On the Monotreme Skull, a Contribution to Mammalian Morphogenesis," 'Phil. Trans.,' Ser. B, vol. 207, pp. 311–374 (1916).

flanges. The anterior and the posterior flanges lie nearly in the same plane and form the outer side of the pillar which is closely applied to the inner surface of the squamosal.

The face between the inner edge and the posterior flange is hollowed out into a wide groove looking backwards into the interior of the skull. This extends down the greater part of the length of the column, expanding below into the general concavity of the base.

The inner edge or ridge enlarges at its base into a short slender bar which runs forwards and inwards to unite with the posterior pillar, just above its base and the foramen for the palatine nerve. This is not the "alisphenoidal spur of the pro-otic" of Parker and Bettany,* for that process extends forwards along the upper edge of the cranial wall while this is directed towards its base. It is notched underneath, just in front of the stapes, for the passage of the seventh nerve, and immediately below its origin the bone is continued backwards as a curved lamella which extends as far as the opisthotic, and contributes to the boundary of the auditory capsule.

The *Stapes* (figs. 6–8, 11, 12, 25, 28).—This elegant little bone resembles a shallow bowl, with a straight handle projecting from the edge. The opercular bowl lies immediately below the posterior lamina of the pro-otic, as though forming its continuation. The handle—"processus opercularis"—is produced from the summit of the anterior edge, and points outwards perpendicular to the wall of the skull. Thus the resemblance of the bone both in form and position to the stapes of a Urodele is complete. In specimen 1 the stapes is displaced, and lies isolated at some distance from the pro-otic. It is traversed by 20 sections (68 to 88), and the vertical diameter is therefore 2 mm. in length; the horizontal diameter measures 2·5 mm. In specimen 2 these quantities become 2 mm. and 1·4 mm. respectively.

The *opisthotic* (figs. 6–8, 26, 27).—Immediately behind the pro-otic is a small

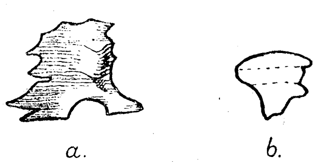

Fig. 27.

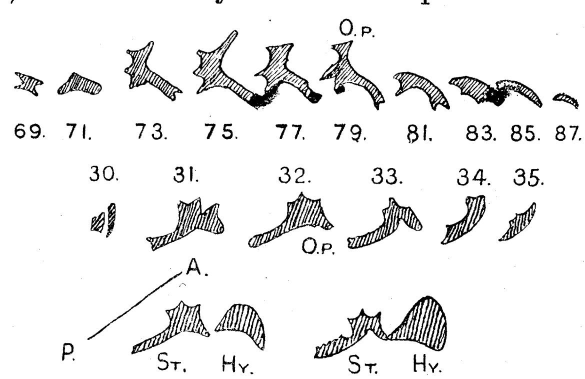

Fig. 28.

Fig. 27.—*a*, Pro-otic and *b*, opisthotic bone, canal through opisthotic indicated by dotted lines. (× 5.)

Fig. 28.—Horizontal sections of the Stapes in order from above downwards. 69 to 87. From specimen 1. (× 4.) 30 to 35. From specimen 2. (× 5.) The sections in the third line show the relation of the Stapes to the Cerato-hyal. *O.P.*, opercular process; *P.—A.*, direction of axis of skull; *P*, posterior; *A*, anterior.

* Parker and Bettany, 'Morphology of the Skull,' London, 1877, p. 115, § 280.

triangular lamina of bone, curved from side to side, and contributing, together with the pro-otic lamina, to the almost semicircular boundary of the auditory recess.

It is supported below by the outer prong, or paroccipital process of the exoccipital foot, and affixed above to the under edge of the tabular lobe of the exoccipital. It thus fills the larger part of the lateral vacuity which lies between these two occipital processes, leaving, however, an open space between its posterior margin and the exoccipital stem. This is nearly divided into two, an upper and a lower portion, by a spur of the opisthotic; it is this lower portion which we identify with the jugular foramen.

It is scarcely necessary to comment on the interest attaching to this additional example of a separate opisthotic bone, common enough, no doubt, among the primitive reptiles of Permian and Carboniferous times—WILLISTON* regards it as one of their constant characters—but subsequently never met wth, except in the Chelonia and Ichthyosauria.

Squamosal (figs. 1, 3, 4, 7, 8, 12, 24, 25, 29).—In this we may distinguish an anterior pedicel from a posterior lamella.

The lamella expands upwards as it proceeds backwards, and is excavated behind by a deep notch with jagged margins. It is firmly wedged in between the pro-otic on the one hand and the supra-temporal on the other.

The pedicel, which in the upper part of its course may be regarded as the thickened edge of the lamella, runs downwards and forwards, and, on passing beyond the lamella, increases in thickness, gives off an alar process from its posterior inner edge, and terminates in a bevelled surface.

The posterior surface of the pedicel is hollowed out by a longitudinal groove, bounded on the inner side by the alar process. Behind this groove, and close to it, rises the ascending ramus of the cerato-hyal. In Necturus and other Urodeles, the epi-hyal end of the cartilaginous hyoid is similarly related to the suspensorium, and the squamosal, which in this form descends as far as the articulation of the lower jaw, is grooved for its attachment.

The squamosal of Lysorophus recalls that of Proteus, as described by PARKER;† the pedicel and lamina corresponding to "the preopercular and supra-temporal halves" and that part of the lamina below the posterior notch to the "spiracular process."

Quadrate (figs. 8, 20, 24, 30).—A four-sided, irregular, columnar bone, 1·8 mm. in height. The front face is free, concave from side to side, and inclined downwards and forwards; the posterior face is also free and similarly inclined, but is more irregular in form. Of the two sides, the inner is bounded by the pterygoid and the outer by the squamosal. Its antero-posterior diameter attains its greatest length in

* WILLISTON, S. F., "Primitive Reptiles," 'Journ. Morphology,' vol. 23, p. 660 (1912).

† PARKER, W. R., 'Phil. Trans.,' vol. 167, p. 571 (1877).

the middle, and diminishes towards each extremity. The lower end was probably invested with cartilage, to complete the articular surface for the articulare.

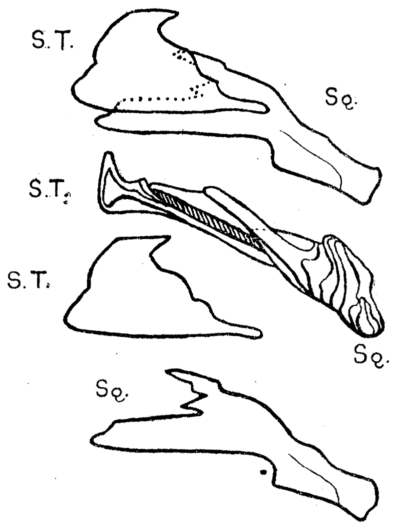

Fig. 29.

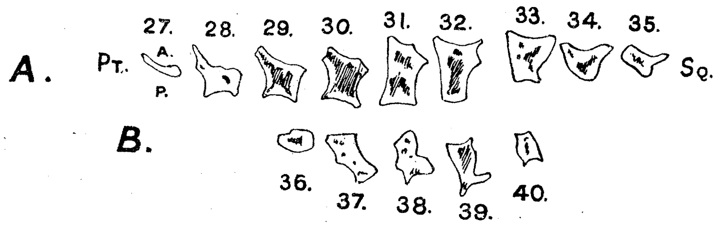

Fig. 30.

Fig. 29.—Supra-temporal and squamosal bones seen from the outer side except the second figure which represents them as looked at from below.

Fig. 30.—A. Horizontal sections (27–35) of the quadrate bone. *A*, anterior aspect; *P*, posterior aspect; *Pt.* pterygoid and *Sq.* squamosal aspects. (×5.)

B. Horizontal sections (36–40) of the articulare.

Supra-temporal (figs. 1, 3, 4, 7, 8, 12, 24, 25, 29).—This is a roughly triangular lamina, thicker behind than in front, with a flat base and a truncated apex.

At the summit it articulates with the posterior process of the parietal, which is excavated to receive it and intervenes between it and the tabulare.

Below the termination of the parietal process the supra-temporal comes into close contact with the tabulare, and remains so as far as that bone descends.

Just before its termination downwards the posterior edge or back of the supra-temporal increases in thickness, and is excavated on the inner side so as to present a hook-like form in transverse section, and here it articulates with both the tabular lobe of the exoccipital and the lower end of the tabulare itself.

In front the supra-temporal extends over the outer surface of the posterior lamella of the squamosal, its lower edge resting on a step-like ledge of that bone. It completely conceals the posterior notch of the lamella as well as the vacuity in the wall of the skull behind the notch.

Pterygoid (figs. 7, 8, 20, 24, 31).—This long, narrow lamina or splint (5 mm. in length, 1·4 mm. in breadth, and 0·4 mm. thick), starts from the region where the pro-otic joins the posterior pillar, runs alongside the parasphenoid, and ends by curving round the anterior edge of that bone to underlie both the vomer and the palatine. From the squamosal it is separated in both specimens by the quadrate. The flank of the splint slopes outwards and downwards, and in the direction of its length it is curved like a bow, *i.e.*, convex outwards at both extremities and concave in the middle. The upper part of the posterior end is twisted outwards at the level of the summit of the quadrate, but beyond this, the bone presents no tendency to assume the triradiate shape so common among the Stegocephalia.

Palatine (figs. 8, 20, 31).—The determination of this bone in all its relations is a rather difficult task, partly in consequence of the less perfect preservation of this region of the skull, a defect which is very common amongst the known specimens of Lysorophus, and partly from the absence of visible sutures, so that in the delimitation of the bone we have only general considerations to guide us.

The best preserved example of the palatine occurs on the left side of specimen 1, where it presents itself as a small more or less triangular lamina, curved outwards from base to summit and with a sinuous margin.

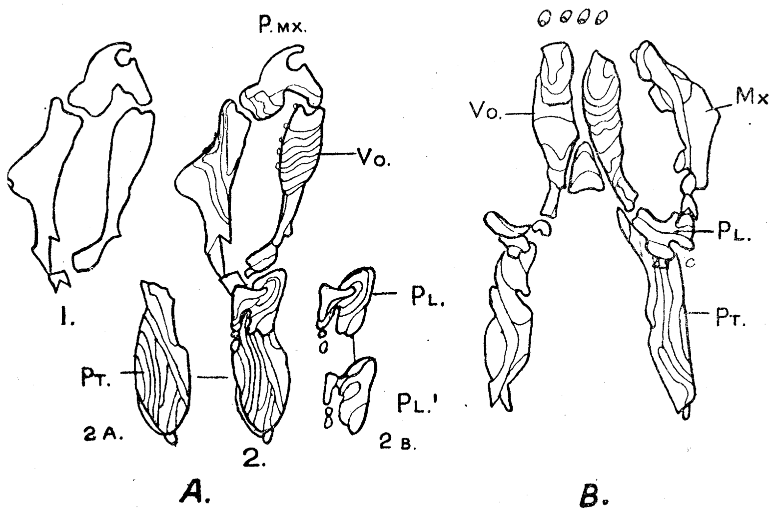

FIG. 31.—The palatine bone, showing its relations to the maxilla, vomer, and pterygoid. A. From specimen 1. (×4.) 1. Outline of premaxilla, maxilla, and vomer. 2. Superposed sections, dorsal surface. 2*A*. *Pt.*, isolated. 2*B*. *Pl.*, dorsal surface, *Pl'*., ventral surface. B. From specimen 2. (×5.)

The base continues the general course of the vomer, and lies near to its posterior termination; the anterior end of the pterygoid underlies the base.

The lamina as it rises from the base curves outwards towards the maxilla, and at the same time assumes the form of a rounded bar which comes in contact with the posterior end of the maxilla, but whether it terminates there or not is uncertain; for what appears to be its continuation, ending freely 0·8 mm. above the point of contact, may prove to be a part of the maxilla which has been separated from the rest by *post-mortem* dissolution.

Dr. BROOM has figured a bone* simpler in form than ours but occupying a similar position and probably representing the outwardly directed process only. This he has

* BROOM, R., *op. cit.*, p. 234, fig. 1.

identified with the palatine. An alternative explanation has been suggested to me by Mr. Goodrich who thinks it possible to regard the posterior limb of the vomer as a confluent palatine, and in that case the supposed palatine would become the transverse bone. The presence of so primitive a bone as the transverse would be quite consistent with the general character of the skull.

The additional information afforded by sections renders possible another interpretation by which the palatine nature of the bone is retained, for its base is found to occupy its proper place as the middle member of the pterygoid-vomer series, while the bone figured by Dr. Broom, if it corresponds, as seems probable, with our rod-like process, is an outgrowth from it, developed to meet the need of the maxilla for support.

The *Vomers* (figs. 7, 20, 31, 32).—These are a pair of slender bones which descend backwards from the præmaxillæ to the anterior termination of the parasphenoid and the pterygoid.

The dentigerous outer border describes a graceful curve, which at first runs nearly parallel with the arc of the premaxillæ, but as it continues backwards it bends towards the middle line till it nearly completes an ellipse, it then broadens out again just in front of the anterior end of the parasphenoid and runs obliquely outwards to meet the palatine and pterygoid.

The original curve is best preserved in specimen 2; in specimen 1 a downward pressure seems to have separated the vomers so that they do not approach so closely behind, and the "waist" of the curve is enlarged.

From the dentigerous border a thin palatal lamina extends towards the middle line where it meets its fellow in a sagittal suture. The lamina is of uniform thickness (0·2 mm.) and there is no thickening next the sagittal suture.

The internal nares cannot have been situated between these bones, but must have opened outside them in the vacuity bounded by the maxilla on one side, the vomer on the other, and the palatine behind.

The length of the vomer in specimen 1 is 6 mm.; in specimen 2, 4·5 mm.

Each vomer bears nine or ten simple conical teeth, from 0·6 mm. to 1 mm. in length. They are attached to the inner side of a thickened outer border.

Premaxillæ (figs. 1, 2, 5–8, 20, 31–33).—These two small bones present, taken together, a bow-shaped outline in front. They are less badly preserved in specimen 1 than specimen 2. Behind they extend backwards for 2 mm., as measured along the middle line, beyond the dentigerous margin to form a thin palatal plate, which articulates with the anterior margin of the vomers. They rise in front in a short vertical wall, 0·5 mm. in height, their total height being 1·3 mm.

Measured along the arc up to its suture with the maxillæ the left premaxilla of specimen 2 is 2·5 mm. in length. The teeth, five in number on each side, are sharply pointed simple cones 0·8 mm. to 0·9 mm. in length and about 0·3 mm. to 0·4 mm. in diameter at the base.

Maxilla (figs. 8, 18, 20, 31, 32).—This bone continues the arc of the premaxilla, but with a greatly diminished curvature, and, bending slightly inwards towards its termination, it gives to the upper jaw a rather elliptical outline.

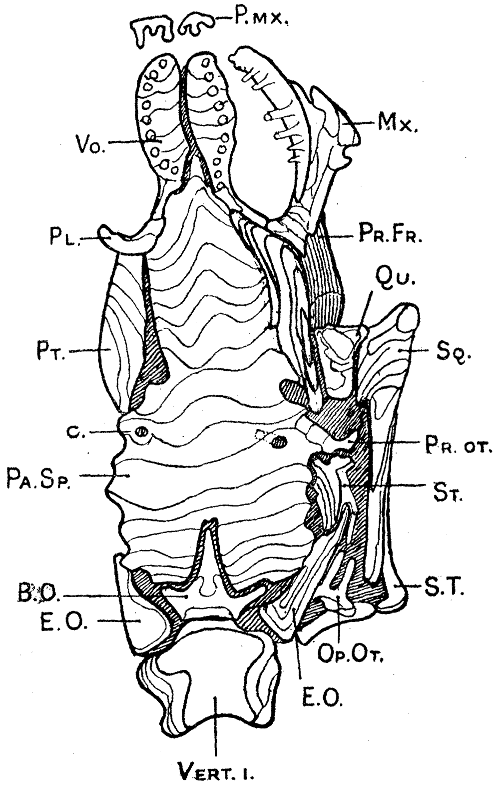

FIG. 32.

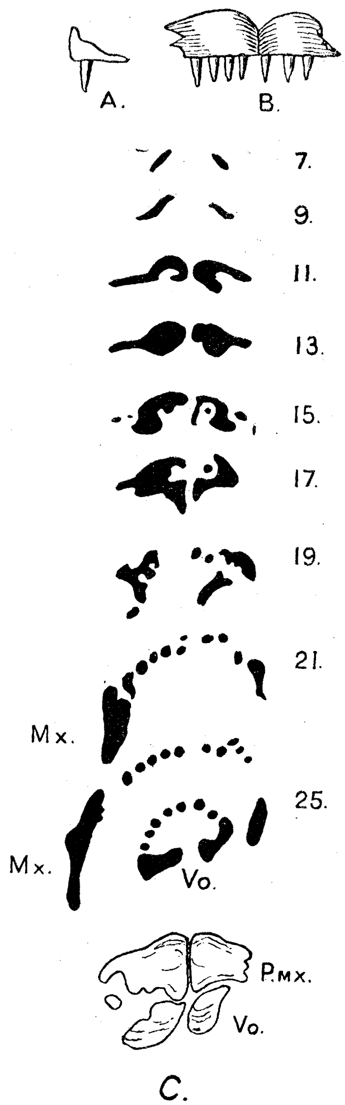

FIG. 33.

FIG. 32.—Ventral surface of the skull (specimen 2). (× 5.)

FIG. 33.—Premaxilla (specimen 1). A. The premaxillæ, vertical longitudinal section. B. Front view; 7 to 25, horizontal sections in series. C. Dorsal view of the premaxillæ and anterior end of the vomers built up from horizontal sections. (× 4.)

The body of the bone is a thin, vertical lamella, very imperfectly preserved, 1·8 mm. in height, 4·5 mm. in length, and about 0·4 mm. in thickness. The teeth are borne on the inner margin, and there is no indication of a palatal plate. The outer lower edge, near the middle of its course, is produced outwards into a rounded shelf, the base of an ascending peg-like process, which articulates by its inner face with the descending process of the prefrontal. By the union of these two processes, an annular band or very short tube is formed on the side of the face, with its axis running parallel to the length of the skull. The ring is not, however, quite complete; it is interrupted on the inner side above by a gap, where the wall of the maxilla which bounds it on the inner side fails to reach the inner margin of the prefrontal.

This remarkable feature recalls in some respects the channel for the tentacle in Ichthyophis, as described by the SARASINS,* but a detailed comparison fails to discover any real resemblance beyond a general similarity in position.

Its lumen was evidently seen by WILLISTON, who describes a narrow space between the maxilla and prefrontal, and suggests that it was occupied by the eye. BROOM† does not accept this interpretation, and is inclined to think that it lodged some other sensory organ. He adds, after discussing the position of the nasal openings, ". . . it is impossible to be quite sure whether the bridge of bone which connects the prefrontal with the maxilla is a part of the prefrontal, or a part of the maxilla, or a small independent bone."

Our sections show, as we have seen, that the bridge is composed of (1) the descending process of the prefrontal, and (2) an ascending process, which we have attributed to the maxilla. I am not, however, without a lingering doubt on the latter point (2), for, in neither of the two cases in which the bridge is preserved, *i.e.*, on the left side of specimen 1 and the right side of specimen 2, have I been able to trace the ascending process into continuity with the shelf-like process of the maxilla; indeed, these two are separated from each other by a slight interval. If this represents a suture, then the ascending process must be an independent bone, perhaps the turbinal of the SARASINS (lacrimal of HUXLEY). The facial ring or tube would then be a narial passage running outside the wall of the maxilla, which it would have to cross in order to open between the maxilla and the vomer.

Appearances, however, suggest a fracture rather than a suture. The shelf-like process is very thin: where the ascending process comes into closest approximation to it no more than 0·1 mm. in thickness. Under the pressure to which both our specimens have been subjected, as their distortion bears witness, the fracture of so fragile a connexion would seem almost inevitable.

The teeth of the maxilla possess the same characters as those of the premaxilla; the left maxilla of specimen 1 bears ten or eleven teeth, the right maxilla of specimen 2 has one or two less.

The *Lower Jaw* (figs. 2, 4, 34–37).—Almost all the accidents which accompany fossilization, and seem designed to mislead the observer, are to be met with in the lower jaw; its analysis, therefore, proved no easy task. Sutures are imitated by little "faults" with a verisimilitude so great that when their true nature is discovered perturbing doubts arise over sutures which are truly genuine. Separate bones may

* SARASIN, PAUL and FRITZ, "Forschungen auf Ceylon," vol. 2, p. 195 *et seq.*, Plates XVIII and XIX. Wiesbaden (1887–1890).

† BROOM, R., *loc. cit.*, pp. 233, 234.

be united by a growth of calcite, and single bones resolved into several by solution. Fortunately, the material for study includes three nearly complete rami and important parts of a fourth; by constant comparison of these one with another it has been possible to arive at definite, and it is to hoped, correct results. The best preserved

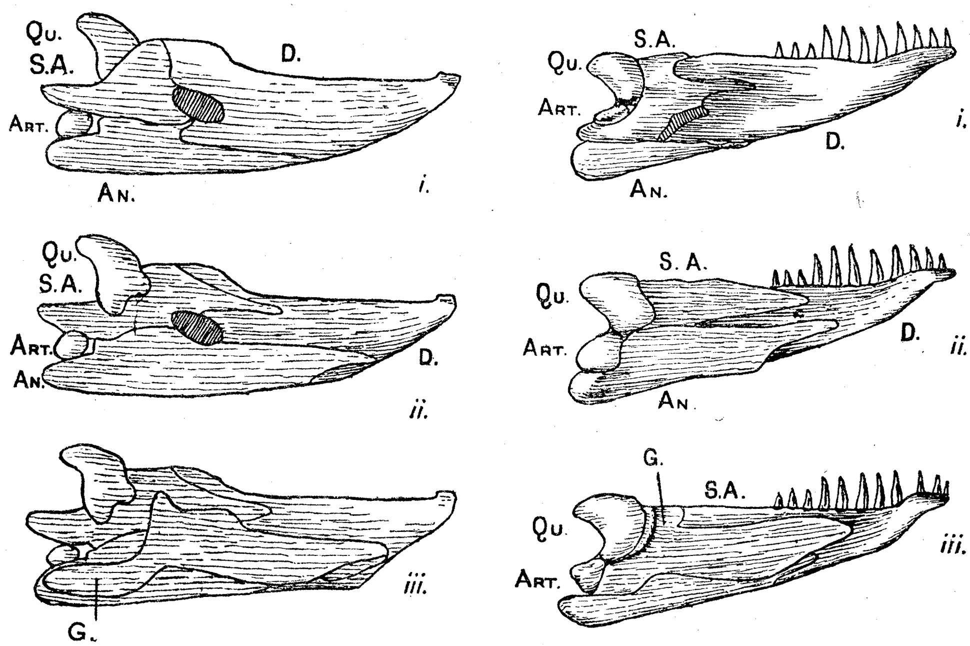

Fig. 34.—The lower jaw. On left from specimen 1. (×4.) On right from specimen 2. (×5.) i, outer; ii, inner side with goniale removed; iii, inner side with the goniale in place.

are the left ramus of specimen 1 (13·2 mm. in length and 4·2 mm. in height) and the right of specimen 2 (10·8 mm. in length and 3·4 mm. in height). These, however, suggested the presence of two bones, a splenial and pre-angular, which the right ramus of specimen 1 proves, I think, to be non-existent. This ramus (fig. 35) has been separated from its fellow, driven out of place so as to lie transverse to the axis of the skull, and squeezed open by a downward pressure which has thus revealed its structure in the clearest manner. If it is as complete as it appears to be our interpretation of the structure of the lower jaw will be relieved of all possibility of error. The left ramus of specimen 2 is very imperfect, but presents a complete row of teeth, and as it is still associated with its fellow, retaining very nearly its correct relative position, it enables us to restore the form of the lower jaw as a whole (fig. 36).

The rami diverge from a rather long and oblique symphysis at an angle of between 55° and 60°. The symphysis was evidently completed by cartilage as is shown by the facility with which the rami have been separated in some cases and displaced before the consolidation of the matrix in which they are embedded.

The *Articulare* (fig. 30, *B*) is a small irregular four-sided prism with truncated upper and lower posterior angles. Its height is 1 mm.; it is seated on the angulare and embraced on one side by that bone and on the other by the goniale. When I previously referred to it elsewhere* as "a comparatively large and important bone," I was unaware that the quadrate which is in close contact with it in specimen 2 is in fact a separate element.

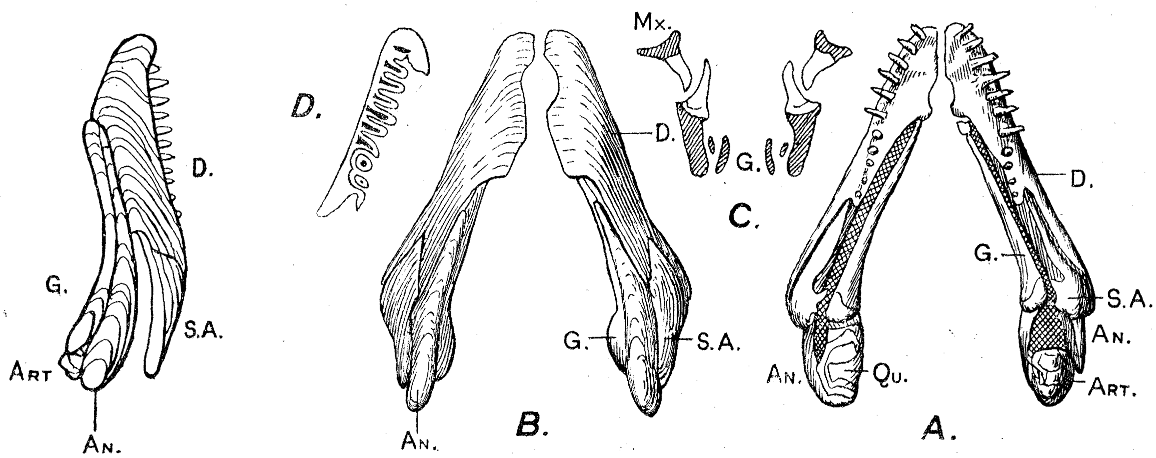

Fig. 35 Fig. 36.

Fig. 35.—Right ramus of lower jaw (specimen 1) squeezed open by vertical pressure, seen from below. (× 4.)

Fig. 36.—Lower jaw (specimen 2). A. Seen from above. B. From below. (× 5.) C. Transverse section through the lower jaw and maxilla of specimen 1 to show the implantation of the teeth. D. Horizontal section through the dentary of specimen 1 showing the base of the teeth. (C and D, × 4.)

The *Surangulare* (fig. 37) is a fairly long splint, thickened behind and produced there into a hook-like process on the inner face, probably for attachment of the masseter muscle.

The posterior margin descends as a vertical wall which rests at the base on the angulare. In specimen 2 the base is produced backwards to form along with the angulare a rather long post-articular process. This is shown also in the figure which Broom gives of the lower jaw. In specimen 1 the angular and surangular elements of the process have been pushed apart from each other; a fortunate accident, affording confirmatory evidence of the precise delimitation of these bones, which might otherwise have been in doubt. The surangulare and the dentary form together a low coronoid process, no doubt for the attachment of the temporal muscle.

The *Angulare* (fig. 37) is a rather thick bone, where it forms the angle of the ramus, but is continued upwards and forwards as a thin lamella lying between the dentary and the goniale and extending as far or almost as far as the goniale to the front. It is excavated on the medial side behind and below to receive the postero-inferior termination of the goniale.

The *Goniale* (fig. 37).—This long splint articulates behind and below with the angulare; it is continued forwards as far as the symphysial margin of the dentary.

* In Broom, *op. cit.*, p. 239.

Just above and in front of its articulation with the angulare the lamella is abruptly truncated behind and the truncated edge is thickened; it rises in a steep wall corresponding to that of the surangulare on the opposite side of the ramus. Near its foot this wall is perforated obliquely by a small foramen, probably the foramen *pro chorda tympani*.

As already mentioned, the posterior extremity of the goniale is applied to the inner side of the articulare.

So far as I can make out a splenial bone is not present. I fancy that the bone which BROOM indicates in his figure of the lower jaw under this name, must be either a part of the angulare or the continuation of the goniale (pre-articulare). If it were really splenial then the pre-articulare shown in the section given by BROOM along the line *a a* of his figure would be splenial also, for the only region where the bone which I have identified as goniale could be resolved into two elements lies considerably behind this line. In this region some of my sections might possibly be taken to represent both elements—splenial and goniale. Indeed, this was the interpretation which at first commended itself to me, but it is in no way confirmed by an examination of the right ramus of specimen 1. On the contrary, this strongly supports the view that of these two bones, splenial and goniale, only one is present, not both. Which of the two it is may be a matter of opinion, but the bone extends so far backwards, almost to the posterior extremity of the jaw, that the presumption is in favour of the goniale.

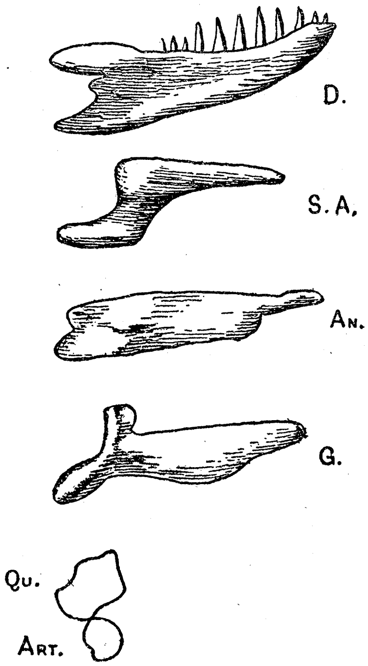

FIG. 37.—The bones of the lower jaw, specimen 2. (×5.)

The *Dentary* (fig. 37) is a large splint-like bone 8 mm. in length, thickened at the distal end, which is excavated by a deep groove for Meckel's cartilage, and expanded above into a horizontal ledge which bears the teeth. It is sutured with the surangulare and overlaps both that bone and the angulare for a great part of their length. In front and below it is in contact with the goniale. Where it meets the surangulare near the angulare is a small external mandibular foramen.

The *Teeth*.—The teeth are simple, hollow, sharply pointed, elongate cones. They are slightly curved (figs. 34, 36), and when attention is confined to horizontal sections they appear to be rather suddenly bent near the base into parallelism with the surface of the bone from which they spring. This would suggest a comparison with the teeth of some Urodeles, such, for instance, as Megalobatrachus, but with this difference, that the opening of the root is not, as it is in that genus, turned away from the outer margin of the dentigerous bone, but in the contrary direction.

Further, when vertical sections are constructed they present no trace of such a suggested bending, the tooth is typically acrodont, and the bending must be interpreted as an elongation of the base (fig. 36, *C*). The teeth are, in fact, more like those of a fish, such as Amia, than a Urodele.

In one instance the tooth appears to have been folded near the base as in some of the simpler Stegocephalian teeth and the teeth of the existing Ceratophrys; such at least appears to be the only possible explanation of such a section as that shown near the letter *D* in Section 27, Plate 70, from the right dentary of specimen 2. Similar but less definite foldings are presented by the roots of all the teeth preserved in the left dentary of the same specimen (Section 29, Plate 70). In order to determine whether the length of the teeth in a series is distributed according to any law the measurements were made which are given in the following Table:—

LENGTH of the Teeth Arranged in Order from before Backwards.

——	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
Pmx., L., specimen 1	0·9	0·9	0·8	0·8	0·8						
Mx., L., specimen 1	0·6	0·6	0·7	0·6	0·8	0·8	0·8	0·7	0·2	0·2	
Mx., R., ,, 2	0·6	0·8	0·8	?	0·6	0·4	0·4	0·6			
Vo., L., ,, 1	0·8	0·6	0·7	0·7	0·6	0·4	0·2	0·2	0·5		
Vo., L., ,, 2	1·0	1·0	0·8	0·8	1·0	1·0	0·6	0·2	0·6		
D., L. ,, 1	0·9	1·1	1·3	1·3	1·5	1·5	1·4	1·2	1·2	1·0	0·9
D., R., ,, 2	0·4	1·0	1·2	1·2	1·2	1·2	1·0	1·0	0·6	0·6	

They are not all of equal value; those taken from specimen 1 are, on the whole, more trustworthy than those of specimen 2; the maxilla and its teeth are badly preserved in specimen 2, and, of the premaxilla, only a trace remains.

It will be seen that the dentary, the only dentigerous bone in the lower jaw of Lysorophus, bears from 10 to 11 teeth, which are generally larger than those of the upper jaw, and that the longest of them are situated in the middle part of the series, the shortest at the ends. WILLISTON found 12 teeth in the specimen described by him.

The Visceral Arches.

The *Hyoid* (figs. 2, 11, 38, 39, 40).—In both specimens the hyoid bones are differently preserved on different sides. In specimen 1 the left hyoid, and in specimen 2 the right, seem to retain very nearly their original form and position. The right hyoid of specimen 1 has been displaced; it lies on its side, and has been flattened out by compression. It was probably a displaced and deformed hyoid that BROILI mistook for a gular plate.

The well preserved examples both present similar characters with slight differences; they consist of a hypohyal and a ceratohyal, the two elements together forming a bone which, in specimen 1, looks very like a lower jaw with a well-marked horizontal and vertical ramus. In specimen 2 the constituent elements are more sharply distinguished from each other. In this the hypohyal is a thin bar, 2·0 mm. in length and 2 mm. in height, straight on the mediad face, curved inwards from side to side on the outer face; it is thickened above, and gives off an uncinate process, which points backwards towards the middle line. The ceratohyal is a large lamellar bone, gently curved from above downwards towards the middle line. It is 2·8 mm. in height and 4·5 mm. in length at the summit, but becomes shorter as it descends by a forward sweep of its posterior edge till it is reduced to 2 mm. in length. Narrow in the middle, it thickens out towards both extremities; in front, for the greater part of its height; behind, directly towards the summit, where it forms what appears to be an articular head, rising 0·6 mm. above the middle region and 0·4 mm. above the anterior end. On its posterior face the head is excavated into a cup-like hollow.

First Branchial Arch (figs. 2, 38, 39, 40).—This includes a ceratobranchial

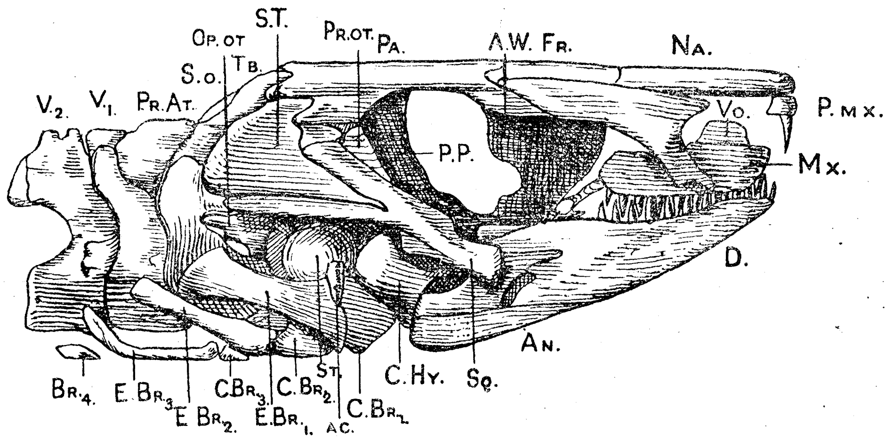

Fig. 38.—The skull with the visceral arches. (× 5.)

and epibranchial member. The two together form a large lamella, curved inwards like the side of a boat, 9 mm. in length, measured along the chord of the arc.

The ceratobranchials of each side, 5 mm. in length and 2 mm. in height, meet with thickened ends in the middle line. The ends bound a concave space in front, which, during life, possibly received the posterior end of a cartilaginous basi-hyal.

As the ceratobranchials pass backwards to their union with the epibranchials, they increase in vertical height, and at the junction on the outside is a little ossicle, which lies along the articular edge from base to summit. This seems to be an accidental bone (*ac.*, figs. 38, 39).

The epibranchial resembles the ceratobranchial, but is shorter, 4 mm. in length, and its posterior end does not approach the middle line.

The first branchial arch of specimen 1 is similar but larger, 11·5 mm. in length, straighter and less incurved. Like the hyoid, it resembles a lower jaw, and the ascending ramus lies inside and a little behind that of the hyoid on the side of the skull.

The *second branchial arch* resembles the first, but is less lamellar and more rod-like at the extremities; the ceratobranchial is 4·4 mm. and the epibranchial 4 mm. in length; towards their articulation with each other they are flattened out in a horizontal plane, possibly as the result of rock pressure.

The *third branchial arch* is similar to the second; the ceratobranchial and the epibranchial are each 4 mm. in length. The epibranchial and the posterior part of the ceratobranchial are much flattened out in a horizontal plane. Although of approximately the same length, these are much feebler bones than those of the second arch. The third ceratobranchials nearly meet in the middle line. Lying between them is a straight minute rod of bone, 1·8 mm. long and 0·4 mm. in diameter, which extends along the middle line, and apparently represents a basi-branchial element. The general character of the arches strongly suggests that, originally, an unbroken series of basi-branchials existed, and completed the branchial skeleton in the middle line; it is possible even that they were more or less ossified, but have subsequently been destroyed by decay and solution.

A *fourth branchial arch* seems to be represented by a train of fragments, which arises within the third arch and runs parallel with it and beyond it as far as the third vertebra.

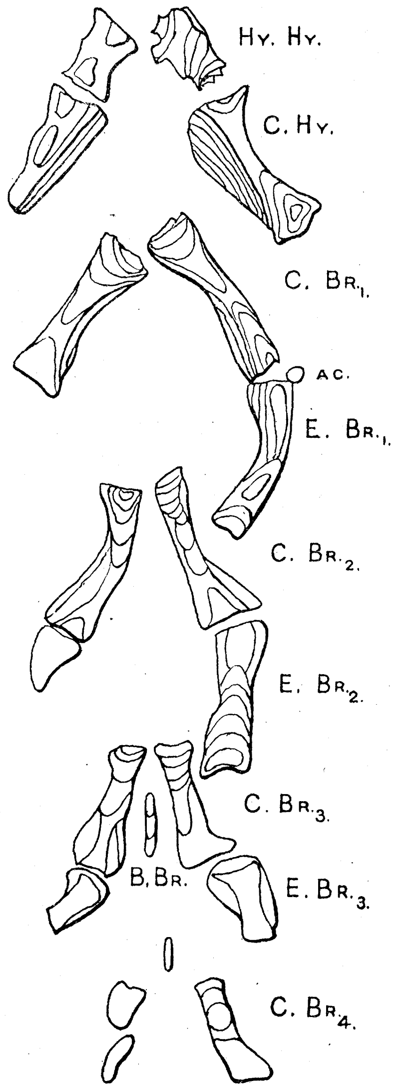

FIG. 39.—The Hyoid and Branchial Arches. *Hy.Hy.*, hypohyal; *C.Hy.*, cerato-hyal; *C.Br.*, cerato-branchial; *E.Br.*, epi-branchial; *B.Br.*, basi-branchial. (×5.) *ac*, an accessory ossicle.

The most remarkable character of the hyoid and first branchial arch is their compressed plate-like form; in this, as in the form of the other branchial arches also, offering a striking contrast to Polypterus; they strongly recall Megalobatrachus with the difference that they do not lie flat or parallel to the ventral surface but make a close approach to the vertical; the second branchial arch is even more similar to that of Megalobatrachus. The hyoid both by its form and position finds its nearest parallel among the bony fishes; an epihyal, however, does not enter into its composition.

The *Vertebral Column.*—For the purpose of description it will be convenient to distinguish the first four vertebræ, which lie in front of the shoulder girdle, as "cervical" and all those behind these, as far as the sacrum, as dorsal vertebræ. Our material may thus be said to include the first and second cervical vertebræ and a series of four dorsal vertebræ in specimen 1, and in specimen 2 all the cervical, including the pro-atlas, and as well two dorsal vertebræ very remote from the head. These were all cut in horizontal sections, except the two last named which were cut transversely.

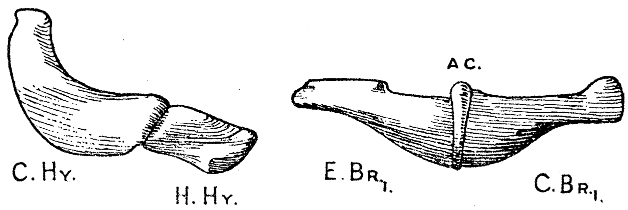

FIG. 40.—i. The hyoid bones from specimen 1. (× 4.) ii. The first branchial arch from specimen 2. (× 5.)

Dorsal Vertebræ.—The centrum is cylindrical, but with two deep depressions on the sides, one, the smaller above the middle and the other the larger below it, so that a transverse section through this region presents the form shown in fig. 43, Nos. 7 and 27.

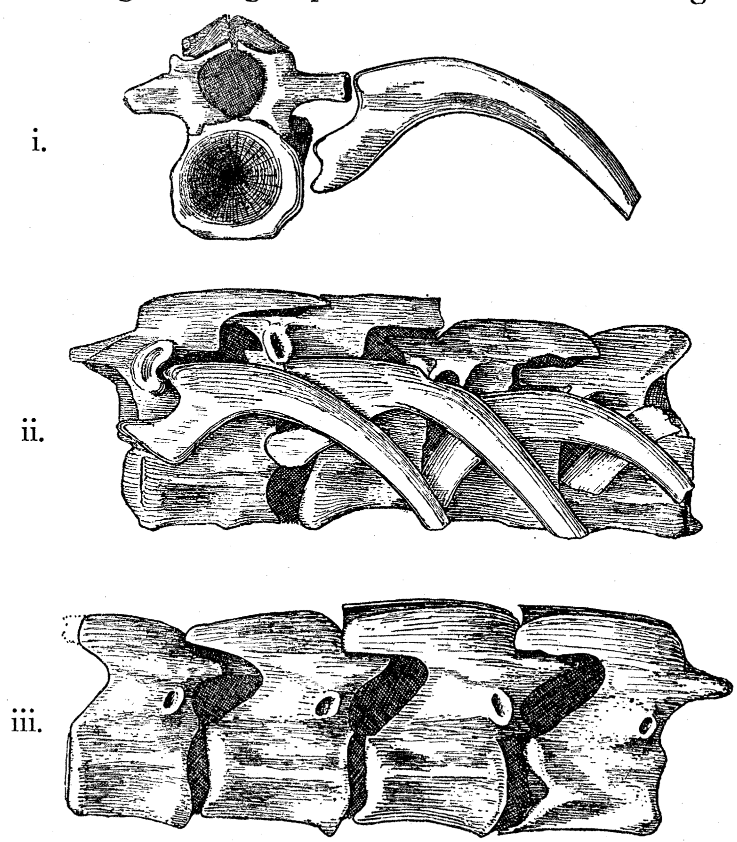

FIG. 41.—Dorsal vertebra. i. Seen from in front and showing the rib placed at right angles to the axis of the vertebra. ii. Lateral view (left side) with the ribs in the position they occupy in the fossil. iii. Lateral view (right side) without the ribs. (× 4.)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

It is deeply amphicœlous and perforate. Its breadth is approximately the same as its length, viz., 5·5 mm. to 6 mm. in specimen 1 which is 4·5 mm. to 5 mm. in height; in specimen 2 the height is 3·6 mm. and the length 4 mm., but in this case not only is the specimen itself smaller but the vertebræ measured lie nearer the head.

The neural arch consists of a pair of lateral elements which appear to have been united with the centrum below and with each other above by synchondrosis. Its height is about the same as that of the centrum; thus in a vertebra 10 mm. in height, the arch measured 5 mm.

The piers of the arch are produced over their anterior half into a stout transverse process. The root of the process is strictly confined to the arch and does not extend downwards over the centrum.

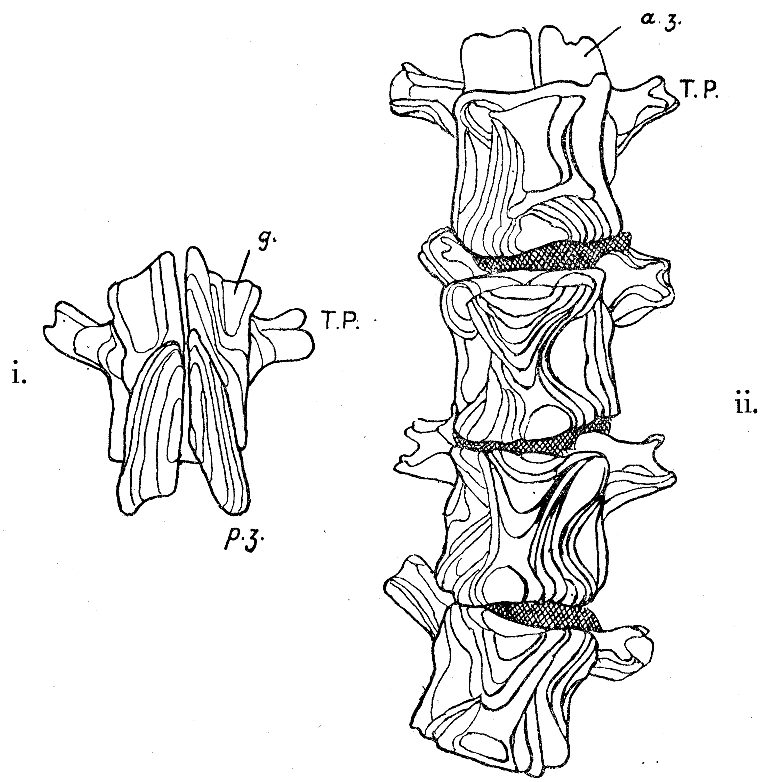

FIG. 42.—i. Dorsal vertebræ of specimen 1 seen from above and built up of superposed sections. (× 4.) ii. Dorsal vertebra of specimen 1 seen from below. (× 4.) T.P., transverse process; *a.z.*, prezygapophysis; *p.z.*, post-zygapophysis; *g.*, groove in prezygapophysis to receive post-zygapophysis.

Behind the transverse process the sides of the arch are rather deeply excavated to form the anterior margin of the intervertebral foramina.

Immediately above the root of the transverse process the sides of the arch rapidly approach each other, roofing over the spinal canal, and extend forwards as a pair of horizontal plates—the anterior zygapophyses—which project a considerable distance beyond the face of the centrum. Each plate bears a wide and shallow groove for articulation with the posterior zygapophyses.

Behind this region the sides of the arch again ascend and rather steeply, forming a vault, closed in front, and resembling the bow of an inverted boat, but without a keel, for a neural spine is not present. The sides of the bow broaden out behind in two diverging wings which, extending beyond the posterior end of the centrum, articulate with the prezygapophyses and ensheath the "bow" of the succeeding arch.

The transverse processes look outwards and slightly forwards. A little pit-like depression in front of the root and another behind suggest the existence of a foramen, of which however there are no other signs. The ends of the processes are excavated for the attachment of articular cartilage.

The whole inner and outer surface of the centrum, including the central perforation, is formed by a layer of dense bone, which is perforated by minute vascular pores, very regularly arranged. Within this layer the structure is cancellous, but at the same time, as shown by transverse sections (fig. 43, Nos. 7, 27), definitely radiate. The chief radii

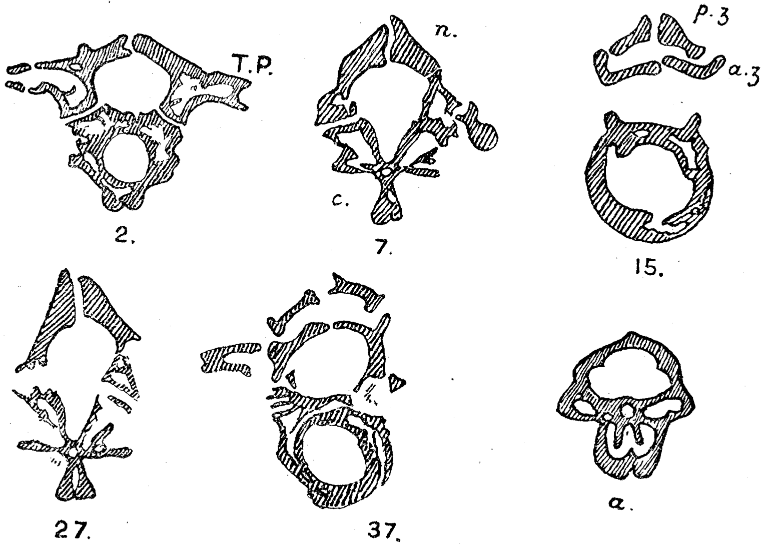

FIG. 43, 2 to 37.—Vertical transverse sections of two dorsal vertebræ of Lysorophus. *a.* Of a dorsal vertebræ of Crypto-branchus; *c.* Centrum; *n.* Neural arch. (× 5.)

are six in number, two lateral and horizontal, two directed upwards and outwards, and two downwards. The descending rays are closely approximated and almost fuse into one, the others make an angle of about 60° with each other. Lysorophus is not the only Amphibian which possesses this piscine character; it is also met with in Cryptobranchus and possibly other Urodeles. In Cryptobranchus also the dense investing layer of bone is perforated by minute pores just as in Lysorophus. It should be added that between the two ascending radii the floor of the spinal canal descends to form a deep pit; and it is in the intervals between adjacent radii that the upper and lower lateral depressions of the centrum are situated. In these details Lysorophus presents a surprising resemblance to some of the bony fishes, such as the Tunny.

As they approach the cervical region the dorsal vertebræ undergo slight changes of form and the transverse processes no longer look forwards but directly outwards. They are associated with stout two-headed ribs, as also is the fourth cervical vertebra.

Cervical Vertebræ.—As we pass from the dorsal series forwards slight modifications set in, which become increasingly marked as we proceed. The third and fourth vertebræ closely resemble the dorsal, differing only in minor details. They are smaller as a whole,* and the height of the arch (3 mm.) exceeds that of the centrum (2 mm. in specimen 2). In the dorsal vertebræ the face of the centrum is larger than the lumen of the spinal canal; in the cervical this relation is reversed.

The zygapophyses are less completely differentiated, so that the articulation assumes still more the character of an ensheathment. At the same time the crest of the arch, formed by the approximation of its sides to the exclusion of the spinal canal beneath, increases in height and diminishes in length.

The transverse processes of the fourth vertebra, as of the dorsal vertebræ immediately succeeding it, are not directed forwards as in the dorsal vertebræ just described, but simply outwards. They are still articulate, however, with two headed ribs. In the second and third vertebræ the transverse processes look outwards and backwards, and the associated ribs, no longer double-headed, are short and slender; thus, in the third vertebra they are 5 mm. in length and less than 3 mm. in the second.

In the *second vertebra* the height of the arch has increased to 3·6 mm., the posterior wings have become shorter, and the crest of the arch is less than half the length of the vertebra behind it. The region of the anterior zygapophyses is still well expressed however by a hood-like extension forwards, which is ensheathed by the arch of the first vertebra.

The *first vertebra* is more profoundly modified. The crest of the arch is now represented by two little cylindrical tubercles, one to each lateral moiety; the transverse process is a mere tubercle, and there are no ribs.

In front the arch no longer projects forwards in definite zygapophyses, or perhaps it should rather be said that these have been shortened to their roots. The piers of the arch are applied in front to the posterior edge of the pillars of the exoccipitals.

"*Pro-atlas.*"—The forward slope of the occiput and the backward slope of the roof of the arch of the first vertebra produce a V-shaped trough, and into this is neatly fitted the paired pro-atlas, which rides like a saddle across the "neck."

The pro-atlas resembles the vault of a vertebral arch, but turned about, *i.e.*, with what would be the anterior face of the arch looking backwards. This is a consequence of its adaptation to the surfaces with which it articulates, the occipital being much

* Thus in specimen 1 we have the following measurements for the centrum :—

	Breadth.	Length.	Height.
Dorsal	5·4	5·5	4·5
Cervical II	3·5	3·4	3·25

broader than the vertebral surface. Its posterior face is moulded on to the face of the first vertebral arch, and its posterior extremity enters the space between the two little tubercles which form the crest of this arch. Its anterior face is applied to the ascending part of the supra-occipital and the medial half of the lamina of the exoccipital. This lamina bears a groove which corresponds with the edge of the surface of articulation.

The two elements of the pro-atlas are articulated together over a broad surface, but readily fall apart, from which we may conclude that they were originally united by synchondrosis. Like so many other paired elements of the skeleton, they are far from being symmetrical one to another on each side of a median plane. The right half is much thicker than the left, and provided more than its share to the articulation with the back of the skull.

Williston, who at first recognised the presence of a pro-atlas,* afterwards stated that "the supposed pro-atlas described by Case and myself is merely the arch of the so-called atlas."† That so acute an observer should have been misled on this point will surprise no one who is familiar with Lysorophus; without the aid of sections it would be next to impossible to arrive at a certain conclusion: these, however, show in the clearest manner that the first vertebra possesses its own arch, and that the pro-atlas is without a visible centrum.

The Centrum of the First Vertebra.

Next to the parasphenoid this and the condyles are perhaps the most amphibian structures in the skeleton. It is opisthocœlous and imperforate, slightly broader than the succeeding vertebra, and higher behind (2 mm.) than in front (1·2 mm.), the upper surface being scooped out by a shallow groove, 4 mm. in breadth and 3 mm. in length, which descends forwards. The hollow cone which forms the anterior face of the other vertebræ is here replaced by a cylindrical convexity, which corresponds to the "odontoid" of the Amphibia, and plays against the nearly flat posterior surface of the basi-occipital. It is composed of slightly denser tissue than the rest of the bone.

On each side of the "odontoid" is a little flange forming the bottom of a shallow recess, which receives the back of the heel of the exoccipital bones.

The condyle of the skull might thus be regarded as tripartite, though the parts are so far from being fused into a single structure that it would seem more appropriate to speak of three condyles than of one. But even if we admit the term "tripartite" as legitimate, it by no means follows that the articulation is in any sense reptilian. It offers indeed a direct contrast to the reptilian articulation for the exoccipital facets look downwards and inwards in Lysorophus instead of outwards as in reptiles, and this difference is directly correlated with another. If, broadly speaking, we may compare the condylar articulation to a ball-and-socket joint, then

* Williston, 'Biol. Bull.,' vol. 15, p. 229 (1908).

† Williston, 'J. Geol.,' vol. 18, p. 600 (1910).

the occipital condyle of a reptile plainly corresponds to the "ball"; in Lysorophus, on the contrary, it supplies the socket, or if we could apply such terms to an articulation we might say that in Lysorophus the joint is procœlous, in the Reptiles opisthocœlous. Thus in this essential particular Lysorophus offers a direct contrast to the Reptilia and it is easy to understand how such an articulation would pass by a reduction of the basi-occipital into that which now characterizes the existent Amphibia. But in Lysorophus the articulation of the skull with the vertebral column is not confined to the centrum of the first vertebra; it extends to the piers of the arch of this vertebra and to the pro-atlas. Such a close association of the whole vertebral front with the back of the skull is a character which irresistibly recalls certain fishes among the Teleosts, in which the first vertebra is similarly plastered on to the occiput. It seems to point to a time when, as my friend Mr. GOODRICH remarks, the limit between skull and vertebræ was in a state of flux.

Caudal Vertebræ.—Unfortunately these are not represented in my sections. By no means anticipating that the specimens would yield so much detailed information, I restricted my attention to the head and its vicinity. Had I known the full value of the material placed in my hands, I should have prepared sections of the entire skeleton. My regret is tempered, however, by the fact that the caudal vertebræ have been described by WILLISTON who asserts that they are without [free] chevrons, and thus definitely Amphibian. They are said to be 17 in number and without ribs or diapophyses.

The *Ribs* (figs. 40, 44).—In all but those of the second and third vertebræ the ribs are two-headed, the tubercular process extending about 4 mm. or 5 mm. beyond the capitulum. All the ribs have suffered some displacement, and are now folded back against the sides of the vertebral column, round which they curl to cross one another below on the ventral surface. This singular disposition has been noticed already by CASE in his specimens. It is probably connected with the fact that the serpentine body is always found closely coiled up; at the same time it suggests that the ribs possessed great freedom of movement and whatever further may be implied by this. The tuberculum lies close to the transverse process, usually just beneath it; the capitulum against the side of the centrum which offers no definite facet for its articulation. Where the rib bends away from the capitulum it is compressed from side to side, so that a transverse section is about twice as high (2 mm.) as broad

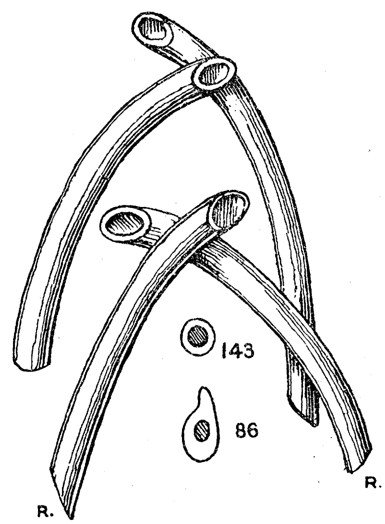

FIG. 44.—*R. R.*, ribs crossing each other below the centra of the vertebræ; 86, oblique section through a rib about 1 mm. beyond the tuberculum; 143, transverse section through the same rib near its distal termination. (All from specimen 1; × 4.)

(1 mm. to 1·25 mm.). It becomes rounder as it proceeds and maintains a diameter of 1·4 mm. for a considerable distance; later it is hollowed out in some cases on one side leaving a ridge to form the posterior edge. The ribs are hollow and the cavity they enclose enlarges by thinning of the wall as they approach their termination. In specimen 1, so far as I can trace them, they are about 11 mm. in length measured along the chord, and 15 mm. along the arc.

Apendicular Skeleton.

Shoulder Girdle (figs. 1 and 2).—The shoulder girdle lies outside the ribs and partly below them. There has evidently been much displacement not far from the third and fourth vertebræ. As in the Urodeles, the dorsal region is not represented by bone.

The *scapula* is a short narrow triangular plate, 2·6 mm. in length; at one corner, now turned forward as a result of displacement, it bears a concave surface, which appears to represent part of the glenoid cavity.

The *clavicle* is a long slender curved rod; its upturned posterior end lies just behind the scapula, thence it curves under that bone, touching it below the articular surface, and runs obliquely downwards and forwards, to end beneath the first rib. At its termination is an elongated triangular plate, lying flat in the ventral plane. Whether this is to be regarded as an expansion of the clavicle or an independent element, there is nothing to show.

A small elongate splint-like bone (*s*, fig. 2) lies in front of the clavicle near the vertebral column, and looks as though it belonged to the shoulder girdle. A cleithrum may possibly be represented either by it or the bone we have assigned to the clavicle.

Fore Limb.—The scattered members of the fore limb lie along a line perpendicular to the direction of the vertebral column.

Humerus.—This is represented by a cylindrical shaft, 3·6 mm. in length, narrowest in the middle, widest at the extremities, which are more or less cup-shaped, owing to the disappearance of the cartilage by which they were originally completed.

A cartilaginous extremity is very characteristic of Urodele limb bones.

The distal end of the humerus is distinguished from the proximal by a rounded swelling on one side.

The long axes of the articular ends lie at right angles to each other, as is shown by the following measurements:—

Breadth of articular end measured from—

	Above downwards.	From side to side.
Proximal end	1·2 m.m.	0·8 m.m.
Distal end	0·8 ,,	1·4 ,,

This is a feature commoner among Mammals and Urodeles than among Reptiles.

Radius.—The radius is a straight slender rod, 2·2 mm. in length, and concave at both ends. It lies on the pre-axial side of the humerus, and points in the same direction as the humerus, but is separated from it by a considerable interval.

The *ulna* is also a slender rod, of about the same length as the radius, but rather strongly curved. It is post-axial, with its proximal articulation near the distal end of the humerus; it has been driven apart from the radius, and lies obliquely to the plane of the sections.

There is no trace of carpal bones, which, as is usual among modern Urodeles, were in all probability cartilaginous.

Metacarpals.—The metacarpals of two digits are preserved as simple rounded rods, lying side by side close together, oblique to the plane of the sections. One is slightly longer (1·4 mm.) than the other (1·2 mm.).

Miss MARIAN FINNEY* examined 200 nodules, containing remains of Lysorophus, in search of limb bones, and found 15 examples, which included some femurs, tibias, and fibulas, two metatarsals, and two phalanges.

Presuming that these determinations, which depend entirely on the form of the bones, are correct, it would follow that Lysorophus was provided with both fore and hind limbs, and, from Miss FINNEY'S observations, it is possible to make some comparison of their length. Thus the femur was found to measure 10·5 mm., while the humerus in our specimen is 3·6 mm. long; similarly, the tibia and fibula are 5 mm. and the radius and ulna 1·8 mm. in length. Unfortunately, nothing is known of the size of the head with which Miss FINNEY'S specimens were once associated, but she mentions the presence of part of a lower jaw, bearing 11 teeth and measuring 8 mm. in length. In the specimen which furnished the fore limb of our description, the dentigerous part of the dentary, measured as far as the 11th tooth, is only 4·6 mm. in length; hence we may conclude that heads, almost twice as long as that of our specimen 2, may have accompanied the bones of the hind limb described by Miss FINNEY.

That such heads exist is beyond doubt; Dr. WATSON is in possession of one which is about 30 mm. in length; nearly twice the size of average specimens, as he remarks, while adding that, on this account, it may prove to belong to a different species.

If we may assume that the ratio of the length of head to limb did not vary greatly with the size of the animal, then we may obtain a rough estimate of the relative length of the femur and humerus by multiplying the length of our humerus by 2, since, as we have seen, the head associated with it is only about one-half the length of that associated with the femur. We should then have humerus 7·2 mm., femur 10·5 mm., a ratio of about 7 : 10; in a specimen of Cryptobranchus, I find it to be 7 : 9, and a similar ratio obtains for Necturus and some other forms. Thus our imperfect data at least suggest that the hind limbs of Lysorophus were longer than the fore limbs.

* FINNEY, MARIAN, "The Limbs of Lysorophus," 'Journ. Morphology,' vol. 23, pp. 664–667 (1912).

A comparison of the relative size of the fore limbs of Lysorophus, two modern Urodeles and a Branchiosaur may not be without interest. Taking the length of the head as a basis, we have the following :—

	Head.	Hu.	Hu × 100/Head. Index.
Cryptobranchus	40 mm.	17 mm.	42·5
Necturus	42 ,,	15 ,,	36
Lysorophus	16·0 ,,	3·6 ,,	22·5
Urocordylus	38 ,,	5 ,,	13

Next taking the length of the humerus as a basis we have :—

	Ra.	Index.	M.ca.	Index.
Cryptobranchus . . .	9 mm.	53	4 mm.	23·5
Necturus	8 ,,	53	4 ,,	26
Lysorophus	1·8 ,,	50	1·4 ,,	39
Urocordylus	3·5 ,,	70		

And finally with the length of the head as a basis we have :—

	Hu + Ra + M.ca.	Index.
Cryptobranchus	30 mm.	75
Necturus	27 ,,	64
Lysorophus	6·8 ,,	42·5

The total length of the fore limb in Lysorophus cannot have been much more than one-half that of the ribs, which, as we have seen, attain a length of 15 mm.

In the light of our present knowledge, Lysorophus stands clearly revealed as a veritable but primitive Amphibian, and no less clearly as a member of the ancestral Urodeles.

Most of the characters by which it differs from existing Urodeles, are such as we might expect to find in a primitive form. The presence, for instance, of a well ossified basi-occipital and supra-occipital, the existence of a foramen for the twelfth nerve, and, possibly connected with this, the presence of a "pro-atlas"; the nature of the condylar articulation of the skull, which represents a stage still existent among the bony fishes, but long since left behind and forgotten in the history of the Amphibia; further, the presence of a separate opisthotic, large tabulares, conspicuous supra-temporal bones, a complex lower jaw, and large well ossified branchial arches.

There are other characters which appear to be peculiar, such as the mode of union of the maxilla with the palatine, and of this bone with the vomer and pterygoid, the nature of the vertebræ, and the well curved form of the long ribs. This last character Lysorophus shares with the Gymnophiona, and so far supports the view long held by distinguished naturalists, that the Gymnophiona stand in close connection with the Urodeles; COPE considered that they were united to the more typical Urodeles by the Amphiumidæ, and the SARASINS not only shared this view but went so far as to include the Gymnophiona and the Amphiumidæ in a single group—one of the two sub-orders which constituted, according to them, the order Urodela.

If this alliance be admitted it would seem clear that the Gymnophiona must have branched off from the main stem prior to Lysorophus, for they still retain important bones, the lacrimal or lateral nasal, postfrontal or postorbital, and jugal which had already been discarded by Lysorophus in Carboniferous bones.

The breach between the Urodeles and the Anura was probably accomplished at a very early date, for all the features of the skeleton which distinguish the Urodeles are already fully expressed in Lysorophus: thus, in the skull the parasphenoid is large and characteristic, the roofing bones are distinct, there is a large prefrontal, a quadrate but no jugal nor quadrato-jugal; and the squamosal is directed forwards as in Siren, Proteus and Necturus. The presence of the tabulare recalls Proteus and Amblystoma.

In the present state of our knowledge speculations on the family history of Lysorophus would seem out of place. That its pedigree included a terrestrial ancestor which used its legs for progression on dry land would seem to be precluded by the persistence of a well-developed branchial apparatus. Its feeble limbs afford but slight ground for argument; we are not entitled to assume, without further evidence, that at some ancestral stage they were more strongly developed. Our knowledge of the steps by which fins were transformed into ambulatory limbs is not advanced enough to justify dogmatism on this point; the earliest limbs may have been feeble organs adapted to progression under water.*

The closely wound coils in which the body is now disposed shows that the vertebral column was capable of freely undulating movements by which in all probability progress in the water was accomplished.

The meaning of the large ribs with their wide range of movement is not clear; it is possible that there also might have been organs of locomotion which were called into play by special circumstances.

The Dipnoi, to which we might turn for some light on the nature of the material from which the early Tetrapods were derived, are already too specialized, at least in known forms, to help us much. Dipterus, which in general plan survives in the existing Ceratodus, presents a parasphenoid which by its breadth makes the nearest approach to the Urodeles; but the peculiarity of its dentition precludes closer comparison. Our knowledge of the palæozoic lung-bearing fishes must be much more extensive before we can speculate profitably on this question, but in any case the

* For an interesting hypothesis on the origin of the Tetrapod limbs, see R. BROOM, "On the Origin of the Cheiropterygium," 'Bull. Amer. Mus. Nat. Hist.,' vol. 32, pp. 459–464 (1913); and B. PETRONIEVICS, "Note on the Pectoral Fin of Eusthenopteron," 'Ann. and Mag. Nat. Hist.,' Ser. 9, vol. ii, pp. 471–476 (1918) (includes an account of the literature).

Dipnoi proper seem to be excluded from the direct line of Amphibian descent by the nature of their ribs.

Dr. WATSON has arrived at important conclusions on the phylogeny of some orders of the Stegocephalia, which at present are only published in abstract. He concludes that in the general course of evolution as illustrated by this group there is a gradual regression and final disappearance from the skull of the foramen for the twelfth nerve, an increase in the size of the interpterygoid vacuities and of the parasphenoidal rostrum, a replacement of the basi-pterygoid processes of the basi-sphenoid by expansions of the parasphenoid and exoccipital, a reduction and final disappearance of the basi-occipital, basi-sphenoid and supra-occipital bones.

If this should prove to truly represent the general trend of evolution, especially as it affects the expansion of the parasphenoid, it might be possible to derive the Urodeles, as MOODIE has done, from the Branchiosauria, though no support to this view is afforded by Lysorophus.

For the fruitful discussion of these problems we need more facts. Much may be revealed by further study of the Devonian fishes, now being so successfully investigated by GOODRICH, WATSON, and DAY,* and we look forward with hope to a time when the internal anatomy of these forms will be as fully exposed as that of Lysorophus.

In conclusion, I should like to express my warm thanks to my friend and former pupil, Mr. LANCELOT SHARPE, B.A., for his skilful assistance in the work of building up some of the reconstructions on which this communication is based.

* GOODRICH, E. S., "Restorations of the Head of Osteolepis," 'Linn. Soc. Journ.—Zoology,' vol. 34, pp. 181–188, figs. (1919); WATSON, D. M. S., and DAY, H., "Notes on some Palæozoic Fishes," 'Mem. and Proc. Manchester Lit. and Phil. Soc.,' vol. 60, No. 2, p. 52, Plates (1916).


9.
Na
Fr.
Pr.Fr.
Pa
Pa.
S.O.
Tb.
11.
Na
Pr.Fr.
Fr.
Pa.
Pa
Pa.
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12.
P.mx
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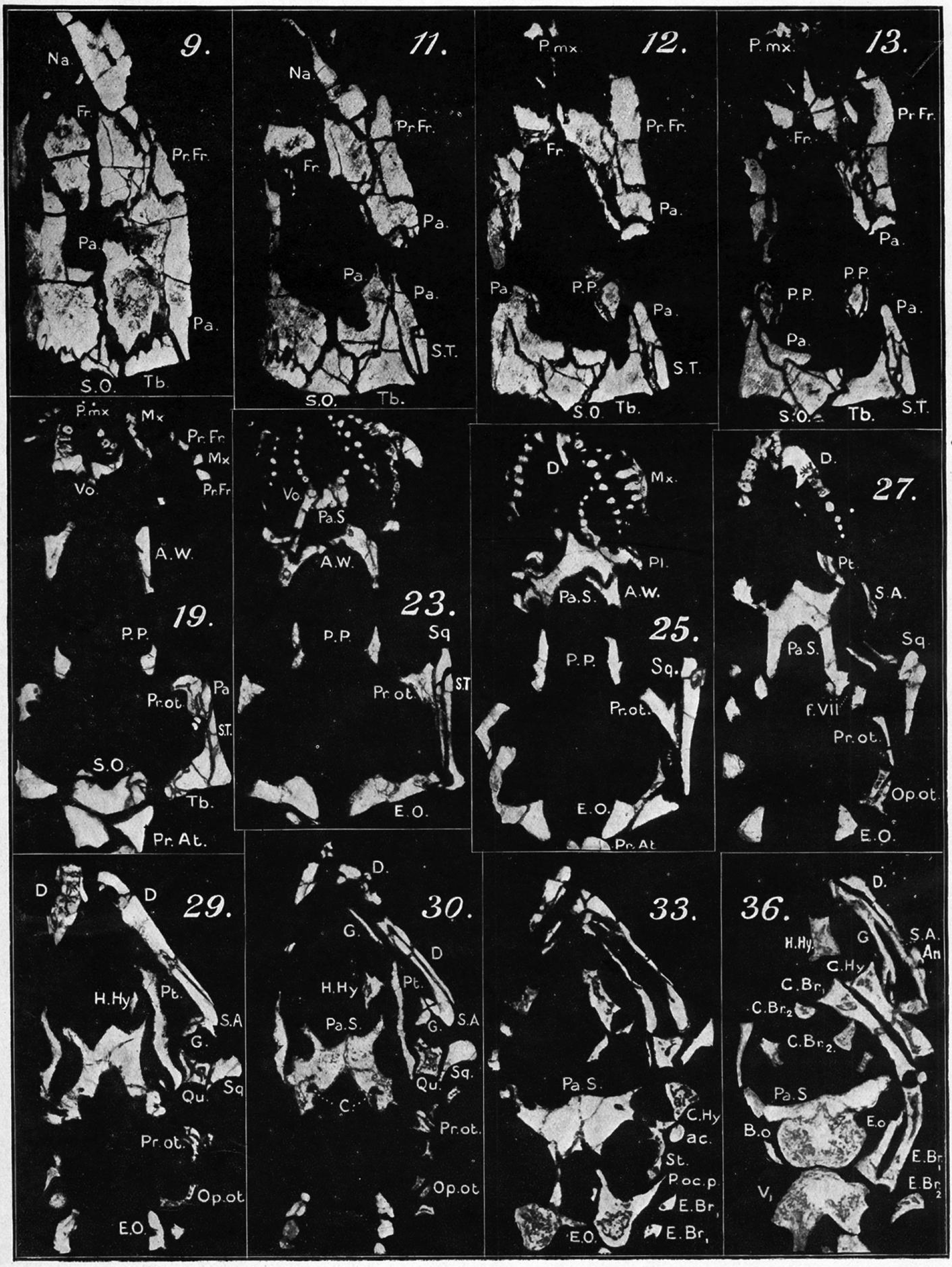
V

EXPLANATION OF PLATE 70.

Twelve horizontal sections through the Skull of Lysorophus (specimen 2), selected from a series of 46, cut at intervals of 0·2 mm. and numbered according to their place in the series.

Abbreviations used in the Plate and Text-figures.

A.V. Anterior vacuity.
A.W. Anterior wall.
ac. Accessory bone.
An. Angulare.
Art. Articulare.
B.Br. Basi-branchial.
B.O. Basi-occipital.
c. Foramen for internal carotid artery.
Cl. Clavicle.
C.Hy. Ceratohyal.
C.Br. Ceratobranchial.
D. Dentary.
E.Br. Epibranchial.
E.O. Exoccipital.
F.pl. Foramen for facial nerve (palatine branch).
F.xii. Foramen for the hypoglossal nerve.
Fr. Frontal.
G. or *Gn.* Goniale.
H.Hy. Hypohyal.
Hu. Humerus.
m.ca. Metacarpal.
M.V. Median vacuity.
Mx. Maxilla.
Na. Nasal.
Op.ot. Opisthotic.
P.oc.p. Paroccipital process.
P.P. Posterior pillar.
P.V. Posterior vacuity.
Pa. Parietal.
Pa.S. Parasphenoid.
Pl. Palatine.
P.mx. Premaxilla.
Pr.At. Pro-atlas.
Pr.Fr. Prefrontal.
Pr.ot. Pro-otic.
Pt. Pterygoid.
Qu. Quadrate.
Ra. Radius.
S.A. Surangulare.
S.O. Supra-occipital.
S.T. Supra-temporal.
Scp. Scapula.
Sq. Squamosal.
St. Stapes.
Tb. Tabulare.
Ul. Ulna.
V_1, V_2. First and second vertebræ.
Vo. Vomer.



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